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Climate Change Threatens the Geographic Distribution of Cupuaçu More Than Cacao: Insights from Ecological Modeling in Brazil

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ABSTRACT

Climate change is reshaping the geographic distribution of plant species, affecting their survival, productivity, and ecological roles. This study assesses the current and future distribution of *Theobroma cacao* (cacao) and *Theobroma grandiflorum* (cupuaçu) in Brazil, two economically and culturally important Amazonian species, using ecological niche modeling based on 33 environmental variables. Species occurrence data and climate-soil interactions were analyzed under different climate change scenarios. Results reveal contrasting patterns between the two species. Cupuaçu, native to the Amazon, exhibits high vulnerability to climatic variations, with projections indicating an expressive reduction of suitable areas, especially in the Amazon and Cerrado biomes. In contrast, cacao shows greater resilience, with potential expansion into other Brazilian regions such as the Atlantic Forest and the Pampa. These divergent trends highlight the importance of targeted conservation strategies tailored to each species' ecological response. The findings underscore the urgency of adopting integrated conservation approaches—*in situ*, *ex-situ*, and *on-farm*—to ensure the long-term viability of these species. Strategies informed by Indigenous knowledge, agroforestry systems, and sustainable land-use practices are essential to mitigate biodiversity loss and promote resilience in the face of climate change. By identifying zones of environmental suitability and vulnerability, this study contributes to guiding public policies and resource management aimed at protecting Brazil's native genetic resources. This work reinforces the critical role of ecological modeling in biodiversity conservation planning, emphasizing the intersection of climate science, sustainable agriculture, and traditional ecological knowledge.

Keywords: Ecological modeling; Biodiversity; Sustainability.

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SIGNIFICANCE STATEMENT

This study investigates the the effect of climate change on the geographic distribution of *Theobroma cacao* (cocoa) and *Theobroma grandiflorum* (cupuaçu) in Brazil and the implications for the conservation and sustainable use of these species. For the analysis, the ecological niche modeling was used, based on environmental data, as well as the occurrence data of species in Brazilian ecosystems. The results show greater vulnerability of cupuaçu compared to cocoa in the Amazon, its center of origin. Cocoa demonstrates greater resilience and potential for expansion to other biomes, such as the Atlantic Forest and the Pampa, while cupuaçu will have greater difficulty perpetuating over the years. The article presents and discusses strategies for the sustainable use and conservation of species of the same genus, considering the relevance of genetic resources from the experience of the original peoples for future generations.

INTRODUCTION

The climate changes that occur worldwide represent a significant threat to the preservation of natural ecosystems, affecting abiotic and biotic components, which leads to changes in temperature regimes, precipitation, and atmospheric concentrations of CO2 (Contreras-Cornejo et al. 2024; Lahlali et al. 2024). These effects tend to influence the performance, growth, and physiological responses of plants over time, varying according to the resilience of each species. In addition, studies show that climate change can favor the emergence of new pests and diseases that compromise the productivity of many crops of commercial interest (Campos et al. 2023; Contreras-Cornejo et al. 2024; Lahlali et al. 2024).

The transformations that occur in the climate have become the subject of research, especially concerning the impact of its effects on agriculture, as it causes a reduction in crop productivity, loss of natural variability in populations, and compromises food security (Grigorieva et al. 2023; Singh et al. 2023; Lahlali et al. 2024). There is great concern about the loss of biodiversity, which is due not only to climate change but also to anthropogenic activities (Zou et al. 2023). Thus, understanding and predicting how plant species respond to climate change becomes essential for developing strategies to mitigate the damage caused by the loss of natural variability (Lan et al. 2022; Sultan et al. 2019).

Several studies have shown that plant species distribution patterns are changing in response to climate variations (Lawlor et al. 2024). Species responses vary according to the environmental variables that most influence their behavior and the period considered in the analysis. Most research emphasizes the consequences of global warming on species distribution, highlighting the loss and division of habitats, which contribute synergistically to biodiversity degradation at species, genetic, and habitat levels (Andres et al. 2023; Rubenstein et al. 2023; Zou et al. 2023).

In this context, ecological niche modeling has proven to be an effective tool, enabling predictions of species distribution based on environmental variables and occurrence records (Thuiller 2024). This approach helps identify areas of current and future climatic suitability, thereby supporting the development of public policies and conservation strategies (Nzei et al. 2022; Franklin 2023). Its application is especially relevant for economically important species that are sensitive to environmental changes, since the characteristics and growing conditions of these crops can be impacted by climate change (Cilas and Bastide 2020; Cordeiro et al. 2023; Marques et al. 2024). Thus, this methodology can be properly applied to studies with the cocoa tree (*Theobroma cacao* L.) and the cupuaçu tree (*Theobroma grandiflorum* (Willd. ex Spreng.) Schum).

The cocoa tree is the most important species of the genus *Theobroma*, considering its socioeconomic importance (Mar et al. 2024), and stands out in the global market for being the main raw material of the chocolate industry (Asiedu 2024), Additionally, it has several applications in the pharmaceutical industry (Loke et al. 2024). According to the International Cocoa Organization (ICCO, 2024), South America contributes approximately 17% of global cocoa production, with Ecuador (5%), Brazil (4,6%), and Peru (2,4%) being the main producers in the region. Brazil has a production of 269,731 tons per year and is considered the second largest producer in South America and the seventh largest in the world (Araújo et al. 2024; Da Silva et al. 2024).

The cupuaçu tree, in turn, is highly valued for its fruits and pulp, which are widely used in the preparation of ice cream, sweets, jams, butter, and juices. These products play an important role in supporting the Amazonian bioeconomy by adding value to native biodiversity and promoting sustainable food innovation (da Conceição das Mercês et al. 2025). In Brazil, the species is important for small farmers working within agroforestry systems, with the primary producers located in the states of Pará, Amazonas, and Bahia. In 2022, Brazilian production reached 28,800 tons (Alves et al. 2024; Bezerra et al. 2024).

Both species face climate-related challenges, including the emergence of pests and diseases, reduced soil fertility, socioeconomic constraints, and reduced yields due to abiotic and biotic stresses. In the case of cocoa trees, there is strong evidence based on the effects of climate change on their productivity, physiology and geographical distribution, which affect long-term sustainability, since the main physiological traits of the species as well as the environmental conditions essential for cultivation are modified, thus representing serious risks to its viability in the coming decades (World Cocoa Foundation 2024; Kongor et al. 2024; Lahive et al. 2019; Cilas and Bastide 2020).

Furthermore, water stress and prolonged periods of drought in the cultivation regions have been identified as primary limiting factors for the culture. Studies also demonstrate evidence of changes and interactions in the behavior of cocoa trees, relating genotypes, physiological characteristics, and climatic variables (Lahive et al. 2019; Cilas and Bastide 2020; Araújo et al. 2024; Ceccarelli et al. 2024).

For cupuaçu tree, although studies on commercial cultivation are still limited, recent research has already addressed the impacts of climate change on wild populations of the species. Molloy et al. (2021), for example, identified significant shifts in the suitable habitat areas of *T. grandiflorum* in future scenarios, highlighting its ecological vulnerability. This information is particularly relevant considering that the models of this study were based on records of occurrence of the species in natural and cultivated environments, without distinction between agricultural areas and wild populations.

Considering the socioeconomic relevance of *T.cacao* and *T.grandiflorum* for Brazil and the risks imposed by global environmental changes, understanding how these species adapt, occur, and predict their current and future distribution, it is essential to ensure their sustainable use and conservation of their genetic source (IPCC 2021; Cilas and Bastide 2020; Araújo et al. 2024). In this context, ecological niche modeling has been shown to be an effective tool for assessing the vulnerability of these species to future climate change scenarios over different periods, becoming crucial for the development of conservation strategies that use geographic coordinates, as well as climatic and edaphic variables (Tomaz et al. 2022; Gomes et al. 2022; Cordeiro et al. 2023; Ceccarelli et al. 2024).

This study aimed to predict the geographic distribution of *T. cacao* and *T. grandiflorum* under current and future climate scenarios using ecological niche modeling, to identify environmentally suitable areas for their cultivation, guiding sustainable land-use strategies, and supporting conservation planning in regions where wild genetic resources may be at risk.

MATERIAL AND METHODS

Characterization of *Theobroma cacao*L. and Theobroma grandiflorum (Willd. ex Spreng.) Schum).

This study focuses on two Amazonian species of *Theobroma*: *T. cacao* and *T. grandiflorum*, selected for their ecological significance, economic value, and contrasting responses to environmental change. Both are perennial, shade-tolerant trees naturally found in humid tropical forests, and are native to the Amazon biome (Nair et al. 2021; Smith 2023). Although taxonomically related, they exhibit distinct ecological behaviors and degrees of domestication, which influence their environmental resilience and management practices.

The cacao tree is distributed across tropical America, particularly in the Amazon basin, and is cultivated globally in equatorial regions. It is the most economically important species of the genus *Theobroma*, serving as the primary raw material for the chocolate industry, with additional applications in pharmaceuticals and cosmetics, and Brazil is among the largest producers in South America (Mar et al. 2024; Loke et al. 2024). The species thrives in regions with annual precipitation between 1,500 and 2,500 mm and average temperatures of 21–32°C, preferring well-drained, nutrient-rich soils. It is a shade-tolerant tree commonly found in the forest understory, exhibiting high genetic and phenotypic diversity due to extensive domestication and breeding programs (Araújo et al. 2024; Lahive et al. 2019).

The cupuaçu tree is considered endemic to the Brazilian Amazon, especially in the states of Pará, Amazonas, and Acre. Its fruits are widely utilized in producing juices, jams, sweets, and cupulate—a chocolate-like product derived from its seeds. The pulp is the most commercially valued part, significantly contributing to the Amazonian bioeconomy and supporting family-based agroforestry systems (Silva et al. 2024; Bezerra et al. 2024). The species has more restricted ecological requirements than cacao, demonstrating lower resilience to climatic variations, particularly regarding water stress and temperature extremes (Molloy et al. 2021; Ceccarelli et al. 2024).

Ecologically, both species occupy the forest understory and are primarily pollinated by small insects (Smith 2023; Jaramillo 2024). They exhibit similar growth habits in shaded environments and depend on specific soil and climatic conditions for optimal development (Lahive et al. 2019; Bezerra et al. 2024). Their reproductive cycles are influenced by climatic factors, and prolonged drought periods may reduce flowering and fruiting rates (Lahive et al. 2019; Mahur et al. 2023; Ceccarelli et al. 2024). While cacao has shown broader climatic plasticity and genetic diversity due to long-standing cultivation and breeding programs (Nousias et al. 2024), cupuaçu remains less domesticated, with fewer selected genotypes available and greater susceptibility to biotic and abiotic stressors (Rosa et al. 2024).

Their ecological, cultural, and economic value, alongside their contrasting vulnerabilities to climate change, justifies their inclusion in ecological niche modeling, providing insights into their environmental requirements and supporting conservation and land-use planning under climate change scenarios

Study area

The study area encompasses Brazil's six primary phytogeographical domains, as officially classified by the Brazilian Institute of Geography and Statistics (IBGE 2019). These include: (i) the Amazon, dominated by humid tropical forests with dense canopies, high rainfall, and exceptional biodiversity; (ii) the Cerrado, a tropical savanna characterized by marked seasonality, frequent fires, and high levels of plant endemism; (iii) the Atlantic Forest, a tropical and subtropical rainforest with high species richness and endemism, now highly fragmented due to historical deforestation; (iv) the Caatinga, a semi-arid region with seasonally dry forests and xerophytic vegetation adapted to water scarcity; (v) the Pampa, in southern Brazil, composed primarily of grasslands and herbaceous species under temperate climatic conditions; and (vi) the Pantanal, the world's largest tropical wetland, featuring seasonal flood dynamics and a mosaic of forested and open vegetation. These domains differ significantly in climatic regimes, edaphic conditions, and vegetation structure, directly influencing ecological processes and species distributions. Their correct ecological characterization is essential to ensure spatial accuracy in niche modeling and to support conservation planning (IBGE 2019; Artaxo et al. 2022; Clement et al. 2021).

Process of obtaining the occurrence points and data cleansing

The occurrence records for *T. cacao* and *T. grandiflorum* were compiled between January and April 2024, at the Plant Genetics Laboratory of the Federal University of Amazonas, encompassing georeferenced data collected from 1970 to 2023. This temporal range was selected to include a sufficient number of validated records while minimizing biases associated with outdated taxonomy or imprecise coordinates. The geographic coordinates were obtained from public databases such as SpeciesLink (CRIA 2023) and the Global Biodiversity Information Facility (GBIF 2023). Additionally, both physical and virtual herbarium collections were consulted, such as REFLORA (2023), the Herbarium of the National Institute of Amazon (INPA), and of the Federal University of Amazonas (UFAM). These collections were selected due to their extensive Amazonian specimens and high-quality georeferenced data. Also, relevant peer-reviewed scientific articles reporting occurrence coordinates were also consulted to supplement the data. These data were utilized during the modeling phase, and the distribution layers of the respective species were analyzed in Brazil using a geographic information system.

For the process of cleansing the data, we conducted a consistency analysis that eliminated duplicates, atypical data, and records from areas where species presence is not viable. This step was essential for creating a reliable consensus model, ensuring that the occurrence points used for model development were accurate and faithfully represented the distribution of species across Brazil. To minimize autocorrelation and avoid sampling bias, we excluded occurrences that were less than 5 km apart. This procedure followed the guidelines set by Aiello-Lammens et al. (2015) and was carried out using the spThin package in RStudio (2024). After data cleansing, spatial thinning, and removal of duplicates and implausible records, a total of 1,014 occurrence points were retained for *T. cacao* and 180 for *T. grandiflorum*, which were used for ecological niche modeling.

To ensure consistency between the modeling process and the available data, the period from 2009 to 2019 was adopted as the reference for the "present" based on the most recent and validated species occurrence records. However, the projections for this period—as well as for future scenarios (2041–2060, 2061–2080, and 2081–2100) —were all based on historical climatic variables from WorldClim (1970–2000), which serve as the baseline for current climate conditions in ecological niche modeling. Thus, the "present period" (2009–2019) refers to the temporal scope of the occurrence records, while the environmental suitability was modeled using historical climate data to allow consistent comparison with future projections.

Environmental variables

For the modeling, two types of environmental data sets were used, covering climatic and soil variables, totaling 33 environmental variables to predict the distribution of *T. cacao* and *T. grandiflorum*.

Among the climatic variables, 19 bioclimatic with spatial resolution of 25 minutes were used, extracted from the Worldclim- Global Climate database (Fick and Hijmans 2017), these data include monthly values of minimum, average and maximum temperatures (°C) and rainfall (mm), based on global historical data from 1970 to 2000, being: AMT: Annual mean temperature (°C); MDR: Mean Diurnal Range (Mean of monthly (max temp - min temp) °C); ISO: Isothermality (MDR/TAR) (*100) (%); TS: Temperature seasonality (standard deviation *100) (%); MTWM: Max temperature of warmest month (°C); MTCM: Min temperature of coldest month (°C); TAR: Temperature annual range (MTWM-MTCM) (°C); MTWQ: Mean temperature of wettest quarter (°C); MTDQ: Mean temperature of driest quarter (°C); MTWQ: Mean temperature of warmest quarter (°C); MTCQ: Mean temperature of coldest quarter (°C); AP: Annual precipitation (mm); PWM: Precipitation of wettest month (mm); PDM: Precipitation of driest month (mm); PS: Precipitation seasonality (coefficient of variation) (mm);PWQ: Precipitation of wettest quarter (mm); PDQ: Precipitation of driest quarter (mm); PWAQ: Precipitation of warmest quarter (mm); PCQ: Precipitation of coldest quarter (mm).

Considering the influence of soil characteristics on plant development (Alvarez et al. 2022), 14 soil properties were incorporated at a depth of 15-30 cm, from the SoilGrids database of the International Soil Reference and Information Centre (ISRIC - World Soil Information) (ISRIC 2020). Among the main variables available are: pH (-$\log_{10}[H^+]$), the organic carbon content in soil (dg/m^3), bulk density, amount of coarse fragments (cm^3/dm^3), sand content (g/kg), silt content (g/kg), clay content (g/kg), cation exchange capacity (mmol(c)/kg), total nitrogen (cg/kg), organic carbon density in soil (hg/m^3), organic carbon stock (t/ha) and estimated probability of occurrence of the horizon To provide a more comprehensive characterization of the environmental niche where the species will present proven occurrence, the variables elevation of the territory and declivities were also included, available in the EarthEnv database (ISRIC 2020). The decision to use soil variables from the 15-30 cm depth layer was based on the fact that this depth corresponds to the effective root zone of most tropical perennial crops, including *T. cacao* and *T. grandiflorum*. This layer is representative of the active soil–plant interface where root nutrient and water uptake are most intense, and where edaphic constraints most directly affect plant development. Previous studies on tropical fruit trees and Amazonian crops have adopted this depth as a reference for modeling purposes due to its agronomic relevance (Alvarez et al. 2022; Ceccarelli et al. 2024).

Data preprocessing and dimensionality reduction

To reduce multicollinearity among predictor variables and improve model efficiency, we performed a Principal Component Analysis (PCA) using the historical environmental dataset (1970–2000), which served as the baseline for modeling species distributions. The PCA was applied to the full set of 33 environmental variables (19 bioclimatic and 14 edaphic) in a single combined analysis, rather than conducting separate PCAs for soil and climate. This approach allowed for an integrated assessment of the main environmental gradients affecting species distributions, capturing interactions between climatic and soil factors.

The PCA was conducted prior to model calibration, as part of the data preparation phase. Only components explaining at least 95% of the total variance were retained, following best practices for dimensionality reduction in ecological niche modeling (Sánchez-Fernández et al. 2013; Velazco et al. 2017). The loadings of each variable on the principal components guided the identification of the most informative axes, which were then used in the modeling framework.

Since future soil projections are not available in the same resolution and format as climatic projections, only the climate-related components of the PCA were projected to the future scenarios (SSP2-4.5 and SSP5-8.5). Soil variables were assumed to remain static across future periods, based on the premise that edaphic factors change more slowly than climatic variables and are less influenced by emission pathway assumptions (Velazco et al. 2017; Alvarez et al. 2022). Therefore, the edaphic component of the environmental niche remained constant in future scenario projections, while climatic conditions were updated accordingly.

This strategy ensured consistency in the variable selection process and allowed the integration of static and dynamic predictors within a robust modeling pipeline.

Prediction of climate data

Among the available Shared Socioeconomic Pathways (SSPs), we selected SSP2-4.5 and SSP5-8.5 to represent an intermediate and a high-end emissions scenario, respectively. SSP2-4.5 assumes moderate mitigation efforts and is often used as a baseline for comparing adaptation strategies. SSP5-8.5, in turn, is the most pessimistic scenario and reflects a fossil-fueled development trajectory with minimal mitigation policies. The combination of both scenarios enables a more comprehensive understanding of species' vulnerability under contrasting global climate futures, as recommended in biodiversity modeling studies (IPCC 2021; Thuiller 2024).

The projection of climate data for future scenarios was based on the IPCC sixth report climate change projections, using reduced climate data from the Coupled Model Intercomparison Project Phase 6 (CMIP6). These data are available in Worldclim- Global Climate database (Fick, Hijmans 2017), and are organized by periods (2041-2060, 2061-2080, 2081-2100). Among the available Shared Socioeconomic Pathways (SSPs), we selected SSP2-4.5 and SSP5-8.5 to represent a scenario of medium and high-level greenhouse gas emissions, respectively. SSP2-4.5 assumes that moderate mitigation efforts are applied and is often used to compare adaptation strategies. SP5-8.5, in turn, is the most pessimistic scenario and reflects a development trajectory with fossil fuels and minimal mitigation policies. The combination of both scenarios allows a more comprehensive understanding of species vulnerability under these global climate changes, as recommended in biodiversity modelling studies and allows a more complete assessment of the potential impacts of these climate changes under distinct socioeconomic and policy trajectories, thus increases the quality of ecological modeling and provides a conservation plan more appropriate for the species studied (IPCC 2021; Thuiller 2024).

Construction of the predictive model

The ecological niche models were developed using R, an open-source programming environment widely used in statistical and ecological modeling, together with the ENMTML (Ecological Niche Models with TheMetaLand) package, a powerful tool for modeling ecological niches and species distributions (Andrade et al. 2020). With the support of the resources and libraries available in RStudio v.4.2, a niche model was developed based on the data series mentioned above.

In total, 13 algorithms available in the ENMTML package were tested to assess their predictive performance in modeling species distributions. From this initial comparison, six algorithms were selected based on their superior evaluation metrics (AUC, TSS, and Sorensen index), ensuring the use of only those with the highest accuracy and consistency. The selected algorithms were Support Vector Machine (SVM), Maximum Entropy Default (MXD), Bioclim (BIO), Random Forest (RDF), Generalized Linear Models (GLM), and Bayesian Gaussian Process (GAU), which together provided robust and complementary modeling strategies. All models were calibrated using the same occurrence dataset and environmental predictors, ensuring consistency across methods.

Algorithms that require presence-only data (e.g., BIO, MXD) and those that require presence–absence data (e.g., GLM, RDF, SVM) were handled by generating pseudo-absence data, following the internal ENMTML routine. This routine randomly generates pseudo-absences from regions outside the environmental envelope of the species, based on a surface range envelope approach that avoids artificially inflating model accuracy. The number of pseudo-absences was standardized to 1,000 for all presence–absence models. The same background area was used for all models and was defined as the extent of the Brazilian territory, excluding oceanic regions and areas above 2,000 meters in altitude, where neither species is known to occur. This background was chosen to reflect both the accessible area for the species and ecological realism, and was used to generate both pseudo-absences and to train presence-only models.

All models were run using the default tuning parameters of the ENMTML package version used, which are optimized for ecological niche modeling applications. The consensus model was then created using a weighted average approach, where each model's contribution was based on its AUC value, as proposed by Marmion et al. (2009), ensuring that models with higher performance had proportionally greater influence in the final prediction.

Elaboration of an integrated model to project the geographic distribution of species

To predict the geographic distribution, a consensus model was created using six different modeling algorithms, including Support Vector Machine (SVM), Maximum Entropy Default (MXD), Bioclim (BIO), Random Forest (RDF), Generalized Linear Models (GLM) and Bayesian Gaussian Process (GAU). The weighted average methodology was applied to develop this consensus model, which, according to Marmion et al. (2009), results in significantly more robust forecasts compared to other consensus methods. This procedure involves a pre-evaluation of the predictive performance of each model. Initially, 50% of models that have higher precision are selected, and then the weighted average is calculated based on the Area Under the Curve (AUC) of these previously evaluated models.

The quality evaluation of the adjusted models was performed based on the calculation of the area under the curve (Area Under the Curve - AUC), obtained from the integration of the Operational Characteristics curve (Receiver Operating Characteristics Curve -ROC). The AUC varies between 0 and 1, with the maximum value of the AUC being theoretically 1.0 and indicating perfect discrimination, while values below 0.5 denote poor modeling performance.

Model performance was evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC), which is widely used in ecological niche modeling to measure the discriminatory capacity of presence–absence models. Models with AUC values 0.7 are considered to have good discriminatory power, and values 0.9 indicate excellent performance (Swets 1988; Jiménez-Valverde 2012). To convert continuous probability outputs into binary presence–absence maps, we used the threshold that maximizes the sum of sensitivity and specificity (MX_TSS), which balances omission and commission errors and is widely recognized as a robust thresholding criterion (Liu et al. 2005; Allouche et al. 2006). The MX_TSS values obtained were 0.81 for *T. cacao* and 0.76 for *T. grandiflorum*, indicating high predictive reliability for both species.

To assess changes in geographic distribution, we calculated the area (in km^2) of environmentally suitable zones predicted by the binary maps generated for each scenario and time period. These calculations were performed using GIS tools within the R environment, overlaying binary presence/absence maps on Brazil's phytogeographic domains. Area values were then compared across periods and scenarios to quantify gains and losses in suitable habitat. The relative balance (net change) was calculated as the difference between gains and losses, expressed as a percentage of the total suitable area in the current scenario.

Finally, binary maps (presence and absence) were generated for each species, which were based on the consensus of models that present good evaluation metrics. In addition, the maximum values of sensitivity and specificity (MX_TSS) were considered. These maps provide a clear visual representation of the predicted geographic distribution of species.

RESULTS AND DISCUSSION

Performance of prediction models

The ecological niche models developed for *T. cacao* and *T. grandiflorum* showed high predictive performance across all selected algorithms. The consensus models achieved excellent discrimination ability, with AUC values above 0.90 for both species. It was verified that for cocoa tree (1.00±0.007) and cupuaçu tree (0.98±0.024), the SVM algorithm and Sorensen metric presented superior metrics with perfect data discrimination. The most influential environmental variables in the species distributions were temperature seasonality, accumulated rainfall in the year, accumulated rainfall in the driest quarter, organic carbon density in the soil, soil pH in water, and elevation.

These variables capture key climatic and edaphic constraints that influence the ecological niches of the two species. A detailed breakdown of model performance metrics and principal components is available in Additional File 1 and 2.

Projection of the occurrence of cupuaçu and cacao trees

After the process of cleansing and spatial reduction of the occurrence data of the species, a final occurrence matrix was obtained with 180 points for cupuaçu tree and 1,014 points for cacao tree (Figure 1a, b).

In the present period, cupuaçu tree and cacao tree showed wide distribution in the Amazon domain, with a presence in the Cerrado, Atlantic Forest, and Pantanal (Figure 2a, b). It was found that the cupuaçu tree does not occur in the Pampa and has low occurrence in the Caatinga and south of the Atlantic Forest (Figure 2a) the cacao tree follows a similar distribution pattern; however, it also occurs in the Atlantic Forest, in the transition areas with the Cerrado, and—unlike cupuaçu—presents limited occurrence in the Pampa domain, as indicated in Table 1.

The projections for the cupuaçu tree in the intermediate scenario SSP245 for the period from 2041 to 2060 indicate a low probability of occurrence of the species in the areas of Caatinga, Pampa, and Pantanal (Figure 3a). It is also observed that the species is distributed longitudinally from the Amazonian biome towards the Atlantic Forest, with a low probability of occurrence in the northwest and northeast regions of the Amazon (Figure 3a, b, c).

In the worst-case scenario, SSP585, there is a progressive reduction of cupuaçu tree presence in the Amazon between 2041-2060 and 2061-2080 (Figure 3d, e), culminating in a sharp reduction from 2081 to 2100 (Figure 3f). The species tends to migrate from the Cerrado to the Atlantic Forest, which results in an increase in population and occurrence in the northwest of the Amazon (Figure 3f).

The projections for the less pessimistic scenario SSP245 in the periods of 2041-2060, 2061-2080 and 2081-2100 show a wide distribution of the cacao tree in Brazil, with high probability of occurrence in the Amazon, Pantanal, Cerrado, Mata Atlântica and Pampa biomes, and lower probability in the Caatinga biome (Figure 3h, i, j). In the most pessimistic scenario, there is a gradual reduction of suitable areas in the Amazon and Cerrado (Figure 3j, k, l). However, some regions show a higher probability of occurrence of the species in areas where it was not previously found, such as the northwestern portion of the Amazon, which has an increase in environmentally suitable areas for the cacao tree (Figure 3k, l).

In percentage, the projections show an increase or reduction of environmentally suitable areas for cocoa cultivation. Only the Amazon biome showed a reduction in these areas, with the largest loss occurring in the most pessimistic scenario SSP585 (14.38%) from 2081 to 2100 (Table 1). The Caatinga, Cerrado, Atlantic Forest, Pampa, and Pantanal biomes had an expansion of suitable areas in both scenarios and the three intervals analyzed. The Pampa stood out with an increase of (+188,249.93%) and the Caatinga with (+116,53%) in the less pessimistic SSP245 scenario for the period from 2041 to 2060 (Table 1). The Pantanal

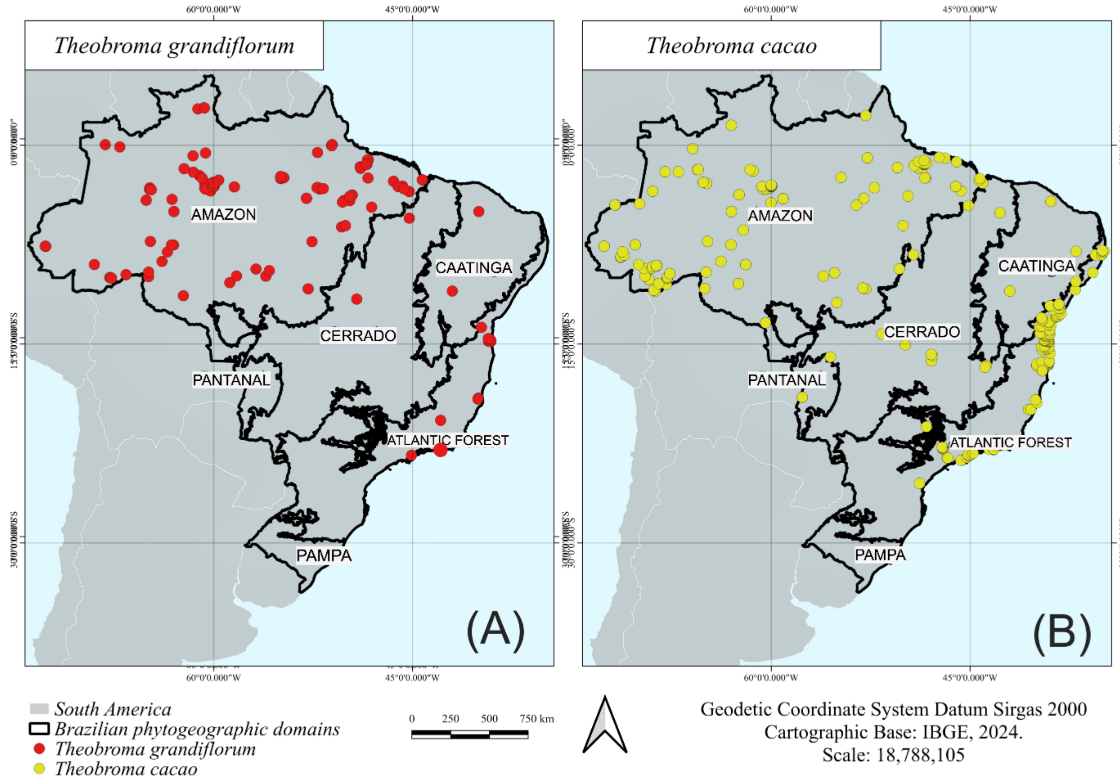

Figure 1. Occurrence points after the analysis of collinearity and spatial reduction and projection for the present period (2009-2019) of a) cupuaçu tree (*Theobroma grandiflorum*), and b) cacao tree (*Theobroma cacao*) in the Brazilian phytogeographic domains.

had a notable increase in suitable areas in the less pessimistic scenario, with growth of (+377.46%) between 2041 and 2060.

The cupuaçu tree showed a different behavior of the cacao tree in future projections, which point to a reduction of suitable areas in the Pantanal (99.45%), Caatinga (91.01%), Amazon (77.18%) and Cerrado (44.17%) biomes between 2081 and 2100 under the most pessimistic scenario, SP585 (Table 1). Only the Atlantic Forest recorded substantial increases in favorable areas in all scenarios and periods evaluated, achieving a growth of (+336.14%) in the most pessimistic scenario SSP585 in the range of 2081-2100 (Table 1). The Pampa biome, on the other hand, did not present adequate areas in the base period nor in future projections (Table 1).

Overall, the projections indicate contrasting trends between the two species. *T. grandiflorum* (cupuaçu) is expected to suffer substantial reductions in total suitable area across Brazil, with a maximum loss of 65.86% under the SSP585 scenario for 2081–2100. In contrast, *T. cacao* (cocoa) shows more resilient behavior, with total suitable areas increasing modestly, reaching up to +18.83% in the SSP245 scenario for 2041–2060. However, this gain decreases over time, dropping to only +1.90% in the most pessimistic scenario (SSP585, 2081–2100). These results highlight the vulnerability of cupuaçu and the comparatively limited expansion potential of cocoa under future climate scenarios.

In addition to changes in total suitable area, the projections revealed spatial displacement in species distribution. For both *T. cacao* and *T. grandiflorum*, suitable zones shifted geographically, particularly from the Amazon toward the Atlantic Forest and transitional zones with the Cerrado. These spatial shifts occurred even in scenarios where the net suitable area remained stable or increased, highlighting the importance of spatially explicit analyses. This behavior reflects ecological migration rather than pure habitat loss or gain, and underscores the relevance of regional conservation planning.

Conservation and sustainability

The overall reduction in suitable area for *T. grandiflorum*, which may reach up to 65% by the end of the century (SSP585) with major concentrations in the Amazon, Cerrado, and Pantanal domains, raises serious concerns regarding the species' long-term viability in its native range. Although *T. cacao* shows

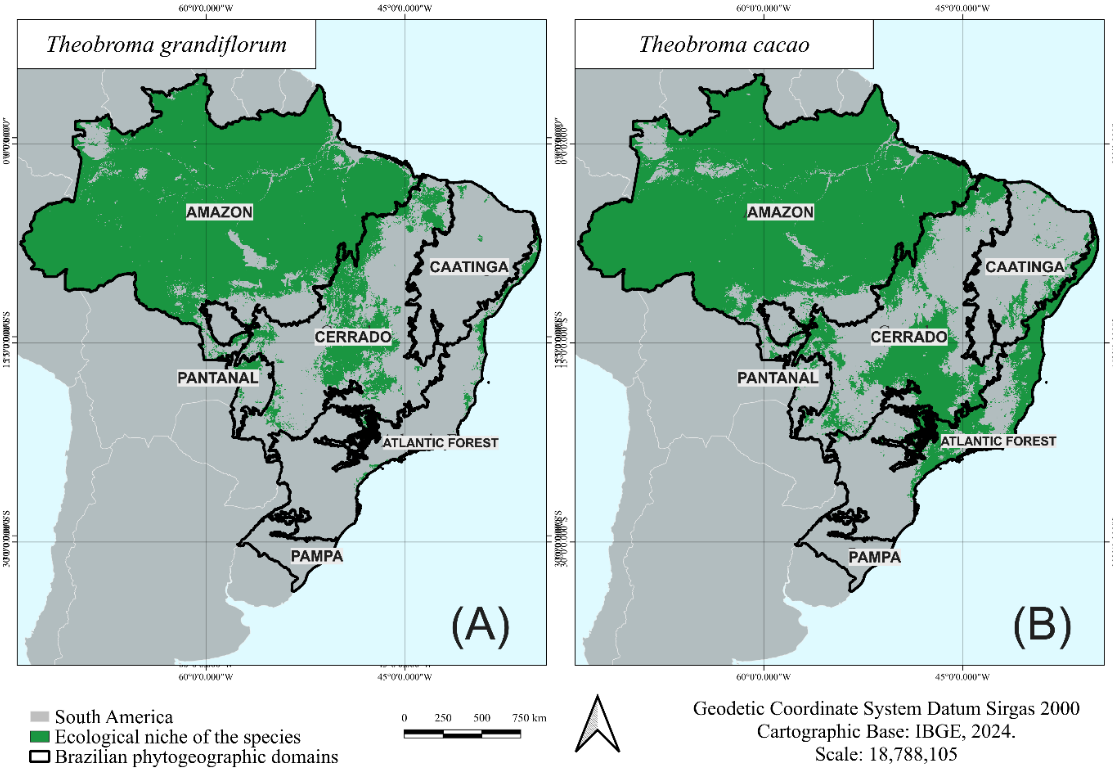

Figure 2. Projection for the current period (2009-2019) for the species: a) Cupuaçu tree (*Theobroma grandiflorum*) and b) Cacao tree (*Theobroma cacao*), modeled using historical climatic variables data from WorldClim (1970-2000). Green areas indicate predicted presence based on the consensus model.

more optimistic trends, with gains in total area, these remain relatively modest and decline progressively under harsher climate scenarios. Such projections emphasize the need for urgent and differentiated conservation strategies for each species.

The ecological niche modeling conducted in this study projects contrasting potential responses of *Theobroma cacao* and *T. grandiflorum* to climate change in Brazil. These results suggest that *T. cacao* possesses a broader climatic tolerance, allowing for an expansion of suitable areas into other biomes, particularly the Atlantic Forest and the Pampa. In contrast, *T. grandiflorum* may experience a marked reduction in suitable habitat, especially under the most pessimistic climate scenario (SSP585) by the end of the century(Ceccarelli et al. 2024; Lahive et al. 2019).

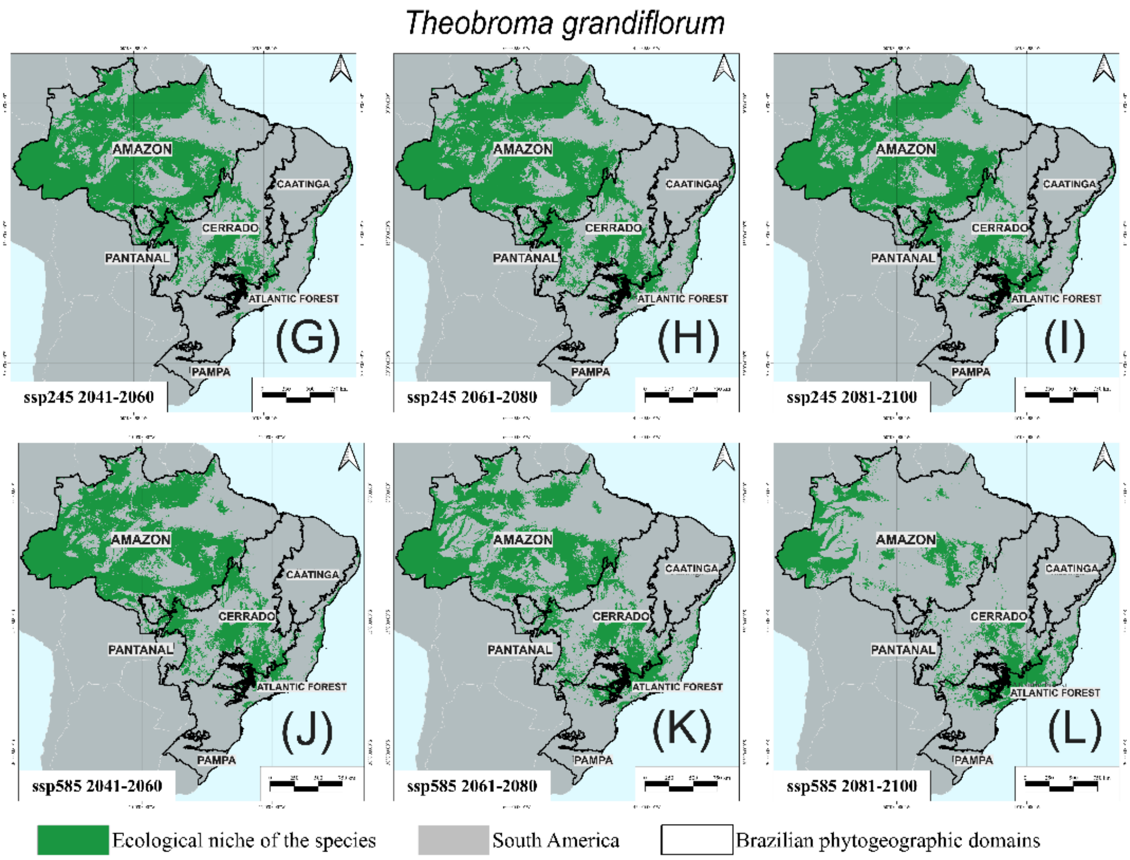

Figure 3. Binary projections of the potential distribution of *Theobroma grandiflorum* (a-f) and *Theobroma cacao* (g-l) in the SSP245 (a-c; g-i) and SSP585 (d-f; j-l) climate scenarios for the periods 2041-2060, 2061-2080 and 2081-2100. The green areas indicate expected presence according to the consensus model. The maps show binary data (presence/absence), and the species names are indicated in the subfigures. The projections consider future climate (CMIP6) based on historical climatic variables (1970-2000), keeping constant the edaphic variables.

Table 1. Projections of increase (+) or loss (-) of environmental suitability area (%) in the SSP245 and SSP585 scenarios in the time intervals 20412060, 20612080, and 20812100, compared to the current period, in the Brazilian phytogeographic domains, for the species *T. cacao* and *T. grandiflorum*

				T. cacao			
			SSP245			SSP585	
Coverage	Current Period (Km^2)	2041-2060	2061-2080	2081-2100	2041-2060	2061-2080	2081-2100
Amazon	3,827,980.50	-2.62	-3.17	-3.36	-3.39	-5.32	-14.38
Caatinga	90,765.01	+116.53	+112.42	+115.91	+108.29	+109.79	+81.87
Cerrado	805,349.70	+67.36	+64.63	+60.80	+64.03	+49.59	+15.90
Atlantic Forest	442,181.26	+72.33	+80.66	+80.07	+75.44	+81.32	+81.07
Pampa	43.37	+113,199.96	+135,299.95	+130,449.95	+128,399.95	+145,799.95	+188,249.93
Pantanal	15,676.80	+377.46	+375.52	+361.00	+368.46	+271.92	+40.25
Total	**5,181,996.64**	**+18.83**	**+18.82**	**+18.02**	**+17.97**	**+14.68**	**+1.90**
				T. grandiflorum			
		SSP245			SSP585		
Coverage	Current Period (Km^2)	2041-2060	2061-2080	2081-2100	2041-2060	2061-2080	2081-2100
Amazon	3.793,200.98	-29.09	-27.87	-32.16	-33.92	-46.39	-77.18
Caatinga	7,719.15	-67.13	-57.30	-56.18	-62.08	-69.94	-91.01
Cerrado	589,170.27	+5.46	+24.82	+8.87	+11.00	+2.97	-44.17
Atlantic Forest	78,470.75	+46.23	+165.65	+152.94	+103.09	+244.71	+336.14
Pampa	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pantanal	35,538.42	-67.66	-62.54	-69.49	-66.75	-86.76	-99.45
Total	**4,504,099.57**	**-23.63**	**-17.93**	**-23.90**	**-25.97**	**-35.22**	**-65.86**

The greater loss of suitable area for *T. grandiflorum* can be attributed to its narrower ecological niche, limited genetic diversity, and higher sensitivity to temperature extremes and water stress. As a species with less domestication history and fewer breeding programs, cupuaçu depends more heavily on stable, humid environments, which are expected to contract under future climate scenarios (Ceccarelli et al. 2024; Rosa et al. 2024). In contrast, *T. cacao* benefits from a long history of cultivation and selection, which has enhanced its adaptive capacity to a wider range of climatic conditions and contributed to its projected expansion (Araújo et al. 2024; Lahive et al. 2019).

These divergent trends have significant implications for food security and the local bioeconomy. Cupuaçu is a key resource for smallholders in the Amazon, and reductions in suitable areas may affect regional income, food diversity, and the availability of non-timber forest products. Conversely, cacao tree's expansion could present new opportunities for cultivation in other Brazilian regions, including the Atlantic Forest, Pampa, and Pantanal, potentially increasing national production. However, this shift must be accompanied by policies that prevent environmental degradation and ensure sustainable land-use practices.

Analysis across Brazil's six phytogeographic domains revealed distinct patterns. For *T. grandiflorum*, the greatest losses occurred in the Amazon (-77.18%), Pantanal (-99.45%), and Caatinga (-91.01%) under SSP585 (2081-2100), highlighting its vulnerability in native and semi-arid regions. The only consistent expansion occurred in the Atlantic Forest, with gains exceeding +300% in some scenarios. For *T. cacao*, gains were recorded in nearly all domains, especially in the Pampa (+188,249.93%) and Atlantic Forest (+81.07%). Even the Caatinga, typically marginal for tropical crops, showed increases of over +80% in suitable area. These findings underscore the need for region-specific conservation and agricultural strategies.

Based on the projections, in-situ conservation efforts should be prioritized in the central-western and southern portions of the Amazon biome, where significant losses in suitable habitat for cupuaçu are expected. These regions represent current strongholds for the species but are projected to become less suitable by the end of the century under SSP585. Ex-situ strategies are recommended for the eastern Amazon and northern Cerrado, where habitat contraction may threaten genetic diversity.

For cacao tree, the Atlantic Forest and Pampa biomes, which show strong suitability gains, may become strategic zones for crop expansion under climate-resilient land-use planning. However, the Amazon region, particularly its southeastern portion, will require the development of genotypes with greater drought and heat resistance, given the projected loss of suitability. These spatial recommendations aim to guide practical conservation, breeding, and agricultural zoning initiatives.

It is important to note that the modeling results reflect potential shifts in environmental suitability, not species migration. For example, the observed change from current suitability in the Cerrado to future suitability in the Atlantic Forest for *T. grandiflorum* represents a shift in climatically favorable conditions, rather than a literal movement of the species. Additionally, the results do not confirm future outcomes but rather indicate probable scenarios based on current climatic projections and species-environment relationships. Although our projections suggest a future reduction in suitable areas for *T. grandiflorum*, previous studies have emphasized the vulnerability of tropical fruit species to climate change, particularly regarding water stress and narrow climatic tolerance ranges. (Ceccarelli et al. 2024; Lahive et al. 2019;).

The Amazon is considered one of the most susceptible regions to climate change (Artaxo et al. 2022), which may lead to shifts in ecological niches toward more suitable environmental conditions (Lawlor et al. 2024; Rubenstein et al. 2023). These processes can occur gradually, over decades or centuries, and are often accompanied by adjustments in phenological cycles and morphological traits that enhance survival in new climatic contexts (Sultan et al. 2019).

Due to the socioeconomic relevance of cocoa and cupuaçu fruits, the conservation of species should be carried out using different strategies, ex-situ, combining the availability of financial resources and area of suitability for soil climate over time. Ex-situ conservation will be necessary to store varieties and genotypes, ensuring the genetic diversity needed for future breeding, especially if the worst period is achieved. Seed banks or plant cloning can preserve genotypes that are resistant to pests, diseases, and the effects of climate change, ensuring a gene bank for future needs.

The on-farm conservation and maintenance of the genetic diversity of plants in the farmers' agricultural systems, their properties, and cultivation systems have already played a distinct role in the center of diversity and dispersion of species. In the case of cocoa and cupuaçu tree, people use the species even for survival, involving sustainable management practices where farmers grow varieties of species in their production systems, often in agroforestry systems. On-farm conservation is advantageous because it maintains genetic diversity while allowing local species to adapt to specific growing conditions and preserves traditional knowledge associated with the management of these crops from local farms (Khoury et al. 2021; Shanley et al. 2016).

The conservation of most plant species is concentrated in natural forests, which are referred to in several ways as intact forest landscapes, primary forests, and wilderness areas. The relationships between indigenous peoples and forest landscapes are based on integrated socio-ecological systems, where cultivated, fallow, and forested areas coexist in a dynamic continuum. These perspectives have been described in detail by authors such as Clement et al. (2021) and Levis et al. (2024), highlighting the role of traditional knowledge in maintaining genetic diversity and supporting in situ conservation. For these groups, each part of the forest mosaic in different stages of socio-ecological succession has different "owners": when people open their gardens, they must respect other forest dwellers, including non-humans, when their gardens are fallow, they allow animals to resume their original roles as managers and conservators of the area. Each succession stage also contains populations of cultivated and domesticated plants for the conservation of genetic resources. Fallow in the field represents on-farm conservation, while the less anthropic parts of the forest mosaic represent in situ conservation (Clement et al. 2021). For the conservation of species such as cocoa and cupuaçu tree in the Amazon, these spaces should be mapped for on-farm and in situ conservation.

The cupuaçu tree is mainly grown by family farmers in the Brazilian Amazon, promotes local development, and strengthens the region's bioeconomy (Silva et al. 2024). The cultivation of this species has presented limitations, especially in the selection of genotypes with high productivity and resistance to the fungus *Moniliophthora perniciosa*, causative of the witch-broom disease, which is the main pest that affects the cupuaçu tree and cacao tree crops (Rosa et al. 2024). The crop also requires efficient soil management since the absence of essential elements such as N, P, K, Ca, Mg, S, and B can negatively affect plant growth, development, and productivity (Silva et al. 2024). It is necessary to ensure that the cultivation of cupuaçu tree receives appropriate management and is conducted in a sustainable manner considering the vulnerability of the species to the effects of climate change and resistance to diseases and pests. Relearning from the indigenous peoples of the Amazon by going to sustainable agroforestry systems can minimize the impacts of cultural development in this region.

Climate change also poses a threat to natural populations and cocoa crops due to the reduction of environmental suitability areas in the Amazon. It will be necessary to adopt differentiated strategies according to each Brazilian region. These strategies that should be adopted for cupuaçu tree in the Amazon would also be valid for the cocoa tree. In traditional cacao-producing regions such as the state of Bahia, the adoption of agroforestry systems presents both opportunities and challenges. Although these systems can enhance biodiversity and ecosystem services, environmental sustainability, their success depends on regional adaptation and socioeconomic feasibility. In this context, the development of high-yielding, drought- and pest-resistant varieties becomes essential to ensure crop resilience and meet the growing demands of the cocoa market, as highlighted by Lahive et al. (2019).

The natural populations of cocoa have wide diversity in their germplasm, resulting from the domestication process carried out by different indigenous groups in tropical America, thus facilitating the adaptation of the species to different environmental conditions (Nousias et al. 2024). The cocoa tree is cultivated in the tropics, and despite the genetic and phenotypic diversity of the species (Araújo et al. 2024), crops are being affected by climate change, especially by the change in water regime and the distribution of pests and diseases (Cilas and Bastide 2020). Water availability is directly related to cocoa productivity, and to ensure the sustainability of its crops, the selection of drought-tolerant genotypes becomes essential during a changing climate (Araújo et al. 2024; Nieves-Ordunã et al. 2024).

There is a need to adopt different strategies for the conservation of cocoa trees due to the high demand for plantations and the socioeconomic relevance of the species for the world population. The cocoa tree has tolerance to periods of drought, which are characteristic of the region. However, prolonged exposure to such limiting factors can impair its biological performance and reduce its productivity (Bossa-Castro et al. 2024). Climate change directly influences the development of cocoa trees, impacting their ecological niche, and it is necessary to consider physiological and phenological responses, as well as the effect of pests and diseases on crops (Cilas and Bastide 2020). The selection of more drought-tolerant and pest and disease-resistant genotypes is essential to ensuring sustainability in cocoa crops (Araújo et al. 2024). To improve production yield, it is essential to understand the reproductive ecology of the species. A recent study about the floral biology of cocoa crops indicated that the cacao tree flowers are most visited during the day by a diversity of insects and in plantations connected to the forest (Jaramillo et al. 2024). The forms of conservation ex-situ, on-farm, and in situ can ensure the perpetuation of the species and survival of crops, as well as direct cultivation with greater sustainability. The adoption of agroforestry systems in cocoa also aims to contribute to the conservation of the species, in addition to performing environmental conservation through improving soil nutrition that is also affected by climate change to promote more sustainable production (Oduro et al. 2024).

The impact of loss for the species of cocoa and cupuaçu tree throughout the climate change process can be minimized with actions that advocate sustainable use and conservation. Strategies like the use of agroforestry practices that promote climate resilience, genetic improvement to develop varieties more resistant to climate change and extreme events, continuous monitoring and agro-ecological zoning to optimize cultivation areas, as well as sustainable soil and water management techniques, are all necessary. Initiatives such as training for producers (farmers), diversifying crops, seeking sustainable markets, the creation of public support policies, such as securing appropriate funding for environmental services in regions studied, can contribute to the adaptation and sustainability of these crops and ensure less damage to the species. It is also noted that such public policies must be designed and implemented to meet the needs of populations who depend on the products of fruit species for survival in the Amazon.

Study limitations and future directions

While ecological niche models are robust tools for predicting species distribution, they have inherent limitations that must be acknowledged. First, our models are based on bioclimatic and edaphic variables, and do not explicitly incorporate physiological or phenological traits of *T. cacao* and *T. grandiflorum*, which are known to influence species adaptation under climate change (Lahive et al. 2019; Ceccarelli et al. 2024). This omission may lead to under- or overestimations of species' adaptive potential in certain environments. Future modeling efforts should integrate mechanistic or process-based approaches that consider species-specific biological responses.

Additionally, the occurrence records used in this study did not distinguish between cultivated and wild populations. Although both types are ecologically relevant, the inability to differentiate them limits our ability to make targeted conservation recommendations. We opted for a broad-scale approach to identify general trends, but we recommend that future research incorporate more refined classifications and metadata regarding land use and cultivation status.

Despite these limitations, we employed rigorous spatial thinning, dimensionality reduction (PCA), and ensemble modeling approaches to minimize bias and increase model robustness. The high AUC and TSS scores support the reliability of the projections, particularly in identifying macroecological trends and vulnerable regions under climate change scenarios.

CONCLUSION

Climate change will impact the distribution of cocoa and cupuaçu tree in Brazil, presenting greater vulnerability to habitat loss, especially in the Amazon and Cerrado while the cocoa tree has greater resilience and potential for expansion to other biomes such as the Atlantic Forest and the Pampa. To mitigate these impacts, the study relates conservation strategies in situ, ex-situ, and on-farm, so that germplasm for future generations. For sustainable management, it presents strategies such as agroforestry systems and sustainable management in natural populations from the teachings of native peoples on land use. These actions are essential to ensure the conservation, and perpetuation of species and reduce impacts on the environment in the face of climate change.

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DATA AVAILABILITY

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

CONTRIBUTION STATEMENT

Conceived of the presented idea: LLM, JST, CSB, MTGL and SLFR. Carried out the experiment: LLM, SFS, RL, AVA.
Carried out the data analysis: LLM, JST, CSB, MTGL, CHSGM and HLVC.
Wrote the first draft of the manuscript: LLM, JST, CSB, SFS and HLVC.
Review and final write of the manuscript: MTGL, RL, CHSGM, AVA and SLFR.
Supervision: MTGL, RL, CHSGM and SLFR.

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Additional Files

Add File 1. Indicator variables and standard deviations (SD) were used to validate six models predicting the potential distribution areas of the *T. cacao* and *T. grandiflorum* species.

	Principal Components					
Variables	**PC19**	**PC21**	**PC22**	**PC23**	**PC24**	**PC26**
AMT	0.07	-0.02	-0.08	-0.01	0.01	0.17
MDR	-0.15	0.06	0.18	-0.19	0.11	0.25
ISO	-0.34	0.17	0.24	0.49	-0.15	-0.14
TS	0.03	0.06	-0.07	0.63	-0.10	0.10
MTWM	0.06	-0.04	-0.07	0.06	-0.13	-0.23
MTCM	0.01	0.00	-0.04	0.01	-0.05	0.06
TAR	0.04	-0.03	0.00	0.04	-0.04	-0.29
MTWQ	0.34	0.10	0.07	-0.13	0.16	-0.12
MTDQ	-0.18	-0.15	-0.28	0.09	0.15	-0.10
MTWQ	0.10	0.01	-0.11	0.24	-0.09	0.14
MTCQ	0.05	-0.02	-0.04	-0.18	0.02	0.07
AP	0.03	-0.07	-0.11	-0.21	-0.72	-0.08
PWM	-0.03	0.03	-0.13	0.13	0.43	0.37
PDM	0.01	-0.01	-0.02	-0.05	0.33	-0.44
PS	0.03	-0.08	0.12	0.01	-0.13	0.00
PWQ	-0.02	0.00	-0.09	0.00	0.13	-0.32
PDQ	0.04	-0.01	-0.06	-0.07	-0.14	0.50
PWAQ	-0.15	0.04	0.19	0.06	0.01	-0.03
PCQ	-0.09	-0.03	0.21	-0.05	0.05	0.00
CTC	0.23	0.02	0.09	-0.03	0.04	0.00
FGV	0.20	0.07	0.26	0.01	-0.02	-0.02
Clay	-0.07	-0.02	0.00	-0.01	-0.03	-0.02
Elevation	0.35	-0.08	-0.62	0.17	0.00	-0.04
Nitrogen	-0.24	-0.18	-0.10	0.13	-0.01	-0.01
DCO	-0.13	0.70	-0.22	-0.12	-0.06	-0.03
ECOS	0.08	-0.56	0.20	0.09	0.00	0.02
Soil pH in water	-0.55	-0.23	-0.33	-0.24	0.02	0.00
Sand	0.06	-0.01	0.00	0.01	0.00	0.00
Silt	-0.02	0.03	-0.01	-0.01	0.03	0.02
Declivity	-0.07	-0.03	0.02	-0.04	0.02	0.01
CCOS	0.09	0.03	-0.02	0.03	0.02	0.00
Classes and probabilities	0.01	0.04	0.00	-0.01	0.00	0.00
Apparent density	-0.19	0.08	0.02	0.02	-0.02	0.00

Legend: AMT: Annual mean temperature (°C); MDR: Mean Diurnal Range (Mean of monthly (max temp - min temp) °C); ISO: Isothermality (MDR/TAR) (*100) (%); TS: Temperature seasonality (standard deviation *100) (%); MTWM: Max temperature of warmest month (°C); MTCM: Min temperature of coldest month (°C); TAR: Temperature annual range (MTWM-MTCM) (°C); MTWQ: Mean temperature of wettest quarter (°C); MTDQ: Mean temperature of driest quarter (°C); MTWQ: Mean temperature of warmest quarter (°C); MTCQ: Mean temperature of coldest quarter (°C); AP: Annual precipitation (mm); PWM: Precipitation of wettest month (mm); PDM: Precipitation of driest month (mm); PS: Precipitation seasonality (coefficient of variation) (mm);PWQ: Precipitation of wettest quarter (mm); PDQ: Precipitation of driest quarter (mm); PWAQ: Precipitation of warmest quarter (mm); PCQ: Precipitation of coldest quarter (mm).CTC = cation exchange capacity at pH 7 (mmol(c)/kg); FGV = volumetric coarse fragments (cm^3/dm^3); COD = organic carbon densities (hg/m^3); ECOS = soil organic carbon stock (t/ha); CCO = soil organic carbon content (dg/kg); CB = "World Reference Base" classes and probabilities.

Add File 2. Indicator variables and standard deviations (SD) were used to validate six models predicting the potential distribution areas of the *T. cacao* and *T. grandiflorum* species.

T. cacao						
Metrics	**BIO[1]**	**GAU[2]**	**GLM[3]**	**MXD[4]**	**RDF[5]**	**SVM[6]**
AUC7	0.98±0.002	0.93±0.003	0.93±0.003	0.93±0.006	0.96±0.002	0.98±0.003
Kappa	0.99±0.024	0.93±0.011	0.93±0.015	0.94±0.020	0.97±0.010	0.99±0.014
TSS8	0.99±0.024	0.94±0.011	0.94±0.015	0.94±0.020	0.97±0.010	0.99±0.014
Jaccard	0.99±0.024	0.91±0.010	0.91±0.015	0.92±0.019	0.96±0.009	0.99±0.013
Sorensen	1.00±0.013	0.95±0.005	0.95±0.008	0.95±0.010	0.98±0.005	1.00±0.007
T. grandiflorum						
Metrics	**BIO[1]**	**GAU[2]**	**GLM[3]**	**MXD[4]**	**RDF[5]**	**SVM[6]**
AUC7	0.93±0.029	0.86±0.022	0.86±0.036	0.86±0.020	0.92±0.018	0.93±0.023
Kappa	0.98±0.058	0.89±0.052	0.89±0.063	0.90±0.045	0.95±0.060	0.98±0.052
TSS8	0.96±0.058	0.88±0.052	0.88±0.063	0.89±0.045	0.94±0.060	0.96±0.052
Jaccard	0.94±0.058	0.80±0.042	0.80±0.055	0.83±0.035	0.91±0.053	0.94±0.043
Sorensen	0.98±0.033	0.89±0.023	0.89±0.031	0.90±0.021	0.95±0.030	0.98±0.024

Legend: [1]BIO = Bioclim; GAU[2] = Bayesian Gaussian Process; [3]GLM = Generalized Linear Models; [4]MXD = Maximum Entropy Default; [5]RDF = Random Forest; [6]SVM = Support Vector Machine; [7]AUC = Area Under the Curve e [8]TSS = True Skill Statistics.