

Past, present, and future potential distributions of the African multipurpose tree *Detarium senegalense* (Fabaceae)

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Abstract

Background and aims – Climate change induces increasing temperatures and drought, with possible profound shifts in species' presence and distribution. Ecological niche models are widely used to assess plant species responses to climate change. However, such data are scarce for West Africa, particularly for vulnerable multipurpose species. This study focuses on modelling the ecological niche and the conservation status of the multipurpose tree *Detarium senegalense* to improve insights into its habitat suitability in West Africa under past, present, and future climatic conditions. This will provide an essential basis for setting up global management plans through efficient conservation and ecological restoration policies.

Material and methods – The potential distribution of *D. senegalense* under past, current, and future climate scenarios were assessed using four algorithms including generalized additive models (GAM), generalized linear models (GLM), random forest (RF), and Maximum Entropy (MaxEnt). We also assessed the shift direction of suitable habitats and the conservation status of the species based on IUCN criteria. Overall, 220 occurrences were combined with a set of five bioclimatic variables to run the models.

Key results – Models performed well with good values of AUC (0.92) and TSS (0.73). Isothermality (41.10%) and Precipitation of Wettest Month (21.50%) contributed most to the distribution of the species. The distribution of *D. senegalense* was relatively constant from the past to the present but could decrease in the next decades. In the future, only 17.70% and 13.98% of the areas were predicted to be suitable under respectively ssp245 and ssp585. In protected areas, the suitable areas under ssp245 were estimated at 21.01% with a decrease of 2.50% and 14.60% with a decrease of 8.61% under ssp585 by 2050. The direction of the distribution shifted to the south-east under future climate scenarios. The conservation status assessment of the species is Least Concern (LC).

Conclusion – This study improves our understanding of the past, present-day, and future distribution of the species and provides support to better manage the conservation of *D. senegalense* in West Africa.

Keywords

centroid, climate, conservation, *Detarium senegalense*, ecological niche modelling

INTRODUCTION

The genus *Detarium* Juss. (Fabaceae) consists of three species found from West Tropical Africa to Sudan and it is introduced in Trinidad and Tobago (WFO 2024). Among them, the Tallow tree (*Detarium senegalense* J.F.Gmel.) is probably one of the most known *Detarium* species. It has a great socio-economic value in West Africa and has the potential to contribute to food security. The species ranks among the highly valued non-timber forest products for its nutritional and medicinal value, and magical and therapeutic uses throughout West Africa (Dassou et al. 2023). The nutritional and medicinal value of the fruit pulp and seed oil are exceptional. For instance, the pulp is rich in vitamin C, with more than 1000 mg / 100 g (Diop et al. 2010), which is about 29, 12, 7, and 5 times higher than in *Citrus × sinensis* (L.) Osbeck, *Citrus × limon* (L.) Osbeck, *Psidium guajava* L., and *Adansonia digitata* L. pulps respectively. It also contains vitamins B1 (thiamin), B2 (riboflavin), B3 (niacin), provitamine A (β-carotene), and essential amino acids (National Research Council 2008; Diop et al. 2010; Ndiaye et al. 2016). The seeds contain various minerals such as potassium (99.26 mg/g), magnesium (77.83 mg/g), calcium (71.11 mg/g), sodium (55.26 mg/g), iron (30.21 mg/g), manganese (7.89 mg/g), zinc (5.26 mg/g), and copper (4.99 mg/g) (Sowemimo et al. 2011). The leaves, bark, roots, pulps, and seeds are rich in therapeutic substances, including powerful anti-bacterial, anti-viral, hypoglycemic, and anti-cancer molecules (Akah et al. 2012; Sanni et al. 2015).

Unfortunately, in addition to the threat of habitat degradation and its exploitation as timber, there is a growing regional trade of its fruits and seeds (Neuenschwander et al. 2011; Houénou et al. 2021). It has been suggested that the high commercial value of the fruits and seeds has stimulated its collection to a level which may threaten the regeneration of the species. Because of this persistent over-exploitation, *D. senegalense* has been reported as a threatened species in Benin (“Endangered”) (Adomou et al. 2009; Neuenschwander et al. 2011) as well as in West Africa (Hawthorne 1996). Moreover, the rate of natural regeneration from seeds, even after dispersal by mammals, is very low (El-Kamali 2011; Houénou et al. 2022). As such, *D. senegalense* risks, in the medium-term, to become very scarce or even disappear locally, although it is classified as “Least Concern” on the IUCN Red List (BGCI and IUCN 2019). While the cultivation of this precious fruit tree is urgent, it is equally important to engage in sustainable conservation strategies to preserve its natural populations. One of the key variables to consider both in cultivation and conservation projects is the species’ responses to climatic variation. Yet, it is still unclear how various climate changes influenced its distribution and how potential areas for its cultivation can change across its distribution range.

Understanding the distribution of key taxa and their response to environmental change is fundamental to their effective management (Acevedo et al. 2012). In West

Africa, patterns of distribution around the Dahomey Gap have been of particular interest to palynologists, archaeologists, and biogeographers as they can help to explain present-day distribution of the Guineo-Congolian closed semi-deciduous humid forests limited to tiny patches, most of them so-called sacred forests in Benin, Togo, and Ghana (Tossou 2002; Adomou 2005; Salzmann and Hoelzmann 2005). The establishment of the Dahomey Gap is favoured by the combined effect of the orientation of the coast in relation to sea currents, which locally modify the climate of the Gulf of Benin, climate change from the Quaternary (especially the Pleistocene and the Holocene), the harmattan, and human activities notably agriculture and forest exploitation (Salzmann and Hoelzmann 2005). Due to these factors, West Africa’s rainforests receded into two major blocks: the western Upper Guinean situated in today’s Ivory Coast/Liberia, and the eastern Lower Guinean/Congolese forest block in southern Cameroon, which are separated by the Dahomey Gap where the savannah reaches the coast (Poorter et al. 2004; Salzmann and Hoelzmann 2005; Giresse 2007). Consequently, in southern Benin and Togo, dense humid forest only exists in the form of islands or relics and the evergreen dense forest unit of dry land is completely absent. Indirectly, the current distribution pattern of forest species in the Dahomey Gap is not only determined by current climatic gradients but also by Quaternary climatic changes. Understanding the specific properties of these changes, which may have an impact on species or their habitats, is central to the sustainable management of species and their ecosystems (Heller and Zavaleta 2009). These climate changes constitute an environmental issue that deserves special attention in the planning of agricultural production, the diversification of agricultural production, and the conservation of species. Fluctuations in climatic variables such as precipitation and temperature are increasingly likely to affect biodiversity and the geographic distribution of favourable habitats for species (IPCC 2007). Information on the impact of climate change on biodiversity is also important to better reason the choices of areas where species can be conserved today and in the future. This is because climate change could generate a spatial dynamic in the geographical distribution of habitats favourable to species and thus make certain regions favourable today, while very unfavourable in the future and vice versa (Hannah et al. 2002). Overlooking this dimension could jeopardize efforts to conserve and cultivate the species.

Species distribution modelling (SDM) is one of the commonly used tools for investigating potential geographical distributions of organisms. SDM can be defined as the prediction of species distribution across the landscape based on the relationship between species occurrence and environmental variables (Guisan et al. 2002). Such distribution models are becoming important tools for survey design and the most popular is the Maximum Entropy (MaxEnt). Modelling the ecological niche and conservation potential of *D. senegalense* in

protected areas under historical, contemporary, and projected West African climates is the main goal of this research. Specifically, this study aims to: (i) identify the environmental variables that significantly influence the distribution of *D. senegalense* in West Africa; (ii) determine the potential habitats favourable to the geographical distribution of *D. senegalense* under past, present, and future climatic conditions; (iii) assess the shift direction in *D. senegalense* distribution in West Africa under past, current, and future climates; and (iv) assess the changes of habitat suitability in the current and future distribution of *D. senegalense* in existent protected areas. We further discuss the implications of these distributions for the conservation, cultivation, and ecological restoration of this important species.

MATERIAL AND METHODS

Study area and species

The study was carried out in West Africa including Senegal, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Burkina Faso, Togo, Benin, and Nigeria (Fig. 1A). In terms of biogeography, four major phytocoria with specific vegetation types can be broadly distinguished: (i) Sahelian savannah (S), (ii) Sudanian savannah (SZ),

(iii) Guinea savannah (SG), (iv) Guineo-Congolian (GC) forest with closed semi-deciduous forests and evergreen forests (Fig. 1A). The African lowland rain forest has three regions, namely Congolia, Upper Guinea, and Lower Guinea, the latter two being separated by the Dahomey Gap (White 1983; Poorter et al. 2004; Leal 2004). The current forest range originated from the dry period in the region during the Quaternary, especially the Pleistocene and the Holocene (Salzmann and Hoelzmann 2005). The Dahomey Gap has been identified as a major ecogeographical impediment to the dispersal of rainforest species in this region and is, as such, of crucial significance for their distribution patterns in West Africa (van Bruggen 1989; Martin 1991; Jenik 1994). The Dahomey Gap experienced a decline in annual precipitation from more than 2000 mm in the rainforest areas of Nigeria and Ivory Coast to about 1200–1000 mm in the savanna region. The GC region is relatively dry and receives between 1600 and 2000 mm of precipitation annually, while the SZ and S zones receive 500–1400 mm and 150–500 mm of annual precipitation respectively.

Detarium senegalense is currently present in a wide geographical range across the four ecological zones: GC, SG, SZ, and S (Fig. 1A). The species is mainly found in Senegal, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Burkina Faso, Togo, Benin, and Nigeria (WFO 2024). The species is a tree with a large leafy crown

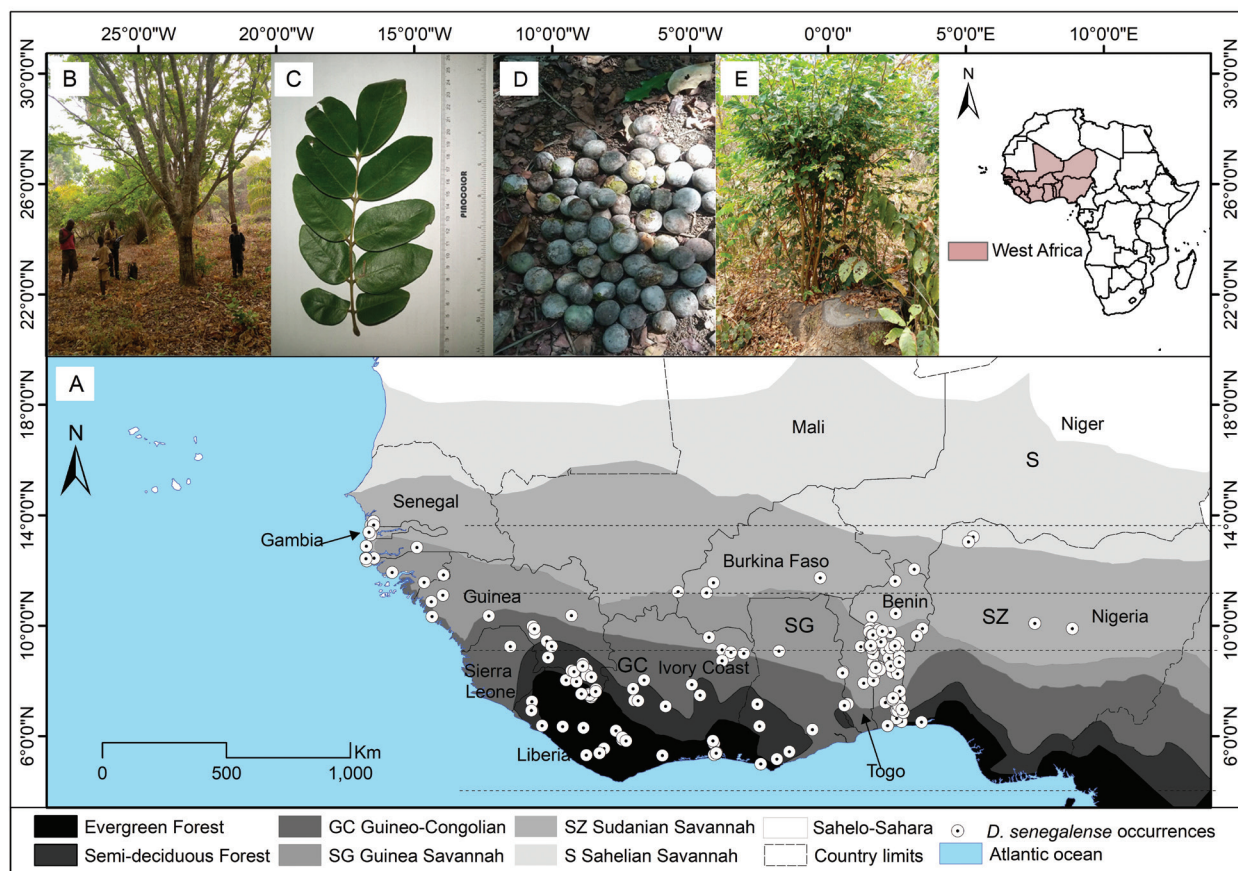


Figure 1. A. Study area with distribution of *Detarium senegalense* across West Africa (white circles). B. Tree. C. Leaf. D. Fruits. E. Suckers. Photographs B–E by G.H. Dassou in 2021.

reaching 10–40 m in height (Fig. 1B) (Akoègninou et al. 2006). The trunk is generally greyish and fairly smooth but covered with fine cracks. The wood is dark reddish brown, hard, and fine-grained. The leaves are bright green, pinnate and have 10 alternate leaflets, which are oval to elliptical, thinly coriaceous, or papery, usually 4–6 cm long and 2.5–3 cm wide, with rather few translucent gland-dots (Fig. 1C). The inflorescence is a panicle or loose axillary fascicle, dense and lax. The apetalous flowers have a calyx with 4 sepals, creamy white, in bud glabrous or sparsely pubescent outside, and 10 stamens. The ovary is ellipsoid, ca 2 mm long, densely hairy, 1-celled, style 3–4 mm long, arched. The fruit is a globose or subglobose drupe, slightly flattened about 5–6 cm in diameter, thick, fleshy (Fig. 1D), and it is divided into three main parts: (i) dark green epicarp, hard for immature fruits, light green tending to brown and brittle for ripe fruits, cracks at maturity, (ii) greenish mesocarp (pulp) intertwined with fibres inserted on the core, (iii) voluminous, woody core covered with fibrous meshes and enclosing a single ovoid and flattened seed of dark brown colour. Flowering occurs from February to May, and fruits take about five to six months to mature. The fruits are dispersed mainly by humans, monkeys, rodents, and parrots (Kouyaté and Lamien 2011). *Detarium senegalense* also holds a high potential to shoot forth suckers (Fig. 1E).

Species occurrence data

Occurrence data were gathered from two sources: online repositories and previously published data. Online data included the records from the Global Biodiversity Information Facility (GBIF.org 2021) and RAINBIO (Dauby et al. 2016). These occurrences were cleaned by removing duplicates and records without geographic coordinates. In addition, older occurrences collected before 1980 were removed to reduce the effects of temporal bias and match occurrence to the climate datasets (Idohou et al. 2017). As for previously published data, occurrences were extracted from two papers, namely Dangbo et al. (2019) and Diop et al. (2010). These coordinates were obtained by georeferencing the maps and digitizing the datapoints. To avoid occurrence bias, the global gazetteer v.2.3 (<http://www.fallingrain.com/world>) was used to assign digital coordinates to the occurrences (Hemami et al. 2020). We projected these coordinates on Google Earth v.7.1 to ensure they matched the target localities. Finally, all occurrences were combined, and we used the occurrence rarefy tool of Spatial Analyst in ArcGIS v.10.8 to reduce autocorrelation among the occurrences. Thus, we kept only one point within each grid cell (5 × 5 km) to be consistent with the environmental layers. Overall, after the cleaning process, 220 occurrences were used to run the models across West Africa: 175 from GBIF, 36 from RAINBIO, and 9 from the two papers (Supplementary material 1).

Environmental data

A total of three sources of environmental layers (bioclimatic, edaphic, and topography) were used. Past, current, and future climatic data were obtained at the spatial resolution of 2.5 minutes (~5 km at the equator) from WorldClim v.2.1 (Fick and Hijmans 2017). The edaphic (Leenaars et al. 2014) whereas elevation variables were taken from the digital elevation model (ASTER DEM) (Fick and Hijmans 2017). Slope data was generated from Google Earth Engine (Gorelick 2013) using a West African boundary. The current variables layers were derived from 1950–2000 climate data (Hijmans et al. 2005). For the past projection, bioclimatic variables layers were obtained from the MIROC-ESM model for the Mid-Holocene (MH, about 6000 years ago) and the Last Glacial Maximum (LGM, about 22,000 years ago). As for the future projection, the MIROC6 model was used to be consistent with the past projection. MIROC are advanced climate models developed by the Atmosphere and Ocean Research Institute (AORI) of the University of Tokyo (Tatebe et al. 2019). The benefit of MIROC6 models is that they have improved climate projections (temperature and precipitation), advanced physical processes, and comprehensive earth system modelling (Tatebe et al. 2019). Past and future layers were also downloaded from the WorldClim website (Fick and Hijmans 2017). The suitable areas were projected under two climate scenarios, ssp245 and ssp585, for the year 2050 (average for 2041–2060). The downloaded variables cut across WA and were resampled at 5 km. We removed four bioclimatic variables (bio8, bio9, bio18, and bio19) because of discontinuities between neighbouring pixels for the African continent (Montoya-Jiménez et al. 2022). The bioclimatic data consisted of 15 bioclimatic variables (Supplementary material 2). Then, we performed the Pearson correlation and jackknife tests (Supplementary materials 3 and 4) using the R package usdm v.2.1-6 (Naimi 2017). These two tests were used to exclude highly correlated variables with the coefficient of correlation (r) value of $[0.7]$ and to highlight those with high contribution. The final candidate factors were selected after reviewing the literature to determine which variables were ecologically significant for the species.

Modelling technique

We modelled the past, current, and future distributions of *D. senegalense* in West Africa. Four machine learning methods were used for this purpose, and the results were averaged for the predictive models. These methods included generalized additive models (GAM) (Wood 2006), generalized linear models (GLM) (Hastie and Tibshirani 1990), maximum entropy (MaxEnt) (Phillips et al. 2006), and random forest (RF) (Breiman 2001). These models were chosen for their effectiveness and robustness (Rong et al. 2020; Daï et al. 2023). The RF is a learning technique that constructs several decision

trees during training and outputs to the class. GAM is a statistical model that is used to link response variables to predictor factors (Wood 2006). The GLM model describes the relationship between the dependent and independent variables (Hastie and Tibshirani 1990). The MaxEnt technique is a probabilistic model that aims to find the probability distribution with the highest entropy (or the least uncertainty) given specific restrictions (Phillips et al. 2006, 2017). All models were run with the R package sdm v.1.1-8 (Naimi and Araújo 2016). Environmental factors were used as independent variables, whereas point locations (geographical coordinates) were used as dependent variables. We also used 10^3 pseudo-absence points since we do not have the real absence data. Furthermore, the occurrences were split into two samples where 70% were used to train the models and 30% to test them. To increase the models' accuracy, each model was replicated 10 times with subsampling and bootstrapping. We assessed the accuracy and the performance of the models using the area under the receiver operating characteristic curve (AUC) and the true skills statistic (TSS) (Allouche et al. 2006). The AUC provides the probability that the predictive power of a model is better than random prediction ($AUC = 0.5$) (Swets 1988). A model with an AUC value close to 1 ($AUC \geq 0.75$) is considered to be a good fit. As for TSS, values range from -1 to 1 and values close to 1 indicate the high performance of the models.

Range dynamics, direction of range shifts, and conservation status

We evaluated the dynamics of the suitable areas and the direction of range shifts using SDMtoolbox v.1.0b (Brown 2014). This toolbox is a python-based GIS software that is capable of describing the magnitude and direction of the predicted change over time by summarizing the core shifts in the species distribution reducing the distribution variation to a single centroid (central) point and generating a vector file (Brown 2014). In our case, the range shifts, as well as range dynamics, were assessed by comparing Mid-Holocene (MH)-current, Last Glacial Maximum (LGM)-current, current-ssp245, and current-ssp585. We also evaluated the dynamics of the suitable areas using Distribution Changes Between Binary SDMs (Brown 2014). The process was the same as described above but here the tool generated a single layer in TIF format and an Excel sheet that held the statistics. Overall, four classes of habitats were automatically generated: contraction, expansion, areas of no change or stability, and no occupancy areas or unsuitable.

The conservation status of *D. senegalense* was evaluated based on the IUCN criteria, especially B. We determined the extent of occurrence (EOO) and the area of occupancy (AOO) with the R package ConR v.1.3.0 (Dauby and Lima 2023). The EOO is a polygon that can be drawn to encompass all the known present occurrences of a species (IUCN 2012). The AOO is related to the area covered by

the number of occupied cells of a grid for a given resolution (IUCN 2012). In this study, we considered grid cells of 2 km², as recommended by IUCN guidelines (IUCN 2024). In addition, the diverse threat levels were measured by estimating the number of locations in protected areas. For this purpose, the occurrence of the species within the West African boundary (<https://geoportal.icpac.net>) and within protected areas (World Database on Protected Areas, UNEP-WCMC 2023) was used.

RESULTS

Factors affecting *D. senegalense* distribution and model accuracy

Overall, five variables were identified to influence the distribution range of *D. senegalense* (Fig. 2A). These variables were related to temperature and precipitation. Isothermality (bio3) was the variable that contributed the most (41.10%). The occurrence probability of the species reached its maximal value when isothermality values were close to 100 (Supplementary material 5). This variable was followed by the Precipitation of Wettest Month (bio13, 21.50%) and the Precipitation Seasonality (bio15, 19.23%). For bio13, the occurrence probability of the species increased when the bio13 values increased. In contrast, species occurrence decreased when the bio15 values varied by around 35%. The Temperature Annual Range (bio7, 10.60%) decreased the occurrence probability of the species with bio7 values below 75 mm (Supplementary material 5). Even though bio7 had a minor impact on species distribution, the occurrence probability of the species tended to increase between values of 10°C and 40°C (Supplementary material 5). Precipitation of Driest Month (bio14) showed the lowest contribution (7.57%). The performance and accuracy of the models showed an average area under the curve (AUC) of 0.92 and a TSS value of 0.73 (Fig. 2B), indicating that the models are of excellent quality.

Potential suitability distribution of *D. senegalense* under past, current, and future climatic conditions

The extent of suitability shown for the four classes (expansion, unsuitable, stable, contraction) for the five time periods (LGM, MH, current, ssp245, ssp585) is documented in Supplementary material 6. In the past, notably at the LGM, the stable ranges of *D. senegalense* distribution, estimated at 1,183,095.65 km² or 21.30% of the study area, mainly occurred from Nigeria to Sierra Leone, and from the Guinean savannah to the evergreen forest ecological zones (Fig. 3A). Overall, *D. senegalense* was found across the SZ to GC zones of Nigeria and Benin, in the SG and GC zones of Togo, and from the SG to the evergreen forest zone of Ivory Coast. The species was also found from the GC to the evergreen forest zone of Guinea and Sierra Leone and the evergreen forest zone of Liberia.

A very slight range expansion of 241,458.47 km² or 0.16% was observed during this period, mainly in the extreme west of Guinea. Meanwhile, the main part of the study area (3,803,962.10 km² or 66.15%) was unsuitable (Fig.

3A, F). The species lost an extent of 807,233.78 km² or 12.39% from the LGM to the current day.

The MH period exhibited a constant favourable range of 1,362,492.32 km² or 21.50% with an unsuitable range of

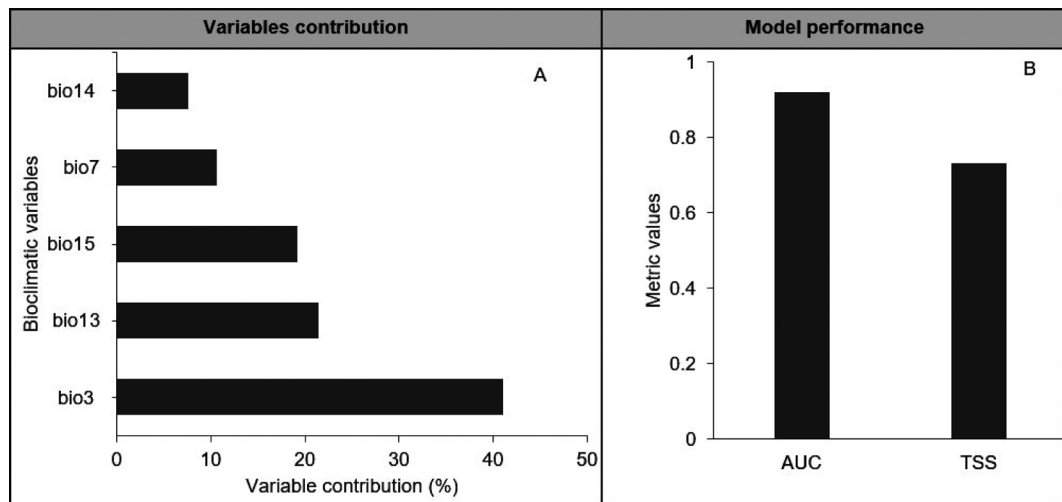


Figure 2. Diagram showing the contribution of the main variables and the performance of the model. **A.** Contribution of the variables involved in the model. Each variable is represented by a code: bio3 = Isothermality, bio7 = Temperature Annual Range, bio13 = Precipitation of Wettest Month, bio14 = Precipitation of Driest Month, bio15 = Precipitation Seasonality. **B.** Performance of the four algorithms. Values in the y-axis represent the average of 10 repetitions related to the two metrics. AUC = Area Under the Curve and TSS = True Skill Statistic.

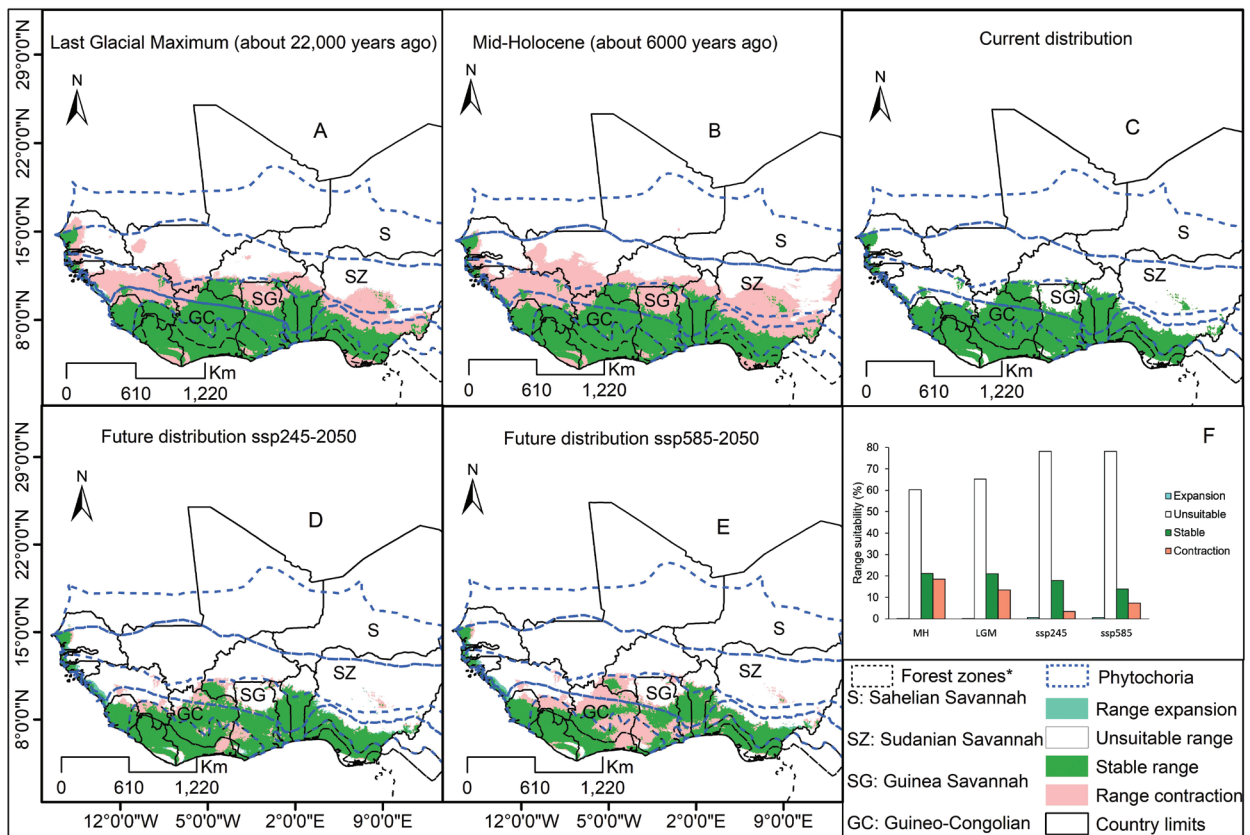


Figure 3. Dynamics of habitat suitability for *Detarium senegalense* across West Africa. **A.** Last Glacial Maximum (about 22,000 years ago). **B.** Mid-Holocene (about 6000 years ago). **C.** Current distribution. **D.** Future distribution ssp245-2050. **E.** Future distribution ssp585-2050. **F.** Range suitability.

3,885,769.34 km² or 60.10% (Fig. 3B). If we compare the MH to the current period, there was no discernible rise in the stable distribution range. The increase was estimated at 62,067.80 km² or 0.03% of the total study area (Fig. 3B, F). The contraction range of the species' distribution area was estimated at 725,420.54 km² or 18.37%.

At present, *D. senegalense* occurs in a large geographical range across Senegal, Guinea, Guinea-Bissau, Sierra Leone, Liberia, Gambia, Ivory Coast, Ghana, Burkina Faso, Togo, Benin, and Nigeria, and spreading across four ecological zones: Guineo-Congolian (GC), Guinea savannah (SG), Sudanian savannah (SZ), and very lower part of the Sahelian savannah (S) zones (Fig. 3C). The species occupies an extent of 1,048,558.40 km² in West Africa. These suitable areas or stable areas for *D. senegalense* distribution under current climatic conditions are located between 5°00'00"N–11°00'00"N and 10°00'00"W–5°00'00"W in the GC and SG zones (Fig. 3C). Countries such as Ivory Coast, Nigeria, Benin, Togo, Ghana, Liberia, and Sierra Leone showed the largest stable ranges. The countries where *D. senegalense* was less represented are Burkina-Faso, Guinea-Bissau, Guinea, Gambia, and Senegal. Overall, 3,954,573.16 km² of the total West Africa was not suitable for the species under current conditions.

Regarding the potential distribution of *D. senegalense* in the future, the stable ranges were 506,147.78 km² or

17.70% under ssp245 and 157,558 km² or 13.98% under ssp585 by horizon-time 2050 (Fig. 3D, E). Results also showed that the unsuitable range predicted for the future appeared to be higher in both scenarios (ssp245 and ssp585) than in the LGM and MH periods respectively. These unsuitable areas were 5,342,985.84 km² or 78.70% and 5,551,460.57 km² or 78.13% under ssp245 and ssp585 respectively. However, these two scenarios showed much smaller contraction ranges than the two previous periods (LGM and MH), with 181,355.14 km² or 2.93% for the ssp245 scenario and 322,893.51 km² or 7.29% for the ssp585 scenario. At the same time, some slight expansions occurred estimating around 5,261.25 km² or 0.67% for ssp245 and 3,837.92 km² or 0.60% for ssp585. In terms of spatial distribution, suitable areas are expected in the SZ to the GC zones of Nigeria and Benin, in the SG and GC zones of Togo, and from the SG to the evergreen forest zone of Ivory Coast. However, the species' suitable areas have shrunk on both sides of the Ivory Coast-Ghana border, with a more pronounced loss in the ssp58 scenario.

Distributional shifts of the centroid of *D. senegalense* in West Africa

The centroid of the suitable area for *D. senegalense* revealed different patterns of range change shift direction (Fig. 4). In past, especially during LGM, range shift directions

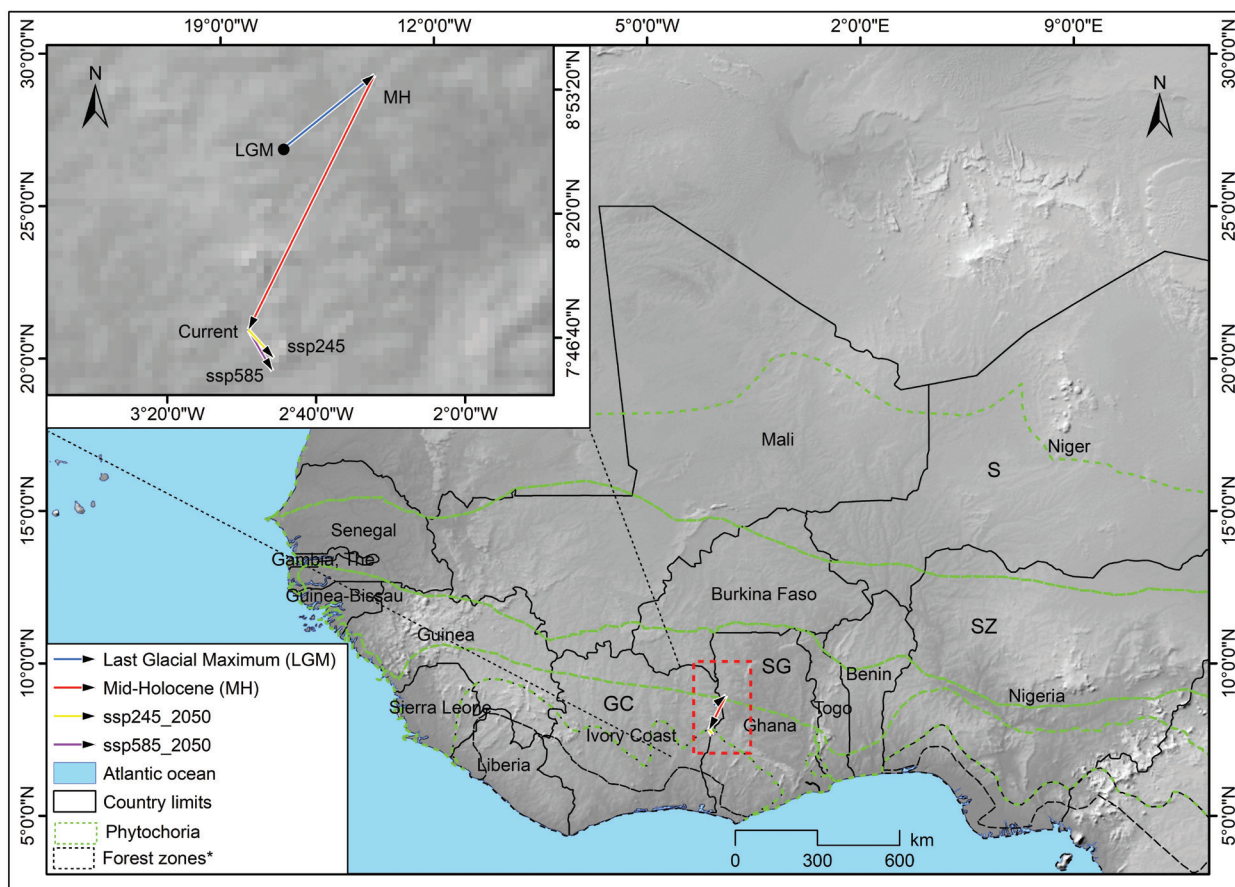


Figure 4. Range shift direction under past (blue and red arrows) and future scenarios (yellow and purple arrows). S: Sahelian Savannah, SZ: Sudanian Savannah, SG: Guinea Savannah, GC: Guineo-Congolian.

tended to be more longitudinal rather than latitudinal, with a north-eastern shift for LGM and a south-western shift for MH. However, both future scenarios showed range shifts to the south-east (Fig. 4). The current centre of distribution of *D. senegalense* was predicted to be in the extreme east of Ivory Coast (Fig. 4).

Distribution analysis of *D. senegalense* within protected areas (PAs) and its conservation assessment

All PAs located between 6°N–13°N and 12°W–10°E were currently suitable for the species (Fig. 5). The models indicated that all PAs in Ivory Coast and Liberia are suitable for the species. In Benin, the PAs suitable for *D. senegalense* were those in the SG and GC zones. There

were no suitable areas in the SZ, including the Pendjari and W parks. Similar observations showed that the PAs in Nigeria, Togo, and Ghana that are currently suitable for *D. senegalense* were located in the SG and GC zones, but more predominantly in the central east and south of the GC zone and in the west of the SG zone of Nigeria, in the south-east of the SG zone and throughout the GC zone of Ghana, and from halfway the SG zone to the GC zone of Togo. In Guinea, the suitable PAs were located in the south-east of the country in the SG and GC zones. Only the PAs along the coast of Senegal, Guinea-Bissau, and Gambia were capable of hosting the species in the present day. In addition, the PAs in the SG zone of Burkina Faso were suitable for the species under current conditions.

According to the future scenario (ssp245), most of the protected areas that are suitable under current conditions

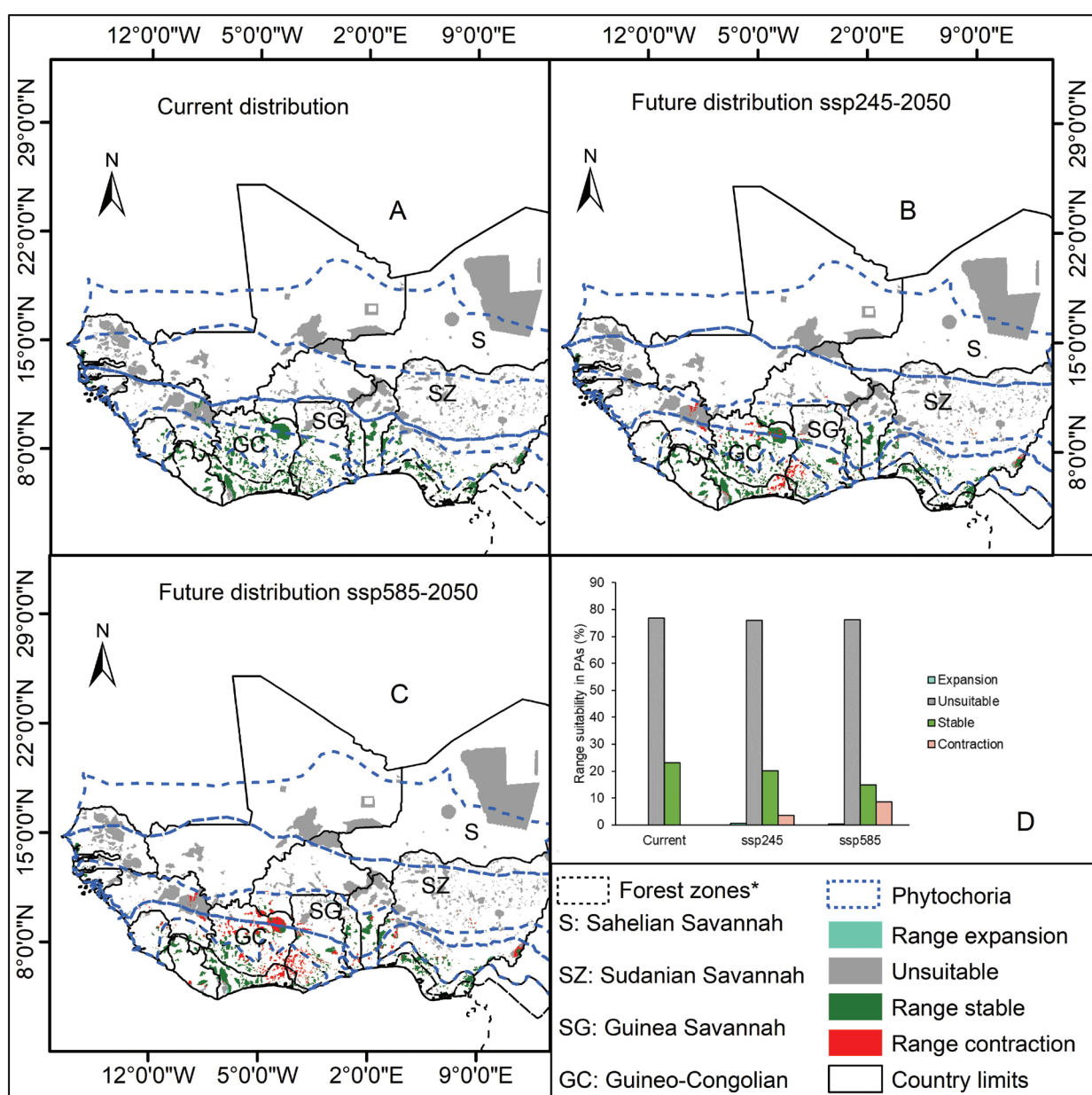


Figure 5. Spatial distribution of *Detarium senegalense* in protected areas under current and future scenarios.

should also be suitable for the species by 2050. However, some unsuitable protected areas are predicted under this scenario. These are located mainly in the south-west and north-west of Ghana and the south-east and north of Ivory Coast, in the SG and GC zones respectively. In addition, some unsuitable PAs are predicted to a slight extent in the SZ zone to the east of the GC zone in Nigeria and in the east of the SG and GC zones in Guinea. The extent of suitability related to each class within the protected areas is provided in Supplementary material 6. The number of protected areas by country as well as their extent were also quantified. Overall, the models indicated that in the present conditions, only 202,569.67 km² or 22.90% of the 2011 PAs of West Africa are suitable for the species. In contrast, 698,554.08 km² or 77.10% of the total extent (i.e. 901,123.75 km²) is not suitable. Moreover, 98,915.92 km² or 21.01% and 27,573.05 km² or 14.60% could be suitable under ssp245 and ssp585 by 2050 respectively. Significant contraction was observed under the ssp585 scenario with 21,714.24 km² or 8.61%. The contraction predicted under ssp585 was 145,798.37 km² or 2.50%. Suitable areas or stable habitats were found especially in Liberia, central and southern Sierra Leone, in the GC zone of southern Nigeria, in the SG zone of Benin and Togo and the south-west of Ivory Coast, and in a few protected areas in central and south-eastern Ghana. The expansion of habitat was estimated at around 413.18 km² or 0.51% and 468.27 km² or 0.35% under ssp245 and ssp585 respectively. As for

unsuitable areas, the estimations were 698,554.08 km² or 77.10% under current conditions. Future scenarios were also high with 655,996.27 km² or 75.98% for ssp245 and 655,941.18 km² or 76.44% under ssp585 by 2050.

The status of *D. senegalense* based on IUCN criteria across West Africa was documented in Fig. 6. The results showed an EOO of 1,958,696 km² (> 20,000 km²) and an AOO of 668 km² (< 2,000 km²). The large EOO points towards Least Concern, while the AOO could indicate Vulnerable (VU). However, the results also indicated that 30.8% of the 220 unique occurrences are located within 44 protected areas. Across the study area, we found 130 subpopulations (considering a 2 km² radius) and 151 locations (considering a grid size of 10 km²). Therefore, the species can be considered as Least Concern in West Africa.

DISCUSSION

Importance of climatic factors on species distribution and model performance

Environmental factors play an important role in forest establishment and persistence (Greve et al. 2011). As a result, under climate change, a set of factors that favour the distribution of a given plant species, particularly multipurpose trees such as *D. senegalense*, may help

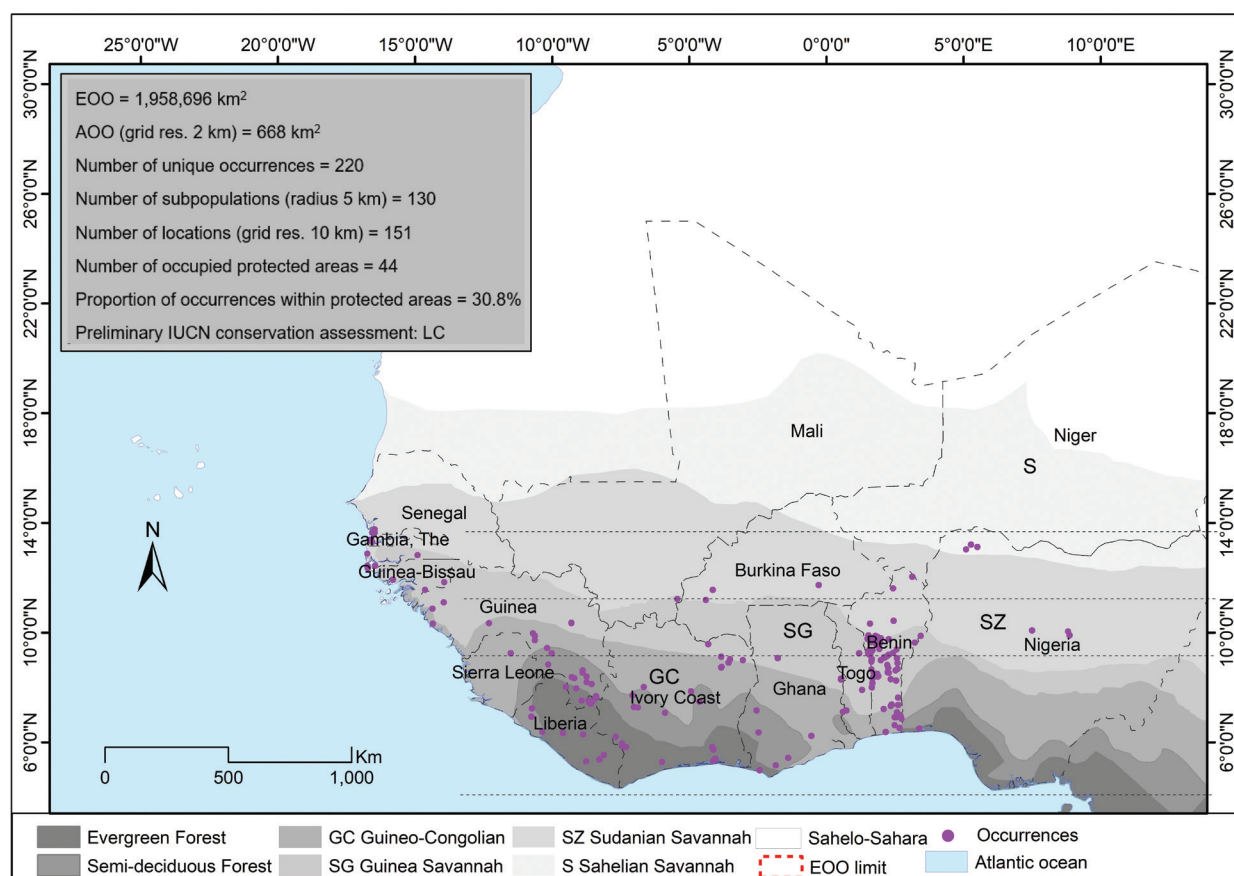


Figure 6. Conservation assessment of *Detarium senegalense* based on IUCN criteria across West Africa.

elucidate its resilience. In this study, climatic factors (temperature and precipitation) were the major variables that explained the species distribution in West Africa consistent with the ecological requirements listed by Diop et al. (2010). However, this finding differs from that of Agbo et al. (2019) who found that soil factors (cation exchange capacity) were important for the distribution of the related species *D. microcarpum* in Benin. Even though soil properties are recommended in plant modelling (Hengl et al. 2017; Zuquim et al. 2020), their incorporation is meaningful in local contexts in contrast to regional ones, as is the case in this study (Pearson and Dawson 2003).

The distribution of *Detarium senegalense* throughout West Africa was mainly affected by isothermality (bio3). Overall, isothermality refers to how similar the average daily maximum and minimum temperatures are throughout the year (O'Donnel and Ignizio 2012). Here, values were close to 100, indicating that the species preferred areas with consistent diurnal temperatures throughout the year. This factor is a determinant of plant distribution in tropical areas including West Africa (Huang et al. 2021). In natural ecosystems, the species is primarily distributed along rivers in gallery forests with an annual precipitation of 800 to 1800 mm, in contrast to *D. microcarpum*, which is more commonly found in open savannah (Dangbo et al. 2019; Houénou et al. 2022). Our findings also showed that species occurrence increased when the precipitation during the wettest month (bio13) increased, which explains why species are more common in rainy ecosystems. In contrast, species occurrence probability decreased when the precipitation of the driest month (bio14) was around 75 mm. Similarly, the occurrence probability decreased for precipitation seasonality (bio15) values of around 35%. This explains how a slight variation in precipitation in a season, particularly during the dry seasons, could influence species seed dispersal, which is facilitated by water and animals. The annual temperature range (bio7) had a minor impact on species distribution, but the occurrence probability of the species increased for temperatures between 10°C and 40°C. These findings suggested that the species may have adapted to the wide range of temperatures under climate change but more research is needed to understand how the species might respond to drought, including germination rates, growth rates, and overall plant health. Moreover, the model performance revealed an AUC value of 0.92, indicating the robustness of the models (Idohou et al. 2017; Agbo et al. 2019). Therefore, they could be considered steady and adequate for constructing the potential ecological niche and conservation ranges of *D. senegalense* through its geographical distribution (Favi et al. 2022).

Impact of climate on species distribution

The current study assessed the dynamics of *D. senegalense* distribution from the past to the predicted

future suitable areas. In general, our findings revealed that the suitability range was relatively stable from the last glacial maximum to the present day. In addition, suitable habitats occurred from Nigeria to Sierra Leone, and from the Guinean savannah to the evergreen forest ecological zones. However, a study of a population in Togo indicated that adult individuals are rare and that there is a low regeneration rate, and thus a predominance of small-diameter trees (Dangbo et al. 2019). Similar results were recently found in Benin by Houénou et al. (2022) and this shows that modelling results need to be considered with caution. Indeed, human pressures on tree species in the Sub-Saharan region, such as illegal cutting and agricultural expansion, have increased ecosystem vulnerability to climate change, affecting their spatial distribution (Gross et al. 2018).

Moreover, the suitable areas of the species shifted from low latitudes to high latitudes from the Last Glacial Maximum to the Mid-Holocene. These findings are consistent with those of Saupe et al. (2019) about the high-latitude migration of tropical species as temperatures rise over geological ages. The Dahomey-gap, which was established during the Holocene, created a unique climate condition in the Guinean Gulf, allowing plant species to spread across a variety of climate zones (Salzmann and Hoelzmann 2005).

According to Trisos et al. (2022), West Africa is one of the most vulnerable zones to climate change. Since the Industrial Revolution, the average annual temperature has risen above 1.1°C, affecting already the growth and productivity of plant species. Global average annual temperature is expected to reach 5°C by 2100 under worse scenarios (Tokarska et al. 2020; Chai et al. 2021). In this context, the models predicted a moderate range decrease for *D. senegalense*, especially under the pessimistic scenario ssp585. In terms of spatial distribution, suitable areas are expected in the SZ to GC zones of Nigeria and Benin, in the SG and GC zones of Togo, and from the SG to the evergreen forest zone of Ivory Coast. Previous studies predicted that the congeneric species *D. microcarpum* could expand in suitable areas (Agbo et al. 2019). Indeed, co-occurring species may react differently in the same envelop spaces, contracting or expanding their suitable areas in response to global climate change (Hällfors et al. 2016). This could be supported by the acclimatization or phenotypic plasticity of species to escape extinction (Silva et al. 2019). Given the increasing warming climate conditions predicted in Africa, most native plant species will experience a decline in the future, e.g. *Parkia biglobosa* (Jacq.) R.Br. ex G.Don (Ayihouenou et al. 2016), and *Borassus aethiopum* Mart. (Salako et al. 2019). Therefore, the hypothesis of a warming climate inducing a decline in the distribution range of a plant species seems to be well-supported (Li et al. 2019; Imorou 2020). Moreover, suitable habitat tends to shift to the south-east (wettest areas or low latitudes) in response to future climate scenarios. *Detarium senegalense* usually occurs in West African riparian forests (Arbonnier 2009), from Upper

and Lower Guinea to the Dahomey Gap, and in Central Africa (Akoègninou et al. 2006; WFO 2024). This region of the continent has a climate with an average annual precipitation of around 1,800 mm, which is ideal for *D. senegalense*, which has moderate water requirements.

Conservation status, implications for cultivation, ecological restoration and efficient conservation, and model limitations

Ecological niche modelling or species niche modelling is a powerful and widely used tool to predict the occurrence of many taxa based on environmental factors (Guisan and Zimmermann 2000). In this study, ENMs were used to have a clear picture of the past, present, and future distribution of *D. senegalense*.

The study also addressed the conservation status of the species under current conditions. Our models predicted the suitable areas for the conservation of the target species were located in the GC zones of Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, Benin, and Nigeria. Furthermore, most protected areas that are suitable under current conditions should be suitable for the species by 2050, except for the south-west and north-west of Ghana and the south-east and north of Ivory Coast, in the SG and Guinean climatic zones, respectively. Based on these findings, we recommend both in situ and ex situ conservation, as the species' suitable habitats are expected to decrease both within and outside of protected areas. According to BGCI and IUCN (2019), the species is of Least Concern. In addition to this statement, they indicated that there are no significant current or future threats to this species. Our findings also classify the species as Least Concern. However, only 30.8% of individuals were found within protected areas. The most important populations are distributed outside protected areas where they are affected by the encroachment due to the agriculture expansion and tree cutting (Dassou et al. 2023). Previous studies also revealed that the commercial exploitation of timber and medicinal products, associated with the growing regional trade of fruits and seeds, and a low potential for natural regeneration of seeds constitute significant threats to *D. senegalense* (El-Kamali 2011; Houénon et al. 2021, 2022). Nowadays, traditional agroforestry systems are another way to preserve tree species within agricultural lands (Sharma et al. 2016). It is also possible to introduce the species in well-protected community and sacred forests in the GC zone. However, for conservation to be effective, greenhouse experiments must be conducted first, as the species has a low natural regeneration. The outputs of these experiments will be a mainstay for the publication of technical manuals for nursery management. The vision would be to share these techniques with various conservation organisations (NGOs, forestry departments) to facilitate seedling production for the National Days of the Tree in its distribution range and to promote the installation of plantations of the species. Implementing

these participatory management policies across local communities and introducing them into agroforestry systems will safely foster species sustainability (Peters and Simaens 2020). The introduction of the species into the botanical gardens must be also envisaged.

Given the usefulness of species distribution models in conservation research (Stockwell and Peterson 2002), the findings of this study are important since they improve insights into the potential changes in *D. senegalense* distribution. The success of model predictions in this study was likely due to the sample size and wider range of data collected, reducing inaccurate predictions caused by incomplete data (Wang et al. 2021). Even though the models showed interesting performance, models can be improved including physiological data, seed dispersal capacity of the species, and local adaptation data (Engler et al. 2012; Adoukonou-Sagbadja et al. 2023). Recently, some new approaches have emerged incorporating intraspecific variation data into the models. For instance, in Benin, the response of the population of *Pterocarpus erinaceus* Poir. to climate change was assessed using this method (Biaou et al. 2023).

CONCLUSION

By reducing areas with suitable climatic conditions, climate change may disrupt key ecological interactions and compromise species sustainability and the dynamics of populations of plants in their geographical ranges. This study revealed that the current suitable environmental areas for *D. senegalense* would contract under future climate change scenarios across West Africa. The increasing unsuitability was also predicted in protected areas, pointing to a need for setting up sustainable management plans. Isothermality and precipitation were shown to be the main factors that govern the distribution of the species and provided insight into their ecological requirements. Given the announced decline in habitat suitability of *D. senegalense* in the future, associated with threats due to overuse for seed trading, timber, and medicinal products, and the low regeneration potential of this species, in situ conservation may not be a one-stop solution but should be complemented with ex situ conservation. More broadly, the findings of this study could lead to consistent knowledge on the future potential distribution of West African species and appear fundamental to reducing species loss through early sustainable management strategies.

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SUPPLEMENTARY MATERIALS

Supplementary material 1

Occurrences dataset.

<https://doi.org/10.5091/plecevo.122470.suppl1>

Supplementary material 2

Description of the environmental variables.

<https://doi.org/10.5091/plecevo.122470.suppl2>

Supplementary material 3

Remaining variables after the Pearson Correlation test.

<https://doi.org/10.5091/plecevo.122470.suppl3>

Supplementary material 4

Variables contributions obtained from the jackknife test.

<https://doi.org/10.5091/plecevo.122470.suppl4>

Supplementary material 5

Average of the response curves for the four models used.

<https://doi.org/10.5091/plecevo.122470.suppl5>

Supplementary material 6

Estimations of suitable area in km² for the whole study area and protected areas.

<https://doi.org/10.5091/plecevo.122470.suppl6>