



Projected effects of climate change on the potential environmental suitability of *Vachellia seyal* (Delile) P. J. H. Hurter in Sudan using MaxEnt species distribution modeling

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Abstract

Climate change may substantially alter the environmental suitability of dryland tree species, with important implications for conservation and restoration. We modelled the current and future potential environmental suitability of *Vachellia seyal* (Delile) P.J.H.Hurter across Sudan using MaxEnt, based on 448 spatially thinned occurrence records and nine climatic, topographic, and edaphic predictors. Future suitability was projected using the ensemble mean of three CMIP6 global climate models under SSP2-4.5 and SSP5-8.5 for 2021–2040 and 2081–2100. Model discrimination was high (mean test AUC=0.944; TSS=0.838±0.02). Isothermality (BIO3; 37.6% contribution), precipitation of the warmest quarter (BIO18; 24.7%), and precipitation seasonality (BIO15; 14.2%) were the principal predictors. Under baseline conditions, 380,890.63 km² (20.22% of Sudan) was classified as environmentally suitable. Under SSP2-4.5, projected suitable area decreased to 177,240.19 km² (9.41%) in 2021–2040 and reached 255,482.20 km² (13.56%) in 2081–2100, remaining below the baseline extent. Under SSP5-8.5, projected suitable area was 350,775.69 km² (18.62%) in 2021–2040 and 306,923.26 km² (16.29%) in 2081–2100. Blue Nile, Gedaref, Sennar, and parts of Kordofan retained comparatively extensive potential suitability, whereas northern Sudan remained predominantly unsuitable. These projections represent potential environmental suitability rather than realized future occupancy and should be interpreted in light of sampling, dispersal, land-use, and climate-model uncertainties. The results provide a spatial basis for prioritizing climate-informed monitoring, conservation, and restoration planning for *V. seyal* in Sudan.

Keywords Climate change · Environmental suitability · Species distribution modeling · Dryland ecosystems · *Vachellia seyal* · MaxEnt · CMIP6 · Conservation planning

Background

Anthropogenic climate change, manifested through rising temperatures, altered precipitation regimes, and changes in the frequency and intensity of climatic extremes, is reshaping ecological processes and modifying species distributions worldwide (IPCC, 2022; Guo et al. 2023; Aguirre-Liguori et al. 2021). As climatic conditions shift, species may experience contraction, expansion, or redistribution of environmentally suitable areas, depending on their ecological tolerances, dispersal capacities, and interactions with other environmental constraints (Rubenstein et al. 2023; Lawlor et al. 2024; Felton et al. 2024; Lyam et al. 2022). Consequently, ecological modelling has become increasingly important for quantifying species–environment relationships and assessing potential distributional responses under

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alternative climate scenarios (Fourcade 2016; Beery et al. 2021; Lawlor et al. 2024; Bachman et al. 2024; Montoya-Jiménez et al. 2022). Historical evidence from tropical ecosystems further demonstrates that climate-associated range shifts can be substantial; for example, elevational shifts exceeding 500 m over approximately two centuries have been documented for tropical vegetation (Morueta-Holme et al. 2015; Martínez Villa et al. 2023). Such changes are particularly important in drylands, where climatic variability interacts with land use and other anthropogenic pressures to influence vegetation dynamics and ecosystem functioning (Foden et al. 2007; Siddig 2014; Zerbo et al. 2023).

African savannas and drylands are particularly responsive to variations in temperature, precipitation, drought, and hydrological conditions, although vegetation responses differ among regions, species, and ecological settings (Trisos et al. 2022; Zerbo et al. 2023; Umuhoza et al. 2025; Patrut et al. 2018). Rainfall amount and seasonality exert strong controls on woody cover in African savannas (Sankaran et al. 2005), while increasing temperatures, recurrent drought, and altered rainfall regimes can affect tree establishment, growth, survival, and recruitment (Mtsetfwa et al. 2023; Ahanger et al. 2021). These processes are especially relevant to Sudan, where substantial spatial and temporal variability in rainfall and temperature has been documented and future precipitation responses are projected to vary among emission scenarios and regions (Alriah et al. 2021, 2022; Hamadalnel et al. 2022; Babiker et al. 2024; Gamreldin and Hamadalnel 2024). Climate-driven changes are therefore unlikely to affect all woody species or regions uniformly. Species-distribution studies of African trees have demonstrated losses, persistence, and potential gains in environmentally suitable areas under future climates, emphasizing species- and scenario-specific responses (Foden et al. 2007; Semu et al. 2021; Wan et al. 2021; Lyam et al. 2022; Atakpama et al. 2023; Hussein and Estifanos 2023; Hamadamin and Khwarahm 2023; Gufi et al. 2023; Mtsetfwa et al. 2023). Recent modelling of *Adansonia digitata* in Sudan similarly indicates substantial spatial reorganization of potential suitability under future climate scenarios (Gadallah et al. 2025). Moreover, even where new areas become environmentally suitable, dispersal limitations, habitat fragmentation, and other non-climatic constraints may prevent species from tracking shifting climatic conditions (Foden et al. 2007; Guo et al. 2023; Peterson et al. 2007).

Vachellia seyal (Delile) P.J.H.Hurter (syn. *Acacia seyal* Delile) is an ecologically and socioeconomically important dryland tree native to Sudan and widely distributed across seasonally dry regions of Africa. In Sudan, the species is an important component of savanna woodland ecosystems and contributes to rural livelihoods through forage, fuelwood, construction materials, forest-based products, and

gum production (Wickens 1995; Gamal et al. 2022; Ghogue 2020; Pretzsch et al. 2011). Although adapted to seasonally dry environments, experimental evidence indicates that its growth and establishment respond to water availability and drought stress (Merine et al. 2015; Ahmed et al. 2020; Elzaki et al. 2023; Ahanger et al. 2021). Consequently, changes in temperature, precipitation amount and seasonality, and drought regimes may alter the geographic distribution of environmental conditions suitable for *V. seyal*, consistent with projected climate responses of other African savanna and dryland trees (Foden et al. 2007; Semu et al. 2021; Wan et al. 2021; Lyam et al. 2022; Atakpama et al. 2023; Mtsetfwa et al. 2023). Changes in its potential distribution could therefore have implications for dryland restoration, sustainable forest management, pastoral systems, and rural livelihoods. The species has also demonstrated potential for the rehabilitation of environmentally stressed soils, further increasing its relevance to dryland restoration and sustainable land management (Thiao et al. 2022; Tesfamariam et al. 2022).

Species distribution models (SDMs) provide a quantitative framework for relating species occurrences to environmental gradients and estimating potential environmental suitability across geographic space and under alternative climatic conditions (Elith et al. 2006; Merow et al. 2013; Pearson et al. 2007; Koreň et al. 2011). Among presence-background approaches, Maximum Entropy (MaxEnt) is widely used because it can estimate relative environmental suitability from presence records and environmental predictors while accommodating nonlinear species–environment relationships (Phillips et al. 2006; Elith et al. 2011; Merow et al. 2013). MaxEnt-based SDMs have consequently been applied to assess climate-related changes in habitat suitability for woody species in Africa and elsewhere (Semu et al. 2021; Gufi et al. 2023; Hosseini et al. 2024; Gadallah et al. 2025; Atakpama et al. 2023; Hussein and Estifanos 2023; Tesfamariam et al. 2022). However, model outputs are sensitive to occurrence-data quality and spatial sampling bias, predictor selection and collinearity, feature specification and regularization, background extent and sampling, evaluation procedures, threshold selection, and environmental differences between calibration and projection conditions (Elith et al. 2010, 2011; Merow et al. 2013; Fourcade 2016; Guisande et al. 2017; Jiménez-Valverde 2014; Peterson et al. 2007; Warren et al. 2021). Explicit reporting of these modelling decisions is therefore essential for reproducibility and for interpreting projections appropriately as estimates of potential environmental suitability rather than predictions of realized future occupancy.

This modelling framework is particularly relevant to Sudan because the country spans pronounced north–south gradients in temperature, precipitation, vegetation, and

soil conditions, while its savanna and dryland ecosystems are exposed to both climatic variability and anthropogenic pressures (Siddig 2014; Mohamed et al. 2016; Hasoba et al. 2025; Harrison and Jackson 1958). Previous research has characterized Sudan's climate variability, vegetation degradation, savanna tree diversity, and climate sensitivity of individual woody species (Hamadalnel et al. 2022; Elzaki et al. 2023; Elhassan et al. 2024; Hasoba et al. 2025; Gam-reldin and Hamadalnel 2024), while recent SDM research has demonstrated the utility of climate-suitability modelling for *A. digitata* in Sudan (Gadallah et al. 2025). Nevertheless, national-scale evidence on the current and future potential environmental suitability of *V. seyal* remains limited. Specifically, it remains unclear how its suitability is structured across Sudan's environmental gradients, which climatic, topographic, and edaphic predictors contribute most strongly to the modelled distribution, and how the magnitude and spatial configuration of suitable areas may change under contrasting CMIP6 climate scenarios. This species-specific knowledge gap is important because responses inferred for other woody species cannot be assumed to represent *V. seyal*, while national-scale summaries alone may obscure substantial state-level differences in suitability loss, persistence, and potential gain.

Accordingly, this study aimed to: (i) estimate the current potential environmental suitability of *V. seyal* across Sudan; (ii) quantify the contributions of climatic, topographic, and edaphic predictors to its modelled suitability; (iii) project changes in potential suitability under SSP2-4.5 and SSP5-8.5 for 2021–2040 and 2081–2100; and (iv) characterize national- and state-level patterns of suitability loss, stability,

gain, and persistent unsuitability. By integrating occurrence records, environmental predictors, MaxEnt modelling, and multi-GCM climate projections, this study provides spatially explicit evidence to support climate-informed conservation, restoration, and sustainable management of *V. seyal* in Sudan.

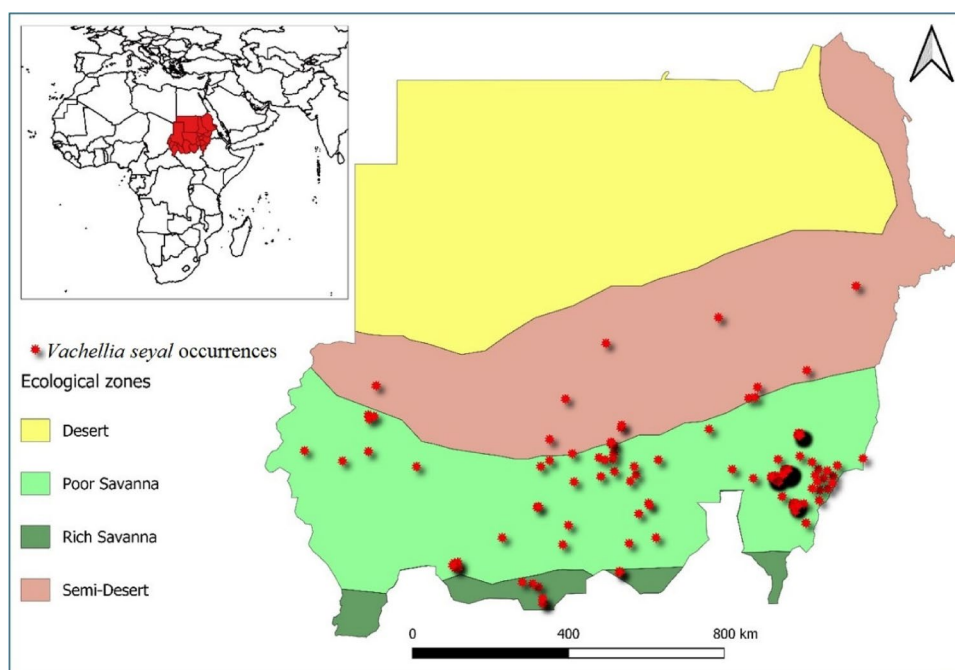
Materials and methods

Study area

Sudan, the third-largest country in Africa by area, spans pronounced latitudinal, climatic, and ecological gradients (Table S1; Fig. 1; Berry 2015). Hyper-arid conditions dominate the north, including the Nubian and Libyan Deserts, where annual precipitation is extremely low and summer temperatures frequently exceed 45 °C. By contrast, southern Sudan experiences comparatively moderate temperatures and substantially greater rainfall (Osman and Ali 2021), supporting savanna vegetation and influencing the biogeography of dryland tree species, including *Vachellia seyal* (Delile) P.J.H.Hurter (syn. *Acacia seyal* Delile).

Rainfall seasonality across Sudan is governed primarily by the annual migration of tropical rain-bearing systems and associated monsoonal circulation. Moist southwesterly airflow during approximately May–October supplies most annual rainfall to central and southern Sudan (Alriah et al. 2021), whereas the November–March period is generally dominated by dry northeasterly airflow and very limited precipitation, particularly in northern Sudan (Elagib and

Fig. 1 Map of the study area illustrating the spatial distribution of *Vachellia seyal* (Delile) occurrence records ($n=448$) across the major ecological zones of Sudan. Occurrence points are displayed on a background comprising bioclimatic gradients and national administrative boundaries, providing spatial context for current environmental conditions relevant to species distribution modelling



Mansell 2000). These strong hydroclimatic gradients are important determinants of savanna productivity, regeneration, and species distributions (Osman and Ali 2021). Climate variability and long-term climatic change may further modify drought and fire regimes, with consequences for vegetation structure and tree recruitment (Hamadanel et al. 2022).

Sudan also exhibits substantial edaphic heterogeneity. Sandy substrates dominate much of the northern and west-central regions, clay-rich Vertisols are widespread across the central belt, lateritic soils occur in the south, and alluvial soils are associated with the White, Blue, and Main Nile systems and major seasonal deltas (SUSIS-ARC 2016; UNEP 2020). Together with climate and topography, this soil variability contributes to broad ecological zonation and may influence the environmental suitability of *V. seyal* across the country.

Vachellia seyal (Delile) P.J.H.Hurter (Fig. 1) is an ecologically important savanna tree native to Sudan's dryland woodlands (Darbyshire et al. 2015; Mohamed et al. 2016; Siddig et al. 2018). Sudan's pronounced climatic, topographic, and edaphic gradients therefore provide an appropriate environmental setting for evaluating the species' potential distribution using a presence-background species distribution modelling framework.

Species occurrence data and spatial filtering

Vachellia seyal (Delile) P.J.H.Hurter is a characteristic tree species of Sudanese savanna ecosystems, occurring widely across semi-arid to sub-humid environments. Given its ecological and socio-economic importance and broad distribution along climatic gradients, the species provides a relevant case for assessing potential shifts in environmental suitability under climate change.

A total of 1,989 raw occurrence records for *V. seyal* were assembled from multiple complementary sources to obtain broad spatial coverage across Sudan (Fig. 1). Primary occurrence data were collected during a field campaign conducted between June and September 2021 in El-Nour Natural Forest Reserve, Blue Nile State, Sudan. During the field survey, individual trees were georeferenced using a handheld Garmin GPS receiver.

Additional presence records were compiled from the National Forest Inventory (NFI; $n=215$; FNC, 2021), the Global Biodiversity Information Facility (GBIF; $n=22$; accessed 10 October 2025), and the International Union for Conservation of Nature (IUCN; $n=22$; accessed 10 October 2025). Further records were obtained from supervised Students' Working Plans archived at the Faculty of Forestry, University of Khartoum ($n=1,254$), and from published studies reporting confirmed occurrences of *V. seyal* in Sudan

($n=275$; Gibreel 2008; FNC, 2021; Gamal et al. 2022; Hasoba et al. 2025). Together with the primary field observations, these sources yielded 1,989 raw presence records before spatial quality control and filtering.

All occurrence coordinates were standardized to decimal degrees and matched to a 1×1 km grid corresponding approximately to the spatial resolution of the environmental predictors. This initial filtering reduced duplicate or spatially redundant observations within individual grid cells. The geographic consistency of the records was subsequently examined in ArcGIS Pro 3.6, and records falling outside Sudan's national boundary were excluded.

To further reduce spatial clustering and the disproportionate influence of intensively sampled locations, occurrence records were spatially thinned using the *spThin* package in R, with a minimum nearest-neighbour distance of 1 km. Following spatial quality control, grid-based filtering, and thinning, 448 occurrence records were retained as the final presence dataset and used for MaxEnt model calibration and evaluation (Fig. 1). Thus, the 1,989 records represent the raw multi-source occurrence dataset, whereas the 448 records represent the spatially filtered dataset used for species distribution modelling. Spatial thinning reduces local clustering and over-representation of intensively sampled areas but does not completely eliminate sampling bias. Because the initial occurrence dataset was assembled from heterogeneous sources with different sampling designs, periods, and levels of accessibility, residual spatial and accessibility biases may remain after filtering. No explicit sampling-bias surface or target-group background was incorporated into the modelling framework; this limitation was therefore considered when interpreting model performance and projected suitability patterns.

Environmental predictors and multicollinearity screening

Environmental predictors represented climate, elevation, and soil conditions (Table S2). Nineteen bioclimatic variables and elevation were obtained from WorldClim 2.1 at 30-arc-second resolution (approximately 1 km at the equator); the bioclimatic variables represent the 1970–2000 climatological baseline (Fick and Hijmans 2017). Soil information was obtained from the WISE/ISRIC database (ISRIC, 2016; Batjes 2016) and harmonized to the same working grid. All predictor layers were clipped to Sudan and aligned to a common extent, cell size, and spatial reference in ArcGIS Pro 3.6 (ESRI 2025). Because the occurrence records were assembled from field observations, inventory data, institutional records, and published sources spanning different periods, their temporal coverage does not correspond exactly to the 1970–2000 climatic baseline. The

baseline model is therefore interpreted as an estimate of the species' broad environmental niche under baseline climatic conditions rather than as a temporally exact reconstruction of occupancy during a single historical period. The soil predictor was represented by the WISE30sec dataset, distributed as a single composite raster at a native resolution of 30×30 arc-seconds (1 km), in which each grid cell is coded with a soil mapping-unit (SMU) identifier. These mapping units integrate estimates for twenty soil physical and chemical properties (including organic carbon, total nitrogen, pH, cation exchange capacity, base saturation, particle-size distribution, bulk density, and available water capacity, among others), with property estimates available for seven standard depth intervals to a maximum of 2 m. The layer corresponding to the 100 cm depth interval was used. The layer matches the resolution and extent of the bioclimatic layers, reprojected to WGS84, and clipped to the Sudan study extent prior to VIF screening and model calibration. To reduce multicollinearity among continuous predictors, variance inflation factor (VIF) screening was conducted in R version 4.4.2 (Guisande et al. 2017; Bhandari 2020). A conservative exclusion threshold of $VIF > 7.5$ was adopted to reduce residual collinearity before model calibration while retaining ecologically informative predictors (Guisande et al. 2017). Twelve bioclimatic variables (BIO1, BIO4, BIO5, BIO6, BIO7, BIO8, BIO9, BIO11, BIO12, BIO13, BIO16, and BIO17) were excluded. The final predictor set comprised nine variables: seven bioclimatic variables (BIO2, BIO3, BIO10, BIO14, BIO15, BIO18, and BIO19), elevation, and the soil predictor (Table S2). Screening was completed before MaxEnt calibration to limit the influence of strongly redundant predictors on model fitting and variable-importance estimates (Guisande et al. 2017).

Future climate projections and GCM ensemble

Future climate conditions were represented using CMIP6 projections (Eyring et al. 2016) for two Shared Socioeconomic Pathways, SSP2-4.5 and SSP5-8.5, and two periods, 2021–2040 and 2081–2100. These pathways represent contrasting radiative-forcing and socioeconomic trajectories, with SSP2-4.5 describing an intermediate stabilization pathway and SSP5-8.5 a high-emissions, fossil-fuel-intensive pathway (Riahi et al. 2017). The two scenarios and time slices were selected to evaluate the sensitivity of projected environmental suitability to both emissions' pathway and projection horizon.

Future climatic predictors were obtained from three CMIP6 global climate models (GCMs): HadGEM3-GC31-LL, MPI-ESM1-2-HR, and IPSL-CM6A-LR. These models have been used in climate assessments for Sudan and the wider East African/MENA region (Mesgari et al. 2022;

Hamadanel et al. 2022; Omay et al. 2023; Babiker et al. 2024). For each SSP and time slice, corresponding climatic layers from the three GCMs were combined using an arithmetic multi-model mean before projection. This procedure reduces dependence on any single GCM but does not quantify the full inter-model spread. Because individual GCM projections were not retained as replicate ecological predictions, GCM-specific uncertainty intervals were not estimated. Accordingly, inter-GCM variability represents an unresolved source of projection uncertainty and is explicitly considered in the interpretation and limitations.

MaxEnt calibration, evaluation, and variable importance

MaxEnt version 3.4.4 was used to relate presence records to the available environmental background because it is designed for presence-background species distribution modelling and can represent nonlinear species-environment relationships (Phillips et al. 2006, 2017; Elith et al. 2011; Merow et al. 2013). MaxEnt output was interpreted as relative environmental suitability rather than as the probability of occurrence or realized future occupancy (Phillips et al. 2022). Accordingly, modelled outputs are described throughout this study as potential environmental suitability. Predictor screening was completed before model calibration to reduce multicollinearity among environmental predictors.

The nine retained predictors and 448 spatially thinned occurrence records were used for MaxEnt calibration and evaluation. Occurrence records were randomly partitioned using the subsample replicate-run type, with 80% used for model training and 20% withheld for evaluation in each of ten replicate runs. Auto features were enabled in MaxEnt, activating linear, quadratic, product, and hinge feature classes while excluding threshold features, consistent with the default auto-feature rule for sample sizes exceeding 80 occurrence records (Phillips and Dudík 2008). Background points were sampled randomly across the full unmasked extent of Sudan rather than being restricted to buffers around occurrence locations, with a mean of 10,000 background points per replicate. The regularization multiplier was set to 1.0. Logistic output was selected, the maximum number of iterations was set to 10,000, and predictions from the ten replicate runs were averaged to generate the final continuous suitability surface. The 10th-percentile training-presence threshold was subsequently applied to generate binary suitable/unsuitable maps for the change analysis.

Model discrimination was evaluated using the area under the receiver operating characteristic curve (AUC) for the training and withheld test records. In a presence-background framework, AUC measures the ability of the model to discriminate observed presences from the environmental

background and is threshold-independent; it should not be interpreted as the percentage of occurrences predicted correctly (Phillips et al. 2006; Elith et al. 2011). Threshold-dependent discrimination was additionally summarized using the True Skill Statistic (TSS), calculated as sensitivity + specificity – 1 (Eq. 1). Sensitivity represents the proportion of observed presences classified as suitable, whereas specificity was calculated relative to the background/negative evaluation locations used in the analysis. Because these locations are not confirmed species absences, TSS is treated as a supplementary discrimination metric rather than as evidence of true absence prediction.

$$\text{TSS} = \text{Sensitivity} + \text{Specificity} - 1 \quad (1)$$

Predictor importance was assessed using MaxEnt's jackknife analysis together with percent contribution and permutation importance. Percent contribution summarizes the contribution of each predictor during model fitting, whereas permutation importance measures the decline in model performance after the values of a predictor are randomly permuted among presence and background locations (Phillips et al. 2006; Howse et al. 2020). These complementary metrics were used to identify predictors most strongly associated with the modelled environmental suitability of *V. seyal*.

Environmental-suitability classification and change analysis

MaxEnt produces a continuous logistic suitability index ranging from 0 to 1. For the primary binary suitable/unsuitable classification used in the change analysis, we applied the 10th-percentile training-presence threshold. This threshold permits a small proportion of training occurrences to fall below the suitability cutoff, thereby reducing sensitivity to positional uncertainty and records from marginal environments, and is commonly used in presence-only SDMs (Liu et al. 2005; Merow et al. 2013). The threshold was selected a priori for the analysis and applied consistently to the baseline and all future projections. Independently, for descriptive visualization and state-level summaries, the continuous MaxEnt output was grouped into four fixed suitability classes (Table 1). These fixed classes were used only for descriptive categorization and were not used to define the binary transition classes in the climate-change analysis;

Table 1 Descriptive suitability classes used to summarize the continuous MaxEnt suitability index

Class	Suitability index	Suitability class
1	0.00–0.20	Unsuitable
2	>0.2–0.40	Low
3	>0.4–0.60	Medium
4	>0.60–1.00	High

neither classification should be interpreted as a probability of occupancy.

Changes in total suitable area were calculated relative to the current baseline using Eq. (2):

$$\text{SACH} = \frac{\text{FSA} - \text{CSA}}{\text{CSA}} \times 100 \quad (2)$$

where *SACH* is the relative percentage change in suitable area between the current baseline and a future climate scenario, *FSA* is the projected future suitable area (km²), and *CSA* is the current suitable area (km²). A positive *SACH* value indicates an increase in projected suitable area relative to the current baseline, whereas a negative value indicates a decrease; a value of zero indicates no net change. The calculation was performed separately for each SSP and projection period, using the current suitable area as the common reference baseline. Changes in the proportion of Sudan's total land area were reported separately as percentage-point differences, thereby distinguishing changes in national land-area proportion from relative percentage changes in suitable area.

Binary baseline and future suitability maps were cross-tabulated into four transition classes: loss (suitable at baseline but unsuitable in the future), stable (suitable in both periods), gain (unsuitable at baseline but suitable in the future), and persistently unsuitable (unsuitable in both periods). These classes describe transitions in modelled environmental suitability and do not imply observed colonization, local extinction, or dispersal. Total suitable area and transition areas were summarized at national and state levels using R-based geospatial procedures and ArcGIS Pro 3.6. Raster reclassification, threshold extraction, and delineation of suitability-transition zones were performed in ArcGIS Pro 3.6.

Results

Model discrimination and evaluation performance

The MaxEnt model showed high discrimination between occurrence and background/evaluation locations, with mean area under the receiver operating characteristic curve (AUC) values of 0.950 for training data and 0.944 for withheld evaluation data across ten replicate runs (Fig. 2). The supplementary True Skill Statistic (TSS) was 0.838 ± 0.02 . These metrics indicate strong discrimination within the evaluation framework used here; they do not represent the percentage of occurrences classified correctly and should not be interpreted as evidence of future occupancy. The

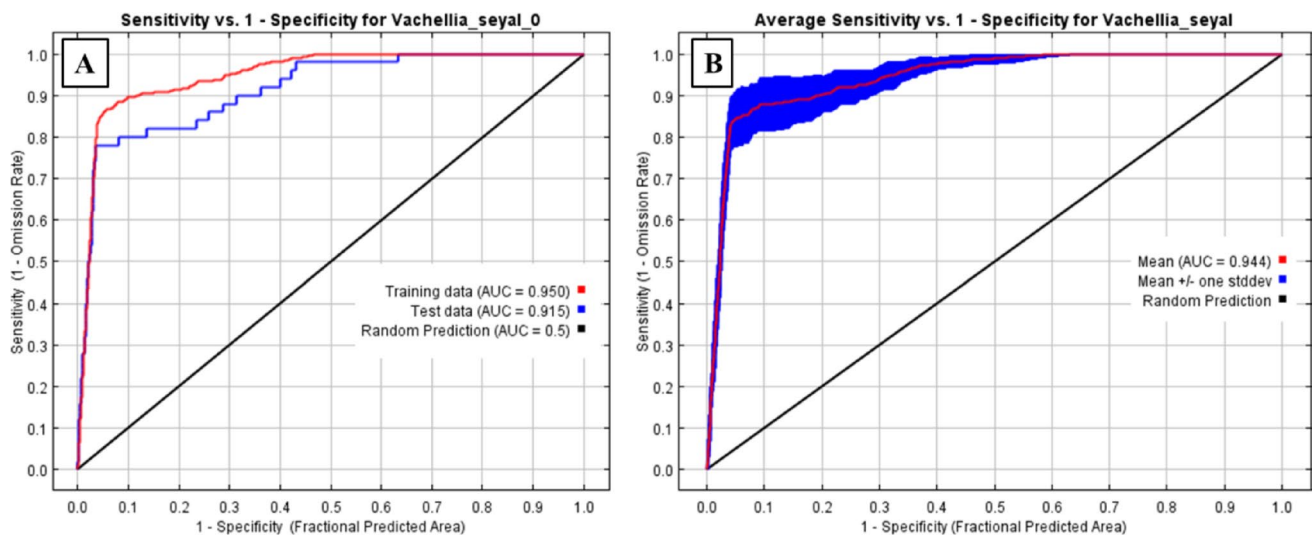


Fig. 2 Performance diagnostics of the MaxEnt model for *Vachellia seyal* in Sudan. **(A)** Omission-rate diagnostics for training and withheld evaluation data relative to the expected omission rate. **(B)** Receiver

operating characteristic performance across replicate runs, showing the mean AUC and associated variability. The diagonal reference denotes discrimination expected under a random classifier (AUC=0.5)

Table 2 Relative percent contribution and permutation importance of all environmental variables retained in the MaxEnt analysis, presented in order of decreasing contribution to model performance

Variable	Bioclimatic Description	Percent Contribution (%)	Permutation Importance (%)
bio3	Isothermality (BIO2/BIO7 × 100)	37.6	4.9
bio18	Precipitation of the warmest quarter	24.7	37.8
bio15	Precipitation seasonality	14.2	24.2
bio2	Mean diurnal range	11.1	0.8
bio10	Mean temperature of warmest quarter	8.8	10.2
Altitude	Elevation	1.9	18.6
Soil	Physical and chemical characteristics	1.0	0.5
bio19	Precipitation of coldest quarter	0.8	3.0
bio14	Precipitation of driest month	0	0

calibrated model was subsequently projected under SSP2-4.5 and SSP5-8.5 for 2021–2040 and 2081–2100.

Across replicate runs, the observed omission pattern was broadly consistent with the expected omission pattern shown in Fig. 2A, while the relatively narrow dispersion around mean AUC indicated limited variation in discriminatory performance among replicates. These diagnostics describe model performance for the available occurrence-background data and are not, by themselves, measures of projection uncertainty under future climates.

Key environmental predictors of *V. seyal* suitability

Nine predictors were retained after VIF screening: BIO2, BIO3, BIO10, BIO14, BIO15, BIO18, BIO19, elevation, and soil (Table 2). Isothermality (BIO3) had the highest MaxEnt percent contribution (37.6%), followed by precipitation of the warmest quarter (BIO18; 24.7%), precipitation seasonality (BIO15; 14.2%), mean diurnal range (BIO2; 11.1%), and mean temperature of the warmest quarter (BIO10; 8.8%). Permutation importance showed a different

ordering: BIO18 was highest (37.8%), followed by BIO15 (24.2%), elevation (18.6%), and BIO10 (10.2%). Elevation therefore had low percent contribution (1.9%) but comparatively high permutation importance (18.6%). Soil, BIO19, and BIO14 contributed little under both measures. The jack-knife analysis (Fig. 3) provided complementary information on the model gain associated with individual predictors and with their omission. Because MaxEnt percent contribution is path-dependent, these values are reported as measures of model contribution rather than causal effects.

Current potential environmental suitability of *V. seyal* in Sudan

Under baseline environmental conditions, 380,890.63 km², equivalent to 20.22% of Sudan's land area, was classified as suitable for *Vachellia seyal*. Within the descriptive suitability classes, 333,663.92 km² was classified as low suitability, 38,167.78 km² as medium suitability, and 9,058.93 km² as high suitability. The remaining 1,502,986.45 km² (79.78%) was classified as unsuitable. Suitable areas were

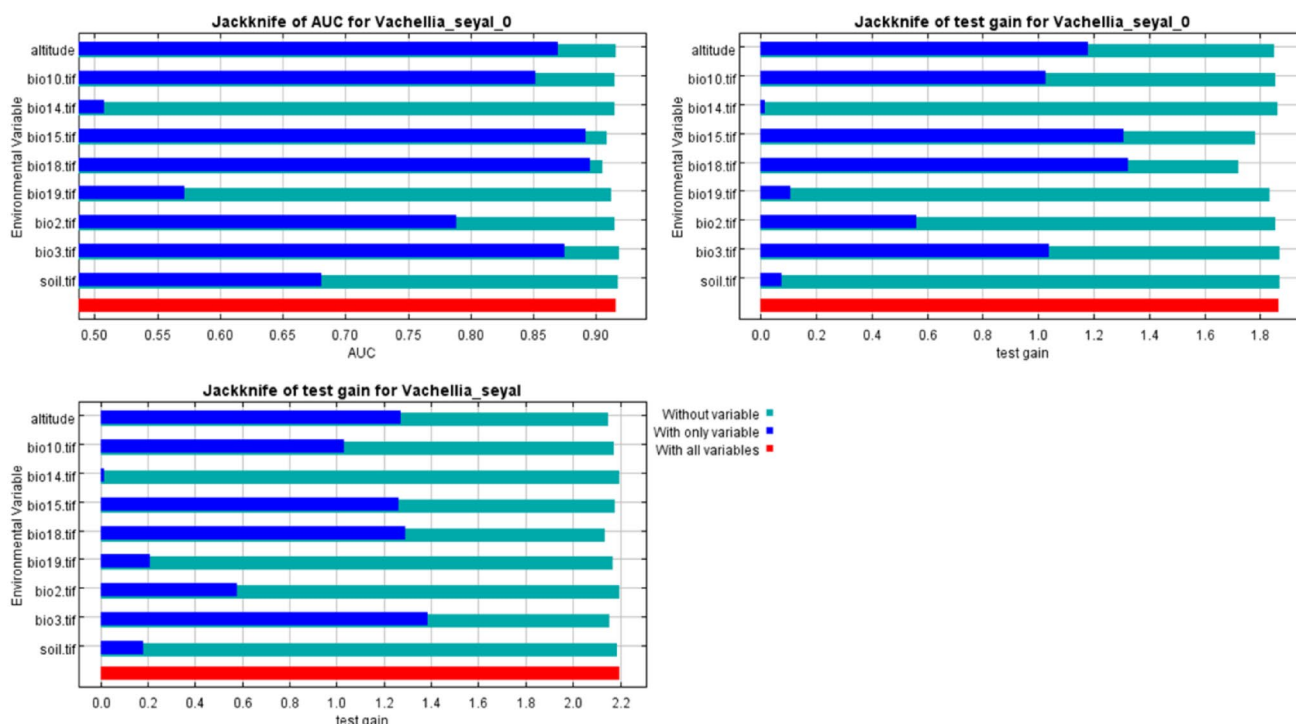


Fig. 3 Jackknife analysis of environmental predictors in the MaxEnt model for *Vachellia seyal*. Bars show model gain when each predictor is used in isolation, when it is omitted, and when all retained predictors are included, as indicated in the figure legend

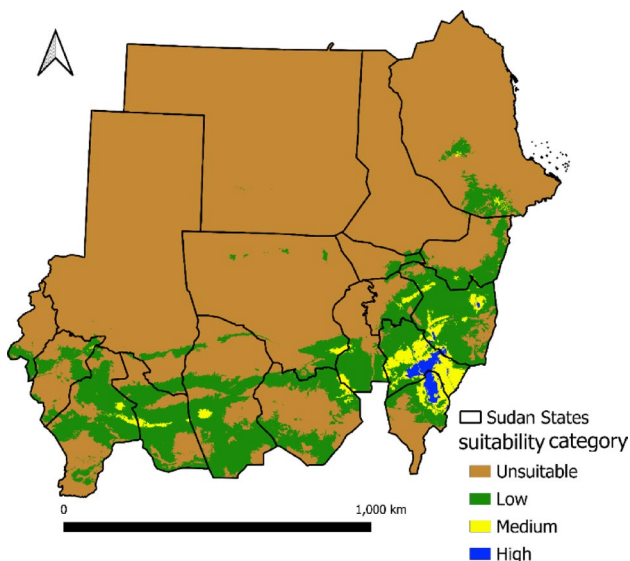


Fig. 4 Baseline potential environmental suitability for *Vachellia seyal* in Sudan, shown using the four descriptive suitability classes (unsuitable, low, medium, and high)

concentrated mainly in central, eastern, and southern parts of Sudan, whereas much of the north and west was classified as unsuitable (Fig. 4). These classes describe modelled environmental suitability and not observed occupancy.

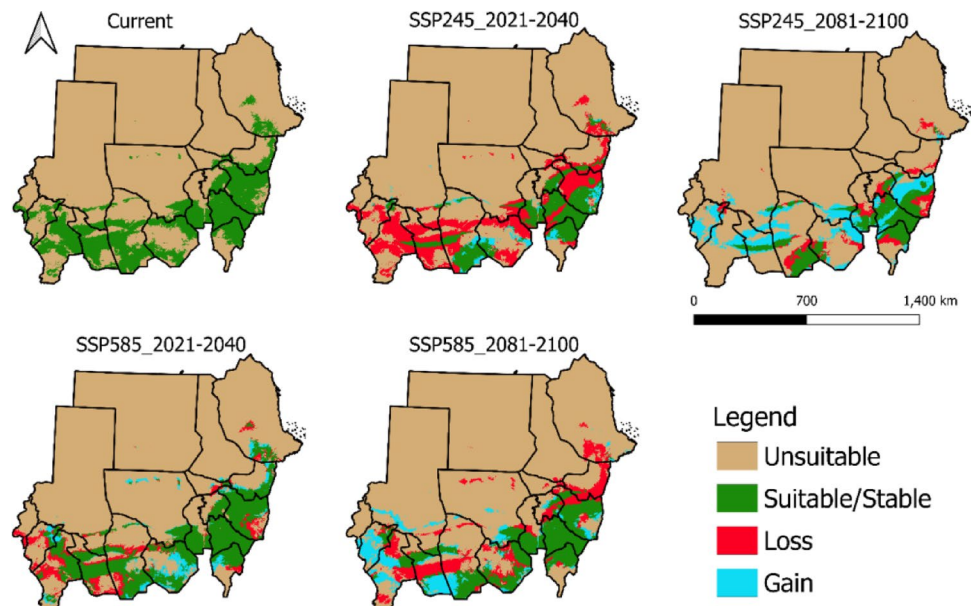
Projected future changes in potential environmental suitability

Projected suitable area was lower than the current baseline under all four scenario-period combinations (Table 3). Under SSP2-4.5, suitable area decreased from 380,890.63 km² (20.22% of Sudan) at baseline to 177,240.19 km² (9.41%) in 2021–2040, a reduction of 203,650.44 km² and a relative change of -53.47%. By 2081–2100, suitable area was projected at 255,482.20 km² (13.56%). Although this represents an increase of 78,242.01 km² relative to the SSP2-4.5 near-future projection, it remains 125,408.43 km² below the current baseline (SACH = -32.93%). The proportion classified as stable suitability was 7.96% in 2021–2040 and 6.47% in 2081–2100, while gain increased from 1.45% to 7.10%.

Under SSP5-8.5, suitable area was projected at 350,775.69 km² (18.62%) in 2021–2040 and 306,923.26 km² (16.29%) in 2081–2100. Relative to the current baseline, these values correspond to reductions of 30,114.94 km² (SACH = -7.91%) and 73,967.37 km² (SACH = -19.42%), respectively. Stable suitability declined from 16.05% in 2021–2040 to 11.16% in 2081–2100, whereas modelled gain increased from 2.57% to 5.13% and loss increased from 4.17% to 7.46%. Thus, the transition maps indicate increasing spatial turnover through time under SSP5-8.5, despite the persistence of suitable areas in parts of the country.

Table 3 National-scale potential suitability and baseline-to-future transitions for *Vachellia seyal* under current and future climate scenarios

Time slice	Total suitable area (km ²)	Total suitable area (%)	Persistently unsuitable (%)	Gain (%)	Loss (%)	Stable (%)
Current	380,890.63	20.22	79.78	0	0	20.22
SSP245_2021–2040	177,240.19	9.41	78.33	1.45	12.26	7.96
Change from current	-203,650.44	-10.81	-1.45	1.45	12.26	-12.26
SSP245_2081–2100	255,482.20	13.56	83.50	7.10	2.94	6.47
Change from current	-125,408.43	-6.66	3.72	7.10	2.94	-13.75
SSP585_2021–2040	350,775.69	18.62	77.21	2.57	4.17	16.05
Change from current	-30,114.94	-1.60	-2.57	2.57	4.17	-4.17
SSP585_2081–2100	306,923.26	16.29	76.25	5.13	7.46	11.16
Change from current	-73,967.37	-3.93	-3.53	5.13	7.46	-9.06

Fig. 5 Baseline suitability and projected suitability transitions for *Vachellia seyal* under SSP2-4.5 and SSP5-8.5 for 2021–2040 and 2081–2100. Transition classes are: stable (suitable at baseline and in the future), loss (suitable at baseline but unsuitable in the future), gain (unsuitable at baseline but suitable in the future), and persistently unsuitable (unsuitable at baseline and in the future)

Overall, the projections indicate both contraction and spatial redistribution of potential environmental suitability. Because total suitable area remained below the current baseline in every scenario-period combination, projected gains in some locations did not offset losses elsewhere.

The transition maps further show that losses, gains, stable suitability, and persistent unsuitability were spatially heterogeneous (Fig. 5). Modelled gains occurred principally in parts of central-eastern Sudan, while losses affected portions of the currently suitable range. These mapped transitions represent changes in modelled environmental suitability only; they do not demonstrate colonization, local extinction, dispersal, or the existence of confirmed climate refugia.

State-level patterns of current and projected suitability

Near-future projections (SSP2-and SSP5-8.5, 2021–2040)

At baseline, state-level summaries showed strong spatial variation in the four descriptive suitability classes

(Fig. 6A). Large areas of Northern, North Darfur, and Red Sea states were classified as unsuitable (367,614, 314,988, and 201,540 km², respectively). In contrast, Blue Nile contained 12,360 km² of low, 5,887 km² of medium, and 3,926 km² of high suitability; Gedaref contained 47,376, 6,439, and 864 km², respectively; and South Kordofan contained 34,479, 1,383, and 8 km², respectively. These values describe the extent of modelled suitability classes and do not indicate observed abundance or population status.

Under SSP2-4.5 for 2021–2040, the distribution among suitability classes changed substantially in several states. West Kordofan was projected to contain 34,949 km² of low and 738 km² of medium suitability, with 77,894 km² classified as unsuitable. Blue Nile was projected to contain 17,333 km² of low, 10,460 km² of medium, and 5,508 km² of high suitability. Gedaref was projected to contain 27,196 km² of low, 2,456 km² of medium, and 859 km² of high suitability. These results demonstrate state-specific reorganization among suitability classes rather than a uniform directional response across Sudan.

Under SSP5-8.5 for 2021–2040, Sennar was projected to contain 20,723 km² of medium and 4,406 km² of high

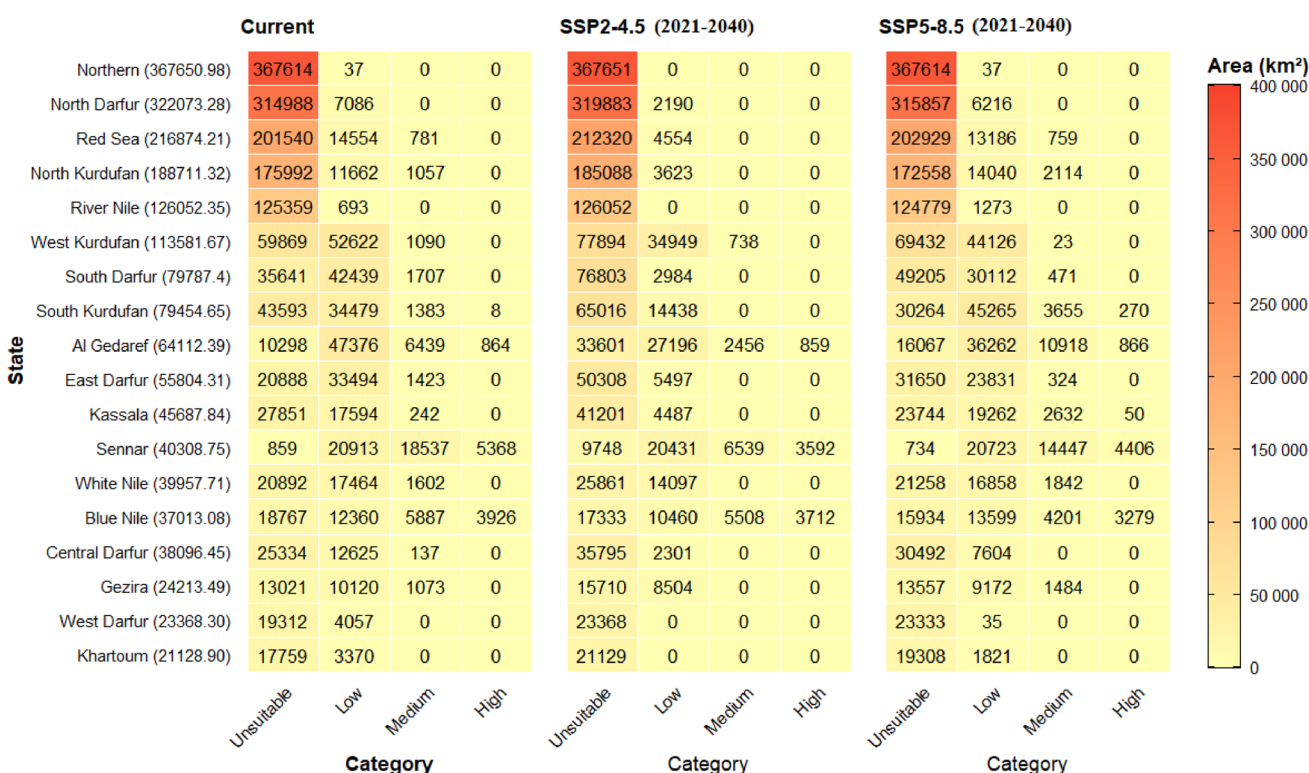


Fig. 6 State-level extent (km²) of the four descriptive *Vachellia seyal* suitability classes under baseline conditions and the near-future SSP2-4.5 and SSP5-8.5 projections (2021–2040)

suitability, while Blue Nile contained 13,599 km² of medium and 3,279 km² of high suitability. Central Darfur was projected to contain 7,604 km² of low suitability and no medium or high-suitability area, whereas Kassala contained 19,262 km² of low, 2,632 km² of medium, and 50 km² of high suitability. The state-level projections therefore show substantial geographic heterogeneity in both the magnitude and class of future suitability.

Across the near-future projections, suitable areas remained concentrated primarily in central, eastern, and southeastern Sudan, whereas large portions of northern and western states remained unsuitable. The direction and magnitude of change nevertheless differed between states and scenarios; consequently, these projections identify areas of modelled persistence, loss, and gain rather than confirmed future refugia or restoration outcomes.

Far-future projections (SSP2-and SSP5-8.5 2081–2100)

Far-future projections retained strong differences among states and scenarios (Figs. 6B and 7). Because baseline state-level patterns are reported above, the far-future comparison focuses on changes in the distribution of suitability classes under SSP2-4.5 and SSP5-8.5 for 2081–2100.

Under SSP2-4.5 for 2081–2100, Blue Nile was projected to contain 10,134 km² of medium and 4,079 km² of high

suitability. The projections also indicated redistribution among suitability classes in Gedaref, West Kordofan, North Kordofan, and Kassala, although the direction and magnitude of these changes varied among states.

Under SSP5-8.5 for 2081–2100, Sennar was projected to contain 13,294 km² of medium and 8,267 km² of high suitability, while Blue Nile contained 11,463 km² of medium and 3,798 km² of high suitability. Central Darfur and Kassala retained comparatively limited medium- and high-suitability areas. These patterns again indicate substantial state-level redistribution rather than a uniform national response.

Across both far-future scenarios, northern and much of western Sudan remained predominantly unsuitable, whereas modelled suitable areas were more prominent in parts of central-eastern and southeastern Sudan (Fig. 7). These geographic contrasts should be interpreted as projected differences in environmental suitability rather than direct evidence of future population persistence, colonization, or local extinction.

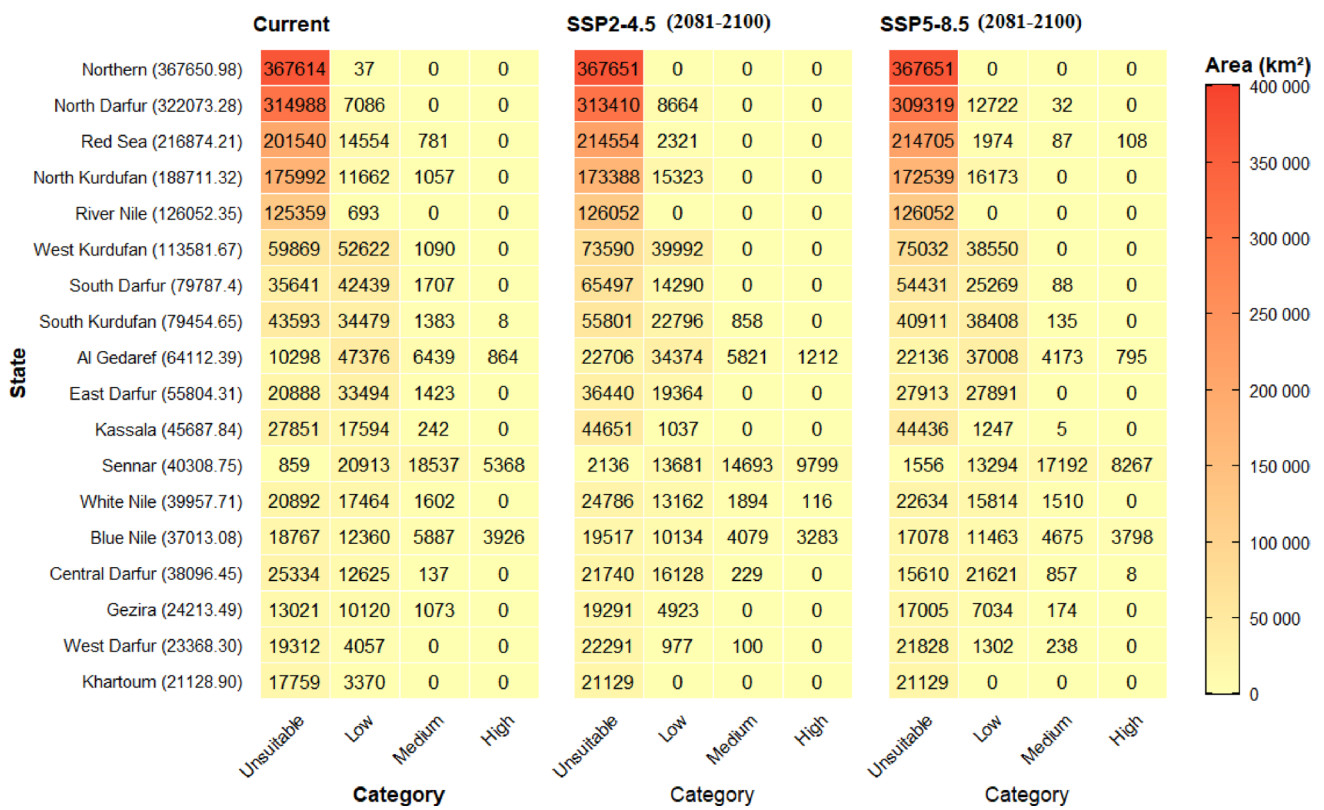
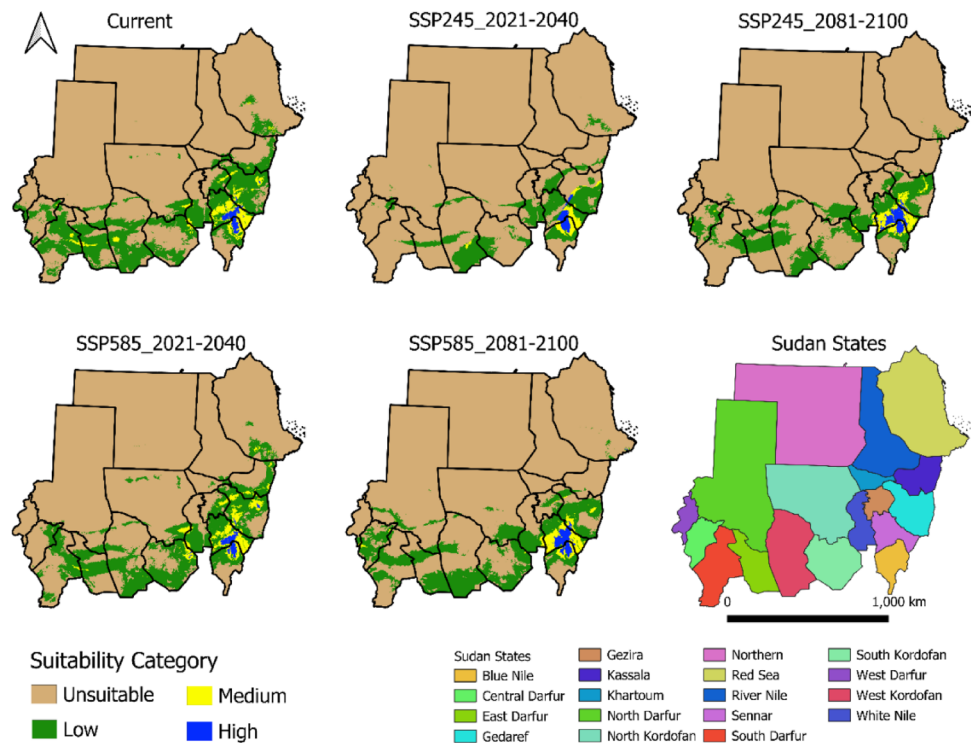


Fig. 7 State-level extent (km²) of the four descriptive *Vachellia seyal* suitability classes under baseline conditions and the far-future SSP2-4.5 and SSP5-8.5 projections (2081–2100)

Fig. 8 Spatial distribution of the four descriptive *Vachellia seyal* suitability classes across Sudanese states under baseline and future climate projections. State boundaries are overlaid for geographic reference



Discussion

Model performance and interpretation of predictive capability

Across ten replicate runs, the MaxEnt model showed high discrimination between withheld occurrence records and the background environment, with mean training and evaluation AUC values of 0.950 and 0.944, respectively, and a mean TSS of 0.838 ± 0.02 (Fig. 2). These statistics indicate strong discriminatory performance within the adopted evaluation framework, but they should not be interpreted as percentages of occurrences correctly classified or as evidence that future projections are accurate. In a presence-background framework, AUC measures the ability to rank occurrence locations above background locations, whereas TSS is supplementary because background locations are not confirmed absences (Elith et al. 2011; Merow et al. 2013; Jiménez-Valverde 2014). The evaluation metrics therefore support the model's capacity to discriminate environmental conditions associated with observed *Vachellia seyal* occurrences within the calibration domain, rather than demonstrating realized occupancy or future persistence.

The relatively small variation among replicate runs indicates consistency under the adopted occurrence partitioning and model settings, but it does not by itself demonstrate absence of overfitting (Pearson et al. 2007; Warren et al. 2021). Comparable MaxEnt applications to African woody species have reported useful discriminatory performance, including *Vachellia negrii* in Ethiopia, *Tamarindus indica* in Ethiopia, and *Adansonia digitata* in Sudan (Semu et al. 2021; Gufi et al. 2023; Gadallah et al. 2025; Montoya-Jiménez et al. 2022). Nevertheless, high discrimination does not eliminate uncertainty associated with occurrence sampling bias, background definition, model specification, temporal mismatch between occurrence records and baseline climate, or transfer to novel future environments (Elith et al. 2010; Merow et al. 2013; Fourcade 2016; Peterson et al. 2007; Warren et al. 2021). Accordingly, all projections in this study are interpreted as estimates of potential environmental suitability rather than forecasts of future geographic occupancy.

Environmental controls on *Vachellia seyal* suitability

The variable-importance metrics indicate that modelled suitability was associated primarily with climatic gradients. Isothermality (BIO3) had the largest percent contribution (37.6%), followed by precipitation of the warmest quarter (BIO18; 24.7%), precipitation seasonality (BIO15; 14.2%), mean diurnal range (BIO2; 11.1%), and mean temperature of the warmest quarter (BIO10; 8.8%). Permutation

importance, however, was highest for BIO18 (37.8%) and BIO15 (24.2%), while elevation showed low percent contribution (1.9%) but comparatively high permutation importance (18.6%). These differences are expected because MaxEnt percent contribution depends on the pathway followed during model fitting, whereas permutation importance evaluates the reduction in predictive performance after values of a predictor are permuted (Phillips et al. 2006; Merow et al. 2013). The two measures are therefore complementary indicators of predictive association and should not be interpreted as independent causal effects.

The prominence of precipitation-related predictors is ecologically plausible for a seasonally dry savanna tree. Experimental and field-based evidence indicates that water availability and drought affect establishment and early growth of *V. seyal* (Merine et al. 2015; Ahmed et al. 2020; Elzaki et al. 2023), while rainfall amount and seasonality exert strong controls on woody vegetation across African savannas (Sankaran et al. 2005; Mtsetfwa et al. 2023). The high importance of BIO18 and BIO15 is therefore consistent with the dependence of establishment and growth on both the amount and seasonal distribution of moisture. Isothermality expresses the relationship between mean diurnal temperature range and annual temperature range; its high contribution indicates that occurrences are strongly associated with the structure of thermal variability across Sudan. This pattern may reflect thermal constraints or covariance with other climatic gradients, but the correlative model cannot establish a physiological mechanism. Experimental or demographic data would be required to determine whether thermal variability directly affects germination, growth, reproduction, or survival.

Elevation contributed little to the model-fitting pathway but had relatively high permutation importance, indicating information that was not fully interchangeable with the other retained predictors. Elevation can integrate local variation in temperature, precipitation, moisture availability, and edaphic conditions, and topographic effects are commonly relevant in species-distribution modelling (Acharya et al. 2025). Conversely, the small contribution of the soil predictor should not be interpreted as evidence that soil is ecologically unimportant; soil conditions can influence belowground ecological processes and ecosystem functioning in forest systems (Duan et al. 2023), while the present result indicates only that the soil layer used here added limited predictive information after the other retained variables were considered. Overall, the results identify a strong climatic component to modelled *V. seyal* suitability while emphasizing that MaxEnt importance statistics quantify associations rather than ecological causation.

Ecological interpretation of current environmental suitability

Under baseline conditions, 380,890.63 km² (20.22% of Sudan) was classified as environmentally suitable for *V. seyal*, with most of this area in the low-suitability class and substantially smaller areas in the medium- and high-suitability classes. The concentration of suitability in central, eastern, and southern Sudan is consistent with the country's pronounced hydroclimatic gradient and the broader distribution of savanna woodland under greater seasonal water availability (Siddig 2014; Mohamed et al. 2016; Hasoba et al. 2025). This pattern is also consistent with the ecology and documented Sudanese distribution of *V. seyal* as a seasonally dry savanna species (Wickens 1995; Ghogue 2020; Gamal et al. 2022). In contrast, much of northern Sudan was classified as unsuitable, corresponding to the more arid end of the national environmental gradient.

The suitability map should not, however, be interpreted as a complete map of occupied habitat. MaxEnt identifies locations whose environmental conditions resemble those associated with the occurrence records and retained predictors, whereas realized distribution additionally depends on dispersal, population dynamics, disturbance, land use, biotic interactions, and historical constraints (Elith et al. 2010; Merow et al. 2013). This distinction is particularly important in Sudan, where woody vegetation is affected by both climatic variability and anthropogenic pressures (Siddig 2014; Hasoba et al. 2025). Areas of higher modelled suitability are therefore best regarded as candidate areas for ecological assessment and field verification, not confirmed population strongholds, genetic reservoirs, or guaranteed restoration sites.

Climate-driven changes in potential environmental suitability

Future projections indicate substantial spatial reorganization rather than a uniform directional response (Table 4; Fig. 5). Relative to the current suitable area of 380,890.63 km², SSP2-4.5 reduced suitable area to 177,240.19 km² in 2021–2040, corresponding to a 53.47% relative reduction and a decline in the proportion of Sudan from 20.22% to 9.41% (10.81% points). By 2081–2100, suitable area under SSP2-4.5 increased to 255,482.20 km² relative to the near-future projection, but remained 32.93% below the current baseline. The late-century increase under SSP2-4.5 therefore represents partial recovery in modelled environmental suitability, not evidence of biological adaptation or a return to current conditions.

Under SSP5-8.5, projected suitable area was 350,775.69 km² in 2021–2040, 7.91% below the current

baseline, and 306,923.26 km² in 2081–2100, 19.42% below baseline. Thus, all four future scenario-period combinations produced less total suitable area than the current baseline, although the magnitude and spatial configuration of change differed markedly. The simultaneous occurrence of stable, lost, and gained suitability is consistent with African woody-species SDMs showing that climate change can reorganize suitable environmental space geographically rather than causing uniform contraction or expansion (Foden et al. 2007; Wan et al. 2021; Lyam et al. 2022; Semu et al. 2021; Atakpama et al. 2023; Hussein and Estifanos 2023; HamadAmin and Khwarahm 2023; Gufi et al. 2023; Mtsetfwa et al. 2023). Suitability gain indicates the emergence of environmental conditions classified as suitable by the model; it does not demonstrate colonization. Likewise, suitability loss does not demonstrate local extinction.

The contrasting trajectories between SSP2-4.5 and SSP5-8.5 also caution against assigning the projected transitions to a single mechanism. Precipitation and temperature gradients were influential correlates in the fitted model, and African dryland research demonstrates the sensitivity of woody vegetation to drought, rainfall variability, and warming (Trisos et al. 2022; Mtsetfwa et al. 2023; Umuhoza et al. 2025). However, the present analysis did not isolate the demographic or physiological causes of individual spatial transitions. Claims of drought-induced mortality, adaptation, dispersal failure, or fragmentation would therefore require independent demographic, physiological, or landscape evidence. The projections show where the multivariate environmental conditions represented by the fitted model become more or less similar to those associated with current *V. seyal* occurrences.

Spatial heterogeneity and state-level implications

The state-level analysis reveals substantial geographic heterogeneity that is obscured by national totals. Blue Nile, Gedaref, Sennar, and parts of the Kordofan region retain or develop comparatively large areas of modelled suitability in at least some future scenario-period combinations, whereas Northern, North Darfur, and Red Sea remain dominated by unsuitable conditions. These contrasts reflect the strong environmental gradient across Sudan and indicate that the direction and magnitude of projected change depend on location, scenario, and projection period. State-level reporting is therefore important for identifying where national-scale contraction co-occurs with localized persistence or gain.

Areas that remain suitable across baseline and future projections may be useful candidates for field-based assessment of persistence and restoration potential (Teshfamar-iam et al. 2022). They should not, however, be labelled

confirmed climate refugia because this analysis does not evaluate population persistence, microclimatic buffering, connectivity, land-use stability, or adaptive genetic variation (Aguirre-Liguori et al. 2021; Lyam et al. 2022). Similarly, areas projected to gain suitability should not automatically be treated as targets for assisted migration. Dispersal limitation and landscape fragmentation can prevent species from tracking shifting environmental conditions (Foden et al. 2007; Guo et al. 2023), and field surveys, regeneration assessments, provenance information, land-use constraints, and local management feasibility are required before translating projected suitability into site-specific interventions (Aguirre-Liguori et al. 2021; Lyam et al. 2022; Tesfamariam et al. 2022).

Implications for conservation, restoration, and climate adaptation

The principal management value of these projections is as a spatial decision-support layer for prioritizing further assessment. Areas with persistent or comparatively high suitability can be screened for field validation, population and regeneration monitoring, seed-source assessment, and the feasibility of assisted natural regeneration (Tesfamariam et al. 2022; Sanchez et al. 2023). Conversely, areas of projected suitability loss can be prioritized for monitoring changes in recruitment, mortality, and disturbance. This approach is more defensible than treating SDM outputs as direct prescriptions because restoration success depends on site conditions, land tenure, disturbance, propagule availability, management capacity, and socioeconomic context in addition to broad-scale environmental suitability (Tesfamariam et al. 2022).

The ecological and livelihood importance of *V. seyal* strengthens the relevance of climate-informed planning. The species contributes to dryland production systems and rural livelihoods and has also been investigated for rehabilitation of environmentally stressed soils (Gamal et al. 2022; Thiao et al. 2022). Consequently, maintaining existing populations and regeneration in environmentally persistent areas may support both conservation and restoration objectives. Potential future gains could inform reconnaissance and field trials, whereas projected losses could guide monitoring and risk assessment. More interventionist measures, including translocation or assisted migration, should be considered only after evaluating provenance, genetic diversity, establishment success, land-use compatibility, and ecological risk (Aguirre-Liguori et al. 2021; Lyam et al. 2022).

Study limitations and future research priorities

Several limitations define the inferential scope of this study. First, MaxEnt is a correlative presence-background approach, and the occurrence records originated from multiple sources and periods, whereas baseline climatic predictors represented 1970–2000 conditions. Although spatial thinning reduced geographic clustering, the absence of an explicit sampling-bias surface or target-group background means that residual survey and accessibility bias may remain (Fourcade 2016; Pearson et al. 2007). Random partitioning may also yield optimistic evaluation when calibration and evaluation records share spatial or environmental structure (Warren et al. 2021). Future studies should therefore consider spatially blocked cross-validation and alternative bias-correction and background-sampling strategies (Fourcade 2016; Warren et al. 2021).

Second, model specification and climate projections introduce additional uncertainty. The analysis used a single SDM algorithm with the specified MaxEnt feature and regularization settings rather than a comparative multi-algorithm or independently tuned modelling framework, while future climate projections were based on the arithmetic mean of three CMIP6 GCMs. Although the multi-GCM mean reduces dependence on any single climate model, it does not quantify inter-model variability. Future analyses should evaluate MaxEnt tuning and alternative SDM algorithms, examine individual GCM projections and their agreement, and assess threshold sensitivity because estimates of suitability loss, persistence, and gain can vary with the selected cutoff (Elith et al. 2011; Bentlage and Shcheglovitova 2012; Merow et al. 2013; Jiménez-Valverde 2014; Warren et al. 2021; Montoya-Jiménez et al. 2022).

Finally, the model estimates potential environmental suitability rather than realized future occupancy and does not explicitly incorporate dispersal, demography, dynamic land-use change, anthropogenic pressures, disturbance, biotic interactions, or future soil changes. Consequently, projected suitability gain or loss should not be interpreted as colonization or local extinction. Transfer to future climates also assumes that the estimated occurrence–environment relationships remain informative under changing conditions (Peterson et al. 2007). Future research integrating land-use and connectivity scenarios, dispersal and demographic processes, independent field validation, and genetic or provenance information would help translate broad-scale suitability patterns into population- and management-relevant assessments (Aguirre-Liguori et al. 2021; Lyam et al. 2022; Moradi et al. 2025). Within these boundaries, the present framework provides a national-scale baseline for identifying areas of projected suitability persistence, loss,

and gain and for prioritizing subsequent monitoring and restoration assessments.

Conclusion

This study provides a national-scale assessment of current and projected potential environmental suitability for *Vachellia seyal* in Sudan using a MaxEnt presence-background framework. Climatic predictors accounted for most of the model-fitting contribution, with isothermality (BIO3), precipitation of the warmest quarter (BIO18), and precipitation seasonality (BIO15) particularly influential. Under baseline conditions, 380,890.63 km² (20.22% of Sudan) was classified as environmentally suitable. All four future scenario-period combinations produced less total suitable area than the current baseline: the largest reduction occurred under SSP2-4.5 in 2021–2040 (53.47% below baseline), followed by a partial late-century recovery that nevertheless remained 32.93% below baseline; SSP5-8.5 produced reductions of 7.91% in 2021–2040 and 19.42% in 2081–2100.

The projections also reveal substantial spatial turnover and state-level heterogeneity, with areas of persistence, loss, and gain occurring simultaneously. These transitions represent changes in modelled environmental suitability and should not be interpreted as inevitable colonization, extinction, adaptation, or future occupancy. The maps can nevertheless inform climate-informed conservation and restoration planning by identifying areas for field verification, monitoring, regeneration assessment, and restoration screening. Their application should be combined with information on population status, dispersal, land use, disturbance, genetic provenance, and management feasibility. By explicitly recognizing these limitations, the study provides a transparent spatial framework for evaluating how the environmental conditions associated with *V. seyal* may be redistributed across Sudan under alternative future climates.

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mel Czimer : writing—review and editing, supervision. All authors have read and agreed to the published version of the manuscript.

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Data availability The data that support the findings of this study are available from the first author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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