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Predicting the habitat suitability of *Vitellaria paradoxa* under climate change scenarios

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ABSTRACT

In Côte d'Ivoire, agroforestry parklands dominated by the *Vitellaria paradoxa* (shea tree) play a role in smallholder agriculture, soil conservation and food security within the Sudanian and Sudan-Guinean zones. Despite its ecological and socio-economic importance, this species, listed as Vulnerable by the IUCN, is increasingly threatened by overexploitation, habitat degradation, recurrent bush fires, poor natural regeneration and climate change, raising concerns about its long-term persistence. To assess the current and future distribution of *V. paradoxa* in Côte d'Ivoire, 135 occurrence records from the CNF herbarium and GBIF were modelled using multiple algorithms and WorldClim v2.1 bioclimatic variables under current and future climate scenarios (SSP245 and SSP585). Multicollinearity was reduced using Pearson correlation coefficients and variance inflation factors ($|r| < 0.7$; $VIF < 8$), and model performance was evaluated through bootstrap-based random subsampling (70% training, 30% validation) using AUC and TSS metrics. The results showed that eight predictors were retained, dominated by temperature variables, particularly temperature seasonality (45%), followed by precipitation. Temperature and precipitation are the dominant drivers, while wind plays a secondary role, indicating a narrow ecological niche and high sensitivity to climate change. Currently, suitable habitats cover 36,673 km² in northern and central Côte d'Ivoire. Projections indicate a northward expansion by 2050, reaching 179,568 km² under SSP-245-2050 and 144,338 km² under SSP-585-2050. They also reveal a more pronounced reduction in habitat suitability as the intensity of climate change increases. These results provide spatially explicit guidance for climate-adaptive agroforestry planning, identifying priority areas for conservation, regeneration, and sustainable shea-based expansion.

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INTRODUCTION

Climate change, characterised by rising temperatures, altered rainfall regimes and an increasing frequency of extreme events, is profoundly reshaping ecological niches and accelerating biodiversity loss worldwide (El-Khalafy *et al.*, 2025). In tropical regions, these changes exert particularly strong pressure on agroforestry systems, whose functioning and sustainability depend heavily on climate sensitive tree species (Mushagalusa *et al.*, 2020). Agroforestry trees deliver essential ecosystem services, including soil stabilisation, microclimate regulation, nutrient cycling and carbon sequestration, while also providing food, medicinal products and income for local communities (Kouassi *et al.*, 2022). As climate variability intensifies, the long-term viability of these systems increasingly hinges on the capacity of key species to maintain suitable habitats under changing environmental conditions.

In West Africa, and especially in Côte d'Ivoire, these challenges are compounded by rapid land use change, agricultural expansion and growing pressure on traditional agroforestry landscapes (Attikora *et al.*, 2023). The country spans a pronounced north to south bioclimatic gradient, from humid Guinean forests in the south to Sudanian savannas in the north (Guillaumet and Adjanohoun, 1971), rendering it particularly sensitive to climate variability and ecological transitions (Traoré *et al.*, 2023). This environmental heterogeneity offers a valuable context for examining climate driven shifts in species distributions, but it also heightens the vulnerability of agroforestry systems to changes in temperature and rainfall regimes. Anticipating such shifts has therefore become a central challenge for sustainable agroforestry planning in Côte d'Ivoire. Although ecological niche modelling has emerged as a powerful framework for quantifying species environment relationships and projecting future habitat suitability (Hamilton *et al.*, 2024), its application to agroforestry species in Côte d'Ivoire and the wider West African region remains limited. Existing studies often focus on wild or forest taxa, while cultivated or semi domesticated species are comparatively neglected,

and methodological constraints continue to reduce the reliability of national scale projections.

Among these species, *Vitellaria paradoxa* C.F. Gaertn., commonly known as the shea tree, occupies a pivotal ecological and socio-economic position in Côte d'Ivoire. A keystone component of traditional parkland agroforestry systems in the northern and central regions, it contributes to soil fertility, moderates microclimatic conditions and supports associated biodiversity, while underpinning rural livelihoods through shea nut and butter production, a strategic source of income and food security, particularly for women (Avaligbé *et al.*, 2021; Attikora *et al.*, 2023). However, the species is increasingly threatened by habitat degradation, agricultural intensification, overexploitation, recurrent bush fires and climate change, and is currently classified as Vulnerable, reflecting a progressive deterioration of its conservation status. Its slow growth, late reproductive maturity, limited dispersal capacity and relatively narrow thermo pluviometric requirements further constrain its ability to respond rapidly to shifting climatic conditions (Raebild *et al.*, 2010; Jepsen *et al.*, 2024). Moreover, pronounced intraspecific variation along Côte d'Ivoire's bioclimatic gradient suggests that local adaptation and phenotypic plasticity play a key role in shaping its response to climate change, underscoring the need for spatially explicit and ecologically robust assessments.

In this context, the present study aims to model the climate-driven habitat suitability of *Vitellaria paradoxa* in Côte d'Ivoire to support agroforestry development under changing climatic conditions. Specifically, it seeks to identify the key environmental drivers shaping the species' current and future distribution, to characterise the climatic gradients and ecological thresholds governing habitat suitability, and to analyse spatial responses of potential distributions under climate change scenarios. In addition, the study assesses the implications of projected habitat changes for the conservation of *Vitellaria paradoxa* and the socio-economic systems that depend on it. By integrating high-quality occurrence data with high-

resolution climate projections, this work provides a robust basis for climate-adaptive agroforestry planning and sustainable land management in Côte d'Ivoire. The resulting insights are intended to inform adaptive agroforestry strategies, strengthen climate-resilient land management and support the long-term sustainability of shea-based livelihood systems in Côte d'Ivoire.

MATERIALS AND METHODS

Study area

Côte d'Ivoire lies between latitudes 4° and 11°30' N and longitudes 8° and 8°30' W. Its climate comprises four main types: the Sudanian climate (1,000–1,700 mm/year, one dry and one wet season), the Baouléen climate (1,500–2,200 mm/year, two dry and two wet seasons), the Attiéen climate (1,300–2,400 mm/year, four seasons), and the montane climate (1,500–2,200 mm/year, one dry and one wet season). Most records are concentrated in the central and northern regions, with only a few isolated occurrences in the east and centre-south. In contrast, the southern and coastal areas show very few, if any, observations (Fig. 1).

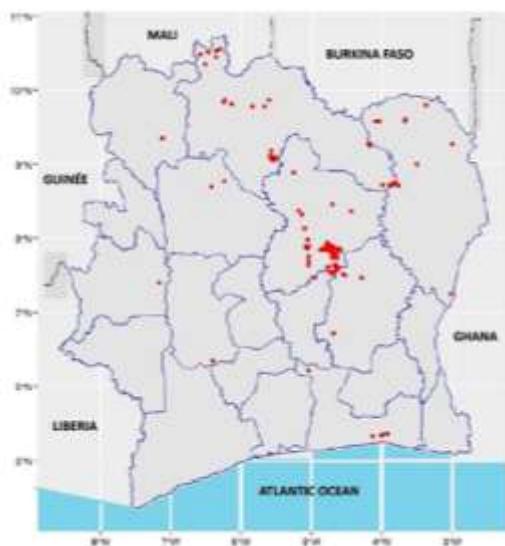


Fig. 1. Location of Côte d'Ivoire and occurrence points of *Vitellaria paradoxa* (●)

Data collection

Occurrence records for *V. paradoxa* were obtained from GBIF (21 November 2025), cleaned to remove duplicates, incomplete data and spatial outliers,

georeferenced with Geolocate, and filtered to exclude imprecise coordinates; no pseudo-absences were generated. After 1 km spatial thinning in SDMToolbox, 135 occurrences were retained. Environmental predictors included 19 bioclimatic variables plus solar radiation, wind speed and vapour pressure from WorldClim v2.1, with future projections (2041–2060, mean 2050) from MPI-ESM1-2-HR under SSP-245 and SSP-58.5. Species distribution modelling was performed in RStudio using RF, MaxEnt, BRT, GAM, GLM, SVM and CART. Suitability maps were binarised using the sensitivity–specificity threshold, model performance assessed with AUC and TSS, and current and future suitability maps with change rates produced in ArcGIS.

Data analyses

Pearson correlation coefficients and Variance Inflation Factors (VIF) were calculated in R using the *usdm* package to detect multicollinearity. Predictors with $|r| \geq 0.7$ or $VIF \geq 8$ were removed. This step improved model stability and reduced bias in suitability estimates (Dakhil *et al.*, 2025). Model performance was evaluated through random subsampling with bootstrapping. Seventy percent of occurrences were used for training and thirty percent for validation. Accuracy was assessed with AUC and TSS. AUC values below 0.7 indicate low accuracy, values between 0.7 and 0.9 indicate good accuracy, and values above 0.9 indicate excellent discrimination (White *et al.*, 2023). TSS ranges from minus one to plus one, with higher values reflecting stronger predictive agreement (Gaire *et al.*, 2022). Variable importance was estimated through permutation-based reductions in AUC. Larger declines indicated stronger influence (Schulze *et al.*, 2023). Response curves were generated to identify ecological thresholds, optima and tolerance limits for *V. paradoxa*. These curves distinguished negligible, monotonic and unimodal relationships (Buermann *et al.*, 2008). The area of each suitability class was calculated directly from the number of pixels in the final prediction grid. The modelling grid covering Côte d'Ivoire (322,463 km²) consisted of 15,194 pixels, giving a pixel area of 21.22 km². The extent of each class (0= unsuitable, 1= suitable) was obtained by

multiplying the number of pixels in each class by the pixel area. This procedure ensured consistent comparisons across current and future (SSP245 and SSP585) scenarios. Continuous suitability values were converted into suitable and unsuitable classes using a threshold of 0.212 (Allal *et al.*, 2011). This conversion enabled the quantification of habitat gains, losses and stable areas across climate scenarios (Doffou *et al.*, 2021). Future habitat change was calculated using the metric $T_c = ((A_2 - A_1) \times A_2 \times 100)$, where A_1 is the current suitable area and A_2 the projected area for 2050. Positive values indicate expansion, while negative values indicate contraction (N'Guessan *et al.*, 2019). This metric provides a clear measure of spatial change and supports conservation and management planning for the species.

RESULTS

Comparative performance of species distribution models

Table 1 shows that Random Forest performs best, with the highest AUC, COR and TSS values and the lowest deviance. BRT, GAM and MaxEnt form an intermediate group, with good discrimination but higher deviance than RF. GLM, SVM and CART perform the weakest, with values below the overall means. The mean metrics (AUC = 0.88, COR = 0.61, TSS = 0.65, Deviance = 0.53) confirm that ensemble methods outperform regression and other machine-learning approaches.

Table 1. Comparative performance of modelling methods based on AUC, COR, TSS and deviance

Methods	AUC	COR	TSS	Deviance
RF	0.93	0.74	0.75	0.35
MaxEnt	0.89	0.58	0.64	0.57
BRT	0.9	0.65	0.67	0.47
GAM	0.9	0.62	0.67	0.72
GLM	0.85	0.5	0.61	0.55
SVM	0.85	0.57	0.61	0.5
CART	0.85	0.62	0.63	0.53
Mean	0.88	0.61	0.65	0.53

Note: The data were generated in RStudio and then exported to Excel for formatting. RF: Random Forest; MaxEnt: Maximum Entropy; BRT: Boosted Regression Trees; GAM: Generalised Additive Model; GLM: Generalised Linear Model; SVM: Support Vector Machines; CART: Classification and Regression Trees.

Selection of environmental predictors and their relative importance in habitat suitability modelling

Fig. 2 identifies the variables with the lowest correlations, and Table 2 provides their corresponding VIF values. Eight predictors are retained for modelling: bio11 (mean temperature of the coldest quarter; VIF= 4.37), bio12 (annual precipitation; VIF= 3.85), bio14 (precipitation of the driest month; VIF= 4.80), bio4 (temperature seasonality; VIF= 2.89), bio5 (maximum temperature of the warmest month; VIF= 7.03), bio8 (mean temperature of the wettest quarter; VIF = 2.26), bio9 (mean temperature of the driest quarter; VIF= 2.10) and wind (mean wind speed; VIF= 5.06). These selected predictors were then used to assess their relative contributions to habitat suitability and to identify the dominant environmental drivers shaping the species distribution.

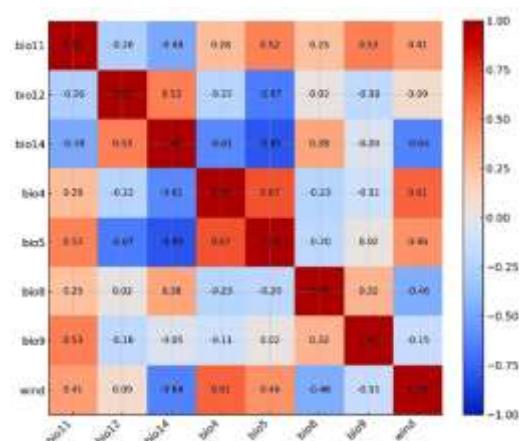


Fig. 2. Correlation matrix of the selected environmental variables

Note: The plot illustrates pairwise Pearson correlation coefficients among the selected environmental variables, with circle size and color representing the strength and direction of the correlations.

The resulting importance analysis reveals a hierarchy among environmental predictors (Fig. 3). Three groups emerge: temperature, precipitation and wind. Temperature is the dominant group. Temperature seasonality (bio4) contributes the most (45%). Mean temperature of the driest quarter follows (bio9, 9.5%), then mean temperature of the coldest quarter (bio11,

8.6%), maximum temperature of the warmest month (bio5, 6.8%) and mean temperature of the wettest quarter (bio8, 3.3%). Precipitation forms the second major group. Precipitation of the driest month contributes 17.4%, and annual precipitation contributes 17.1%. Both variables strongly influence suitability. Wind contributes only 3.4%, showing a much weaker effect.

Table 2. Environmental predictors retained and their corresponding VIF values

Code Designation	VIF
bio11 Temperature of the coldest quarter	4.372
bio12 Annual precipitation	3.853
bio14 Precipitation of the driest month	4.805
bio4 Temperature seasonality	2.897
bio5 Maximum temperature of the warmest month	7.034
bio8 Mean temperature of the wettest quarter	2.264
bio9 Mean temperature of the driest quarter	2.100
wind Mean wind speed	5.064

Note: The data were generated in RStudio and then exported to Excel for formatting. All variables retained for modelling exhibit VIF values below the critical threshold of 8, indicating an absence of problematic multicollinearity and ensuring robust predictor independence.

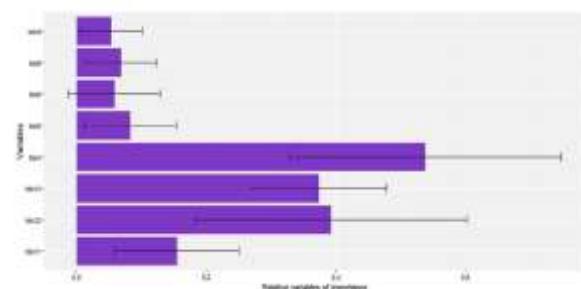


Fig. 3. Contribution of environmental variables to model performance

Note: The figure was generated in R using the packages sdm, terra, raster, dismo and sp, based on permutation-based variable importance calculations.

Climatic optima and ecological thresholds derived from response curves of *Vitellaria paradoxa*

The response curves in Fig. 4 show that the environmental suitability of *Vitellaria paradoxa* varies along climatic gradients and exhibits clear

non-linear patterns. Suitability increases with the mean temperature of the coldest quarter, rising from approximately 21 to 25 °C, and then stabilises around 27 °C. The maximum temperature of the warmest month shows a narrow optimum between 32 and 36 °C, followed by a sharp decline above 38 °C. Temperature seasonality is associated with increasing suitability between about 1.2 and 1.5 °C, with an optimum between 1.6 and 1.8 °C. The mean temperatures of the wettest and driest quarters also present narrow optima, centred around 26–28 °C and approximately 27 °C, respectively. Precipitation variables also influence habitat suitability. Annual precipitation displays a unimodal response, with maximum suitability occurring between 1,200 and 1,300 mm and a decline beyond 1,400 mm. Precipitation of the driest month shows an optimum range between 10- and 20-mm. Wind has a weaker but detectable effect on suitability. The response follows a bell-shaped curve, with optimal suitability observed at wind speeds between 1.70 and 1.75 m·s⁻¹, followed by a decrease at higher wind speeds.

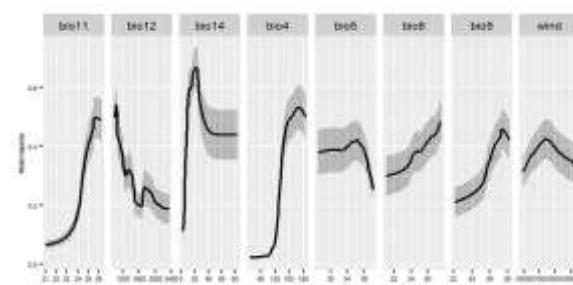


Fig. 4. Response curves of *Vitellaria paradoxa* for the selected environmental predictors

Note: The figure was generated in R using the packages sdm, terra, raster, dismo and sp, based on permutation-based variable importance calculations.

Projected spatial shifts in habitat suitability of *Vitellaria paradoxa* under SSP-245 and SSP-585 by 2050

V. paradoxa is currently confined to the Sudanian and Sudan–Guinean zones of northern and central Côte d'Ivoire (Fig. 5; Table 3), while the more humid southern regions remain unsuitable.

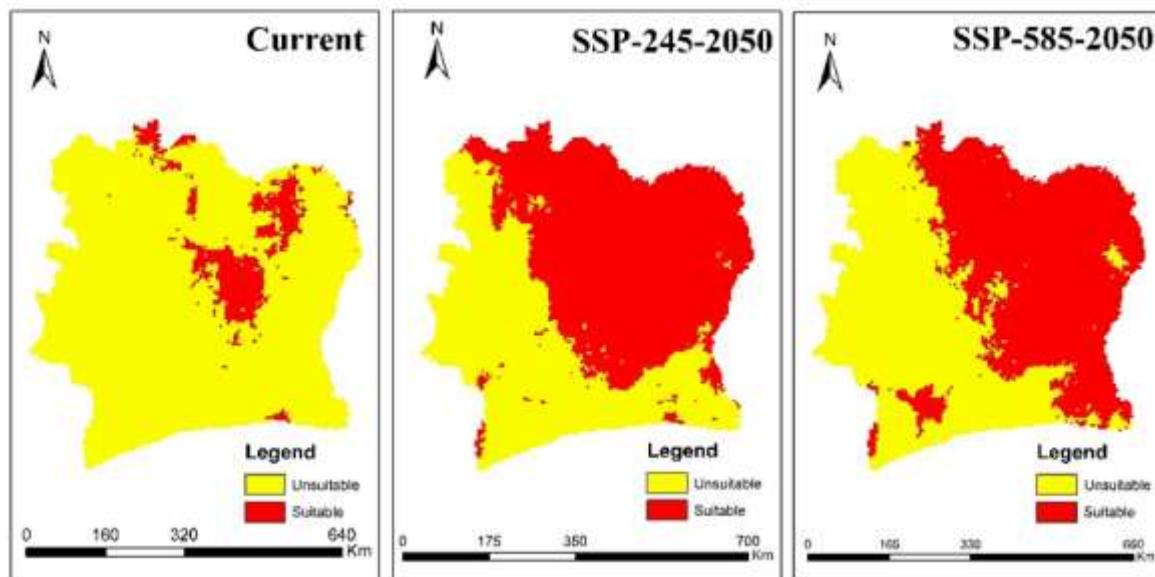


Fig. 5. Current and future habitat suitability for *Vitellaria paradoxa* under SSP2-4.5 and SSP5-8.5 climate Scenarios

Note. The map was generated in R using the packages sdm, terra, raster, dismo and sp, and subsequently finalised in ArcGIS for cartographic refinement.

Table 3. Changes in suitable and unsuitable areas for *Vitellaria paradoxa* in Côte d'Ivoire under SSP2-4.5 and SSP5-8.5 climate scenarios by 2050

Characteristics	Unsuitable areas	Suitable areas
Number of pixels	Current	13466
	SSP245_2050	6733
	SSP585_2050	8393
Number of pixels	Current	285790
	SSP245_2050	142895
	SSP585_2050	178125
Rate of change	SSP245_2050	-50
	SSP585_2050	+390
		-38
		+294

Note: Values come from ArcGIS suitability maps; areas were computed from pixel counts, and change rates follow the Methods formula, with negative values indicating losses and positive values indicating gains.

Suitable habitats presently cover 36,673 km², compared with 285,790 km² classified as unsuitable. Under the SSP-245-2050, suitable habitats expand to 179,568 km², representing an increase of +390 %, while unsuitable areas decline by -50 %. This expansion occurs mainly towards the north and northeast of the country. Under the SSP-585-2050, the expansion of suitable habitats is more limited. Suitable areas reach 144,338 km², corresponding to an increase of +294 %, and unsuitable habitats decrease by -38 %.

Overall, the spatial projections indicate contrasting changes in habitat suitability between the two climate scenarios, with greater expansion under SSP-245-2050 than under SSP-585-2050.

DISCUSSION

The findings confirm the strong advantage of ensemble learning for ecological niche prediction in heterogeneous tropical agro-ecosystems. Among the evaluated algorithms, Random Forest achieved the strongest predictive performance, combining excellent discrimination ability (high AUC, COR, and TSS) with low deviance, reflecting high robustness and reduced generalisation error. These results are consistent with previous studies showing that ensemble approaches better capture complex, non-linear species–environment relationships while limiting model variance and improving prediction stability (Deekshith, 2016). Boosted Regression Trees (BRT), Generalised Additive Models (GAM), and MaxEnt exhibited intermediate accuracy, reaffirming their continued relevance in species distribution modelling due to their ability to model non-linear ecological responses. However, their comparatively higher deviance indicates increased sensitivity to sampling bias and reduced extrapolation strength

when dealing with multi-scale climatic hierarchies and interaction-driven suitability collapse. By contrast, models such as GLM, SVM, and CART performed the weakest, likely due to their reliance on parametric assumptions or simple decision boundaries, which restrict their capacity to capture non-linear climatic constraints, ecological thresholds, and complex interaction effects, particularly in tropical agricultural landscapes characterised by high environmental heterogeneity. Random Forest's superior performance can be explained by its multi-tree aggregation structure, which captures multi-scale climatic interactions while reducing overfitting risk, reinforcing its increasing adoption in SDM and climate-impact suitability inference (Ahmed *et al.*, 2024; Mohammadagha, 2025). Because model reliability depends not only on algorithmic structure but also on predictor independence, the next analytical step required robust variable screening to stabilise climatic inference. Consequently, the deliberate reduction of predictors through VIF-based multicollinearity screening ensured that retained bioclimatic variables provided unique, non-redundant, and ecologically meaningful information, strengthening numerical stability, computational efficiency, and model transferability (Hamilton *et al.*, 2024; Blońska *et al.*, 2025). Indeed, multicollinearity is widely recognised as a major source of uncertainty in SDM, inflating parameter instability, weakening ecological inference, and reducing model interpretability, particularly in climate-driven niche projections (Júnior and Nóbrega, 2018). On the basis of this screened predictor set, the variable-importance hierarchy revealed a dominant influence of temperature-related variables, reflecting the species' strong sensitivity to thermal regulation of physiological performance, phenology, growth cycles, and intra-annual thermal oscillation. Precipitation variables formed the second most influential group, confirming the fundamental role of total annual rainfall, dry-season moisture balance, and seasonal hydrological stress in defining the realised ecological niche of *V. paradoxa*, a seasonal tropical tree species known to be constrained by intensifying aridity and increasing rainfall variability. Although wind showed

lower relative importance at the regional scale, its contribution remains ecologically meaningful locally, acting as a micro-climatic modifier through indirect effects on evapotranspiration, moisture loss, and mechanical stress, particularly in open or fragmented shea parklands (Cidores *et al.*, 2020; Tang *et al.*, 2022). Because climatic gradients shape suitability through sharp ecological limits, the next step is to interpret how *V. paradoxa* responds to these thresholds under scenario-dependent climatic oscillations. Suitability response curves indicate that *V. paradoxa* operates within relatively narrow ecological optima governed by strong non-linear responses and clearly defined climatic thresholds. The sharp decline in suitability beyond upper thermal limits suggests limited tolerance to extreme heat, reinforcing its vulnerability to increasing temperature seasonality, a pattern also reported for tropical taxa under climatic instability (Tagliari *et al.*, 2021; Chevalier *et al.*, 2022). Similarly, precipitation constraints modulate suitability through strong dependence on both total annual rainfall and dry-season moisture input, confirming sensitivity to intensified aridity and seasonal hydrological imbalance (Salamanca *et al.*, 2023; Song *et al.*, 2024). The preference for moderate wind regimes further suggests that wind may act as a local stress amplifier under future extremes, indirectly restricting tree performance at finer spatial scales. These threshold-dependent response patterns reaffirm the necessity of using robust ensemble SDM algorithms, particularly Random Forest, BRT, and MaxEnt, which efficiently capture non-linear suitability collapse when anticipating climate-driven range oscillations (Ganglo, 2023; Teixeira *et al.*, 2025). Yet, beyond model choice, future projections must also consider scenario-dependent climatic windows to avoid misleading resilience conclusions. Under the current climate, suitable shea habitat is largely restricted to the Sudanian and Sudan-Guinean zones of Côte d'Ivoire, indicating poor adaptation to humid southern environments where moisture regimes likely exceed its tolerance envelope. Future climate scenarios reveal a non-linear response to warming. Moderate warming may temporarily shift conditions

closer to intermediate thermal optima, enabling partial northward expansion of suitable habitat, a response documented for species whose climatic windows broaden under moderate warming before becoming constrained under stronger extremes (Dyderski *et al.*, 2024). However, under stronger warming trajectories, this flexibility diminishes, where extreme heat and hydrological imbalance restrict further expansion, offsetting any intermediate warming benefit. These contrasting responses confirm that multi-scenario modelling is essential for robust SDM projections of seasonal tropical trees such as *V. paradoxa* (Salamanca *et al.*, 2023). Therefore, beyond scenario-dependent range oscillation, the projected contraction of stable suitability zones raises urgent conservation and socio-economic concerns for long-term shea-based agroforestry persistence. Accordingly, the projected loss of climatically suitable habitat highlights serious concerns for biodiversity conservation and for the ecosystem services and livelihoods that depend on shea fruit harvesting and butter value chains. The contraction of stable suitability zones requires a reassessment of current management strategies, including agroforestry zoning, fire-controlled regeneration pathways, and corridor-guided conservation planning. Adaptation strategies should prioritise climatically stable refugia, identify ecological corridors for assisted regeneration, promote diversified shea-based agroforestry systems to buffer climatic stress, and support the development and dissemination of heat- and drought-tolerant shea genotypes to mitigate climatic suitability collapse. In parallel, the integration of local ecological knowledge, participatory fire management, and community-driven conservation governance remains essential for ensuring sustainable, culturally appropriate restoration of shea landscapes in Côte d'Ivoire. Taken together, these findings confirm that thermal, hydrological, and wind-mediated micro-climatic regulation interact through non-linear climatic hierarchies, reinforcing the necessity of robust ensemble SDM algorithms, careful predictor screening, and scenario-informed agroforestry

adaptation planning to sustain *Vitellaria paradoxa* and the socio-ecological systems that depend on it.

CONCLUSION

This study assessed the current and future climatic suitability of *Vitellaria paradoxa* in Côte d'Ivoire in order to support agroforestry development under a changing climate. By identifying the main climatic factors governing the species' distribution, particularly temperature seasonality, annual precipitation and dry season moisture availability, the study improves understanding of its climatic envelope and anticipates potential spatial shifts in suitable habitats. The projections suggest a possible redistribution of suitable areas, with a tendency towards increased suitability in the northern regions of the country. These findings provide a relevant spatial framework for climate adaptive agroforestry planning by facilitating the identification of priority areas for conservation, assisted regeneration and sustainable development of shea-based agroforestry systems. They also offer a scientific basis for field validation and long-term monitoring, thereby contributing to evidence informed strategies aimed at strengthening the resilience and sustainability of shea dependent livelihoods in the face of ongoing climatic change.

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