Habitat suitability of subpopulations of Adansonia digitata L. in West Africa: Implications for conservation and domestication

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ABSTRACT

For an adaptive policy to be effective, it is crucial to divide species populations into subpopulations, especially for species with diverse environmental conditions. In this study, occurrence data of Adansonia digitata L., a multipurpose tree species, were collected from the Global Biodiversity Information Facility portal (1513), fieldwork (421), and other studies (195) throughout the West Africa scale. Principal Component Analysis was used to discriminate the sample into four subpopulations based on 19 bioclimatic variables, elevation, and soil data. Using a Stack Species Distribution Modelling (SSDM) approach, nine modeling algorithms were performed for each subpopulation and the global sample. The results showed that the distribution of subpopulations was latitudinally dependent, with niches differentiated and not overlapping. Environmental variables contributed differently according to the subpopulations. Overall, it was found that 47.63% of West Africa was unsuitable for the cultivation and conservation of the species, while 15.38% was highly suitable. Among the most suitable countries were Burkina Faso, Benin, Senegal, and Togo.

1. Introduction

Studies focused on suitable habitats and the impact of climate change on the future distribution of biodiversity are increasingly becoming a reliable tool to predict the impact of climate change on biodiversity. Several studies have been conducted and are ongoing on native plant species in Africa, as well as on non-timber forest products (NTFPs) (Sanchez et al., 2010; Birhane et al., 2020; Dimobe et al., 2020; Dimobe et al., 2022). Occurrences used to implement models sometimes considered each target species population as a single sample for the study countries. However, intraspecific morphological, physiological, and genetic characteristics are observed throughout the distribution range of these species (Assogbadjo et al., 2006; De Smedt et al., 2010; Fandohan et al., 2010; Assogbadjo et al., 2011). Consequently, failing to consider these variations could introduce bias in models (Hällfors et al., 2016).

Individuals within a population of the same species develop different strategies for survival against environmental constraints depending on the conditions they are exposed to (Fandohan et al., 2010). These

strategies can be transmitted to their descendants. However, intraspecific diversity is often unknown or only studied in limited samples and locations (Assogbadjo et al., 2009; Maguire et al., 2018; Chládová et al., 2019), especially in Africa where genetic studies on native trees are lacking. Nevertheless, intraspecific genetic diversity is crucial for addressing evolutionary ecology facing climate change uncertainty and biotic constraints (Prasad and Potter, 2017).

According to Smith et al. (2019), species-level niche models may overlook local adaptive circumstances, and species distribution models (SDMs) can be affected by the complexity of scheduling plant species dispersal and biotic interaction (Hällfors et al., 2016). Therefore, ecological niche models that incorporate local adaptive factors can provide insights into species responses to climate environments (Banta et al., 2012) and reduce management efforts (Hällfors et al., 2016).

The African baobab (*Adansonia digitata* L.) is a native multipurpose tree that occurs from the coast and forest stands with abundant rain and low temperature to the Sahel arid areas. Given its importance, its integration as a dietary protected agroforestry plant species in West Africa (Eyog-Matig et al., 2002), growing interest (Russo et al., 2019), and the

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potential impact of human and climate threats on its population (Birhane et al., 2020), it is crucial to scrutinize its management based on strong knowledge of its habitat for cultivation. The importance of the African baobab for the local populations justifies the numerical studies devoted to this species to promote its valorisation, cultivation, and lasting management (Eyog-Matig et al., 2002; Assogbadjo and Loo, 2011; Kebenzikato et al., 2015; Birhane et al., 2020). All plant parts of the species are useful for dietary, pharmacopeia, and cosmetic purposes (Kebenzikato et al., 2015; Russo et al., 2019). The most commercially valuable organs are leaves and fruits (Kebenzikato et al., 2015).

Several studies have assessed the morphological phenotype variation of this species in different locations (De Smedt et al., 2010; Sanchez et al., 2011; Munthali et al., 2012), suggesting an impact of the local environment. Genetic studies conducted in Kenya have shown differentiation between coastal and inland populations (Chládová et al., 2019). Consequently, a local adaptive strategy showing species plasticity and the variation of micropopulation response against climate conditions has emerged. This calls for the necessity to account for these variations in niche modeling to reduce bias. In the absence of formal genetic characterization at the scale of large populations, the use of environment variables prevailing on species occurrence could help discriminate subpopulations to improve predictive models.

An earlier study conducted at the continental scale by Sanchez et al. (2010) identified suitable habitats for the cultivation of the species and factors shaping its distribution. Globally, this study contributes to improving plant species valorization and management in West Africa. In particular, it aims to (i) determine potential subpopulations of A. digitata based on environmental variables and (ii) assess how taking these subpopulations into account improves habitat models for the species in West Africa. We hypothesize that (i) A. digitata may be more abundant in regions with a hot and dry climate, as it is adapted to surviving long periods of drought through its deep root system and thick, spongy bark; (ii) the tree may be limited in its distribution by temperature, with a preference for warm to hot climates; and (iii) *A. digitata* populations in different regions may be genetically distinct due to isolation and adaptation to local bioclimatic conditions. This could lead to the evolution of different subpopulations with unique characteristics that are adapted to their specific environment.

2. Material and methods

2.1. Study area

The study was conducted in West Africa, which is located between -15o and 15o W longitudes, and 5o to 26o N latitudes. Five main agroecological zones characterize West Africa : desert, arid, semi-arid, sub-humid, and humid (Gravel, 2016). This implies various environmental conditions, especially rainfall, temperature, vegetation, and soil. The total annual rainfall ranges from less than 200 mm in the Sahara Desert in the north to over 2000 mm in the coastal area in the south (Ojo et al., 2004), especially in the Guinean zone. The rainfall lasts for about 6–12 months from the south of 12 N latitude and less than 4 months in the arid and semi-arid areas in the northern part. The dense forest and Guinean savannas correspond to the humid zone, while the forest-savannas belong to the semi-humid zone in the south of 12° N. The Soudan and Sahelian savannas mainly cover the semi-arid zone and the Sahelian savannas cover the arid area (Bocksberger et al., 2016; Gravel, 2016). Boffa (2000) reported that diversified and vast agroforestry parklands also covered these latter areas.

2.2. Description of Adansonia digitata L

Adansonia digitata L. syn. Adansonia sphaerocarpa A.Chev. or baobab is a multipurpose savanna tree species belonging to the Malvaceae family (APG IV, 2016). It is a mesophanerophyte that can grow up to 25 m in height and has a maximum stem diameter at the breast height

of 20 m (Akoégninou et al., 2006). Its leaves are composed and digitate with an alternate phyllotaxis (Fig.1). The species flowers are large and white, and bats are their primary pollinators. Flowering usually starts before the rainy season and before the appearance of new leaves. It is considered a priority diet plant species in some subregions (Eyog-Matig et al., 2002).

2.3. Occurrence and environmental data

The species occurrence data were collected from various databases and covered West Africa. The first cleaning of the data consisted of the deletion of duplicated, doubtful, non-valid, and mismatched country occurrence coordinates. Overall, 2129 occurrence points of A. digitata were considered for this study after crosschecking and removing duplicated and incorrect occurrences. Of the 2129 occurrences, 71.07% (1513) were obtained from the Global Biodiversity Information Facilities (GBIF) database (http://www.gbif.org), and 28.95% (616) from extensive fieldwork in Burkina Faso, Benin, and Togo.

The study relied on environmental data, which comprised 19 bioclimatic variables, elevation derived from the Radar Topography Mission (SRTM) digital elevation model, and soil data. The bioclimatic and elevation variables were obtained from version 2.1 of the WorldClim database, accessed from https://www.worldclim.org/data/worldclim21.html (Fick and Hijmans, 2017). Soil types were sourced from version 1.2 of the Harmonized World Soil Database, accessible at http://www.fao.org/land-water/databases-and-software/hwsd/en/ (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). The bioclimatic variables, soil data, and elevation data were extracted using West Africa as a mask, and then converted into ASCII format with the aid of QGIS. A total of 21 environmental variables were employed in this study, comprising one categorical and 20 continuous variables (Table 1). All variables used in the study had a spatial resolution of 30 s (ca. 1 km).

2.4. Discrimination of species subpopulation

The discrimination of potential subpopulations of *A. digitata*, based on environmental variables considered here, was performed using the ''*FactoMineR*'' and ''*Factoshiny*'' packages in the R statistical software (Husson et al., 2020). The first two axes of the Principal Component Analysis (PCA) (Axis 1 = 52.50% and Axis 2 = 19.45%) allowed the discrimination of four subpopulations of the species in West Africa with a 95 % confidence interval of clustering. Thereafter, the identified subpopulations were subjected to Linear Discriminant Analysis (LDA) to measure the distance between them.

2.5. Global and subpopulation distribution modelling

All modeling analyses were performed using the R statistical software with the 'Stack Species Distribution Modelling (SSDM)'' package (Schmitt et al., 2017) for the global sample data at the species level and for each discriminated subpopulation. Habitat suitability models were generated using nine modeling algorithms: Generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), artificial neural networks (ANN), classification tree analysis (CTA), general boosting method (GBM), random forests (RF), support vector machine (SVM), and maximum entropy (MAXENT). Each modeling algorithm has its advantages and limitations. Combining several algorithms could improve the performance of models but also increase the computation time (Breiner et al., 2015; Breiner et al., 2018). For this study, all environmental variables were considered (Feng et al., 2019; Moukrim et al., 2020) instead of correlative analysis and the choice of variables, as done in several previous studies (Dimobe et al., 2020). The R Shiny web application (Chang et al., 2016) was used as a graphical interface for data loading, analysis, and results display.

To assess the predictive capacity of the models, the occurrence data were randomly split into 75–25% training and validation subsets ten
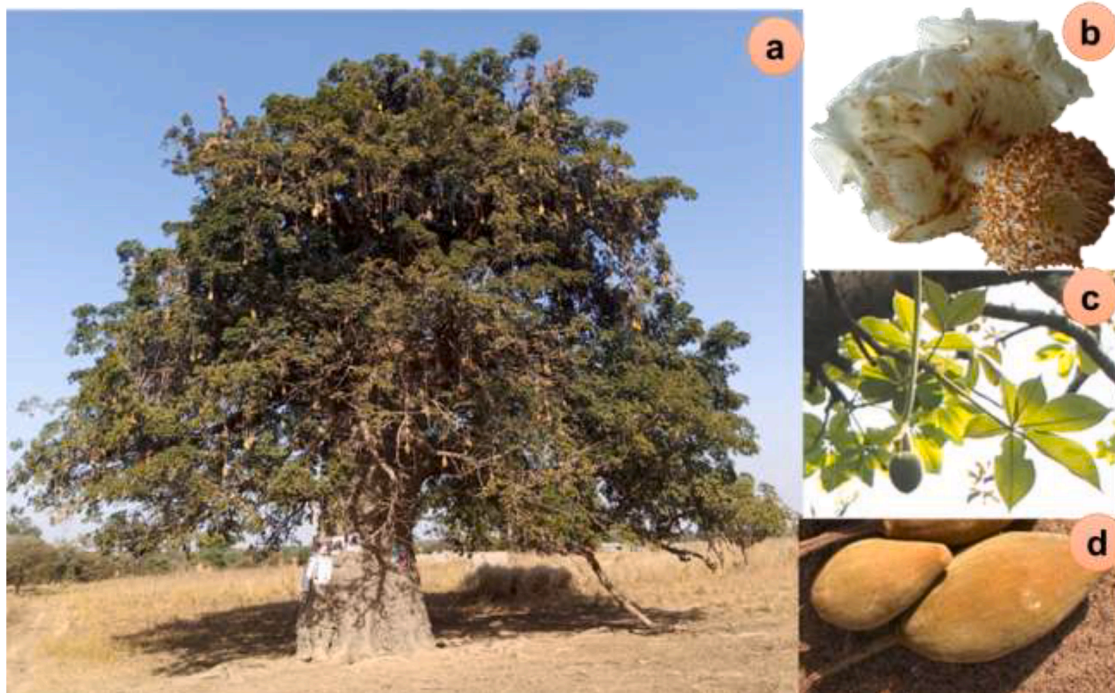
Fig. 1. Adansonia digitata (A: mature tree in an agroforestry parkland, B: flower, C: leafy branches with a young fruit, and D: dried fruits).

Table 1
List of environmental variables used in the study.

Codes	Variables	Units
Elev	Elevation	m
soil	Soil types	−
bio 01	Annual Mean Temperature	°C
bio 02	Mean Diurnal Range (Means of monthly (max temp - min temp))	°C
bio 03	Isothermality (BIO2/BIO7) (* 100)	%
bio 04	Temperature Seasonality (standard deviation × 100)	°C
bio 05	Max Temperature of Warmest Month	°C
bio 06	Min Temperature of Coldest Month	°C
bio 07	Temperature Annual Range (BIO5-BIO6)	°C
bio 08	Mean Temperature of the Wettest Quarter	°C
bio 09	Mean Temperature of the Driest Quarter	°C
bio 10	Mean Temperature of Warmest Quarter	°C
bio 11	Mean Temperature of the Coldest Quarter	°C
bio 12	Annual Precipitation	mm
bio 13	Precipitation of Wettest Month	mm
bio 14	Precipitation of the Driest Month	mm
bio 15	Precipitation Seasonality (Coefficient of Variation)	mm
bio 16	Precipitation of Wettest Quarter	mm
bio 17	Precipitation of the Driest Quarter	mm
bio 18	Precipitation of the Warmest Quarter	mm
bio 19	Precipitation of the Coldest Quarter	mm

times. Raster outputs of probability distributions were imported into QGIS to classify the habitat suitability of the species. Two maps were produced: one for global habitat suitability in West Africa and another for specific habitat suitability for each subpopulation. Suitable global habitats were mapped by merging subpopulation maps. This map was then compared with the one created using all the occurrence records at the species level.

The appropriate habitat was mapped based on the output of the binary map of presence/absence produced using the "10 percentile training presences"(Phillips and Dudík, 2008). Three habitat suitability classes were then defined across the study area using a threshold value (T) (Moukrim et al., 2020): $p \geq T$ corresponds to high probability of presence, $T/2 \leq p < T$ to mean probability, and $T/4 \leq p < T/2$ to low probability.

2.6. Model evaluation and validation

The relative contribution of each environmental variable to the model's accuracy was measured using Pearson's correlation coefficients (Thuiller et al., 2009). Pearson's correlation coefficient predicts the accuracy of the full model with a target variable and the one without a variable. The higher the value, the greater the influence of the variable on the model. The accuracy of the model was assessed using Area Under the Curve (AUC), Kappa, and True Skill Statistic (TSS) (Thuiller et al., 2009). In addition, the Symmetric Extremal Dependence Index (SEDI) was used as a complementary and better metric measure (Ferro and Stephenson, 2011; Wunderlich et al., 2019). Although the Odds Ratio Skill Score (ORSS) is considered better than SEDI, the present study justified the use of SEDI because only presence data were used for modeling, and real absence data was not required for ORSS computation (Wunderlich et al., 2019). The TSS and SEDI indices were computed based on the sensitivity (true positive fraction) and specificity values. The maximum value of SEDI is close to 1 when the model is perfect (Ferro and Stephenson, 2011).

To determine if the subpopulations discriminated are reliable, ENMTools (Warren et al., 2010) estimated pairwise measure of niche similarity using the output of species probability models. The niche similarity measure is based on Schoener's D and I indices, assuming respectability suitability scores are proportional to species abundance and suitability scores as a probability, with values ranging from 0 indicating no niche equivalence to 1 indicating absolute niche correspondence (Warren et al., 2010). Schoener's D value p above 0.95 supports niche conservatism, while values below 0.95 support niche divergence. Additionally, $p > 0.05$ shows that there is no more similarity (Zhao et al., 2019).

3. Results

3.1. Distribution of subpopulations

The PCA distinguishes four subpopulations of *A. digitata* in West Africa based on environmental variables, as shown in Figs. 2a and b. The analysis reveals that species individuals are discriminated along
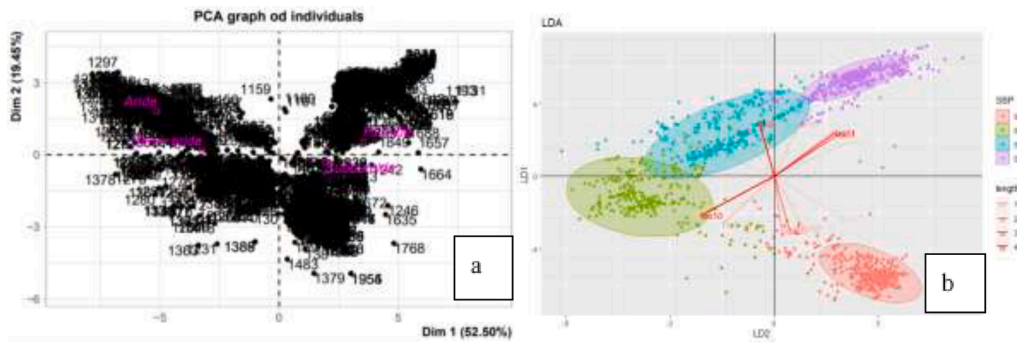
Fig. 2. Discrimination of A. digitata subpopulations using environmental variables: (a) Principal Component Analysis and (b) Linear Discriminant Analysis.

agroecological zones. Although there are some disparities between arid and semi-arid subpopulations, there still exists a strong connection between them. As can be observed in Fig. 2b, the LDA clearly highlights this relationship. In contrast, a significant difference exists between subpopulations of the humid zone in the southern part (hereinafter "sbp1"), and the arid zone in the northern part (referred to as "Sbp4"), of the region, as shown in Figs. 2 and 3. The geographical distribution of subpopulations across the West African region is presented in Fig. 4.

Visually, there is a significant difference between the subpopulations of the humid zone (Sbp1) and the others when all environmental variables are considered. The ANOVA two-way statistical analysis revealed a significant difference (*p-value=0.00*) among the four groups. However, a pairwise comparison of subpopulations shows that the mean values and the statistical difference significantly vary (p < 0.001).

The mean values of altitude for the subpopulations are presented in Table S1, with Sbp2 having the highest mean value and Sbp1 having the lowest. The mean annual temperature (bio 01), mean temperature of the wettest quarter (bio 08), mean temperature of the warmest quarter (bio 10), and precipitation of the wettest quarter (bio 16) are all highest in Sbp4 and lowest in Sbp2. in contrast, annual precipitation (bio 12) is higher in Sbp2 and lower in Sbp4.

Other environmental variables show different patterns across subpopulations. The mean diurnal range of temperature (bio 02), temperature seasonality (bio 04), maximum temperature of the warmest month (boi05), annual temperature range (bio 07), and precipitation seasonality (bio 15) all increase from Sbp1 to Sbp4, while isothermally (bio 03), mean temperature of the coldest month (bio 06), precipitation of the driest quarter (bio 17), and precipitation of the warmest quarter (bio 18) all decrease.

Despite significant differences between subpopulations, Sbp2 and Sbp3 have statistically similar mean values for the mean temperature of the driest quarter (MTDQ, bio 09). Sbp4 has the highest mean value, whereas Sbp1 has the lowest. Sbp3, like Sbp1, has a higher mean temperature of the coldest quarter (bio 11) than Sbp2.

The precipitation of the wettest month and the driest month (bio 13 & 14) was higher in Sbp1 than in other subpopulations. The lowest and comparable values were found in Sbp3 and Sbp4, respectively. The precipitation of the coldest quarter (bio 19) is higher in Sbp2 and lower in Sbp4. The mean values in Sbp1 and Sbp3 were comparable.

3.1.1. Model performance

Two types of results were obtained: the Stack Species Distribution Model (SSDM) and the Ensemble Species Distribution Models (ESDMs) for each subpopulation. The ESDMs demonstrated success, as indicated
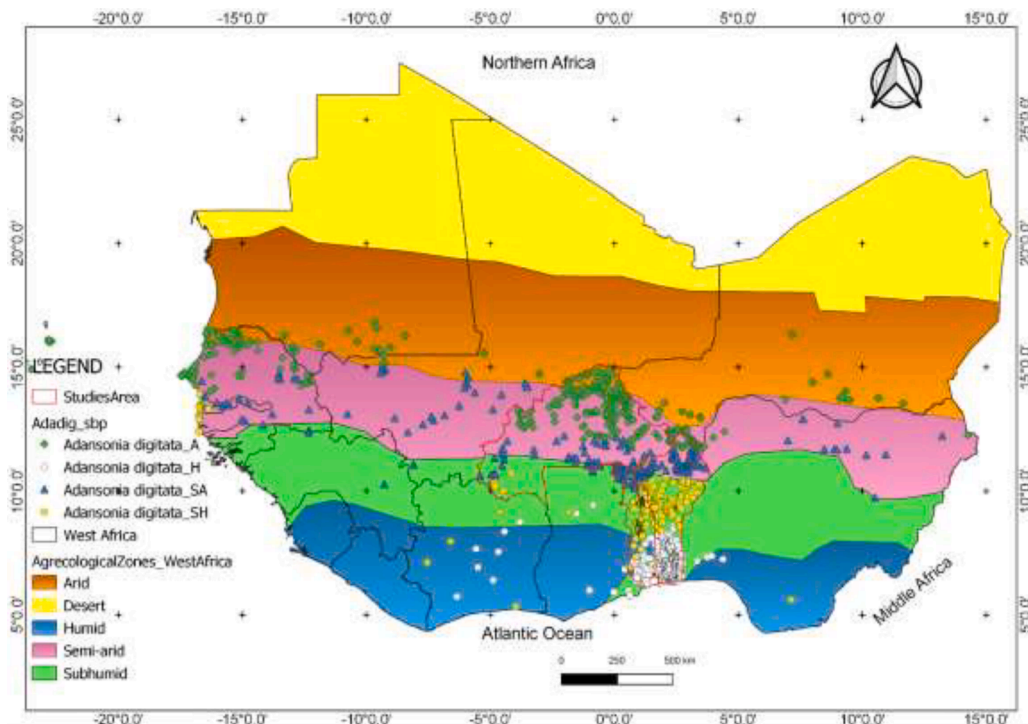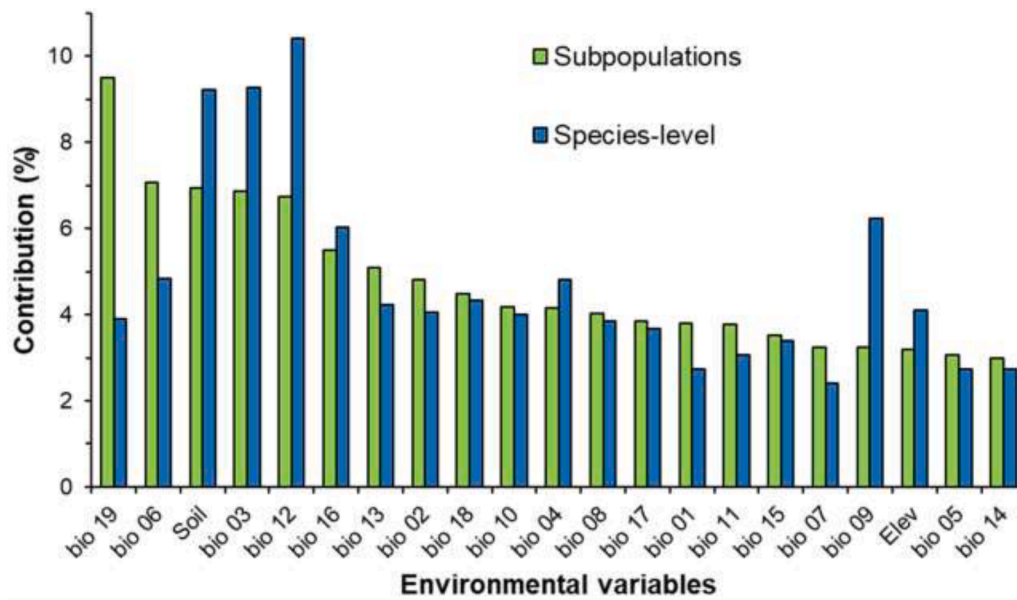

Fig. 3. Geographical distribution of Adansonia digitata subpopulations in West Africa.

Fig. 4. Contribution (%) of the selected environmental variables to the distribution of *Adansonia digitata* model in West Africa: subpopulations (green colour) and species level (blue colour).

by their high metric values (see Table 2). However, the predictive ability of Sbp3 (AUC=0.89, Kappa = 0.69) was comparatively weaker than that of the other models, where the AUC and Kappa values were both greater than 0.90 and 0.77, respectively.

Following the prediction of the SSDM, the employed metrics demonstrated good performance (p = 0.96 ± 0.09). This confirmed an ecological dissociation between subpopulations, as evidenced by the Marczewski-Steinhaus distance (Jaccard index) based on presence/absence data, Cj = 0.92 ± 0.21. Additionally, the subpopulation patterns were highlighted by the overall TSS and SEDI values, which corresponded to 0.94 and 0.98, respectively. Notably, the global model constructed using subpopulations was more accurate than the model created using all occurrences considered at the species level, with the latter model achieving AUC, TSS, and SEDI values of 0.89, 0.78, and 0.90, respectively.

3.1.2. The relative importance of environmental variables

The distribution pattern of *A. digitata* subpopulations is shaped by environmental variables, with varying contributions from one population to another. In general, the precipitation of the coldest quarter (bio 19, PCQ) is the variable with the highest contribution rate of 9.5. It is followed by the mean temperature of the coldest month (bio 06, MTCM), soil, isothermality (bio 06), and annual precipitation (bio 12) (Fig. 4). However, this trend changes when considering the model constructed using samples at the species level. In this case, PCQ and MTCM are less emphasized, with the most influential variables are annual precipitation, isothermality, and soil.

The model in the arid zone was shaped by three primary variables: soil, followed by precipitation of the coldest quarter (bio19) and mean temperature of the coldest month (bio06) (Fig. S1). In the humid zone,

the variable that contributed the most to the model was the mean temperature of the coldest month (bio 06, 13.73%). In the subhumid zone, the precipitation of the coldest quarter (bio 19) and isothermality (bio 03) were the most important variables of the model, with contributions of 16.45% and 12.53%, respectively. The contribution of bio 06 was minimal. The most influential variable in the semi-arid zone was annual precipitation (bio 12, 09.05).

3.1.3. Suitable habitats for A. digitata in West Africa

Fig. 5 depicts the distribution of suitable habitats for the subpopulations of *A. digitata* in West Africa. The "*10 percentile threshold*" for all subpopulations except for Sbp3 is 0.49. For Sbp3 it is 0.40. Probabilities (*p*) above the *10 percentile threshold* were considered highly suitable and correspond to 90% of occurrences, while *p* below the value *T* represents the remaining 10% of occurrences.

Of the four subpopulations, Sbp3 has the largest distribution range in the semi-arid zone, whereas Sbp1 and Sbp2 have the least distribution range in the humid and sub-humid zones (Fig. 5). The most suitable countries for the cultivation and conservation of the species are Burkina Faso, Benin, Togo, and Senegal (Fig. 5 & 6). Burkina Faso and Senegal are the most suitable countries for the cultivation and conservation of Sbp3 and Sbp4, while Benin is suitable for all subpopulations. However, the habitats found in Togo are not suitable for Sbp4. The southern parts of Mali and Niger are very suitable for Sbp3 and Sbp4, respectively, while Sierra Leone and Liberia are not as suitable. Additionally, a significant portion of these countries is projected to be unsuitable.

The overlapping niche analysis revealed less similarity among the four subpopulations. The most reconcilable similarity was found between Sbp1 and Sbp2, and between Sbp2 and Sbp3 and Sbp4, with respective *D* index values of 0.49, 0.42 and 0.37. In contrast, the

Table 2
Performance of ensemble species distribution models.

Subpopulations	T	AUC	Omission rate	H	S	F	prop. correct	K	TSS	SEDI
Sbp1	0.49	0.97	0.02	0.98	0.96	0.04	0.96	0.90	0.93	0.98
Sbp2	0.49	0.95	0.04	0.96	0.94	0.06	0.95	0.87	0.90	0.97
Sbp3	0.40	0.89	0.07	0.93	0.86	0.14	0.88	0.69	0.79	0.91
Sbp4	0.49	0.92	0.07	0.93	0.90	0.10	0.91	0.78	0.83	0.93

T = Threshold, AUC = Area Under Curve, H = sensitivity, S = specificity, F = False positive rate, K = Kappa, TSS = True Skill Statistic, SEDI = Symmetric Extremal Dependence Index
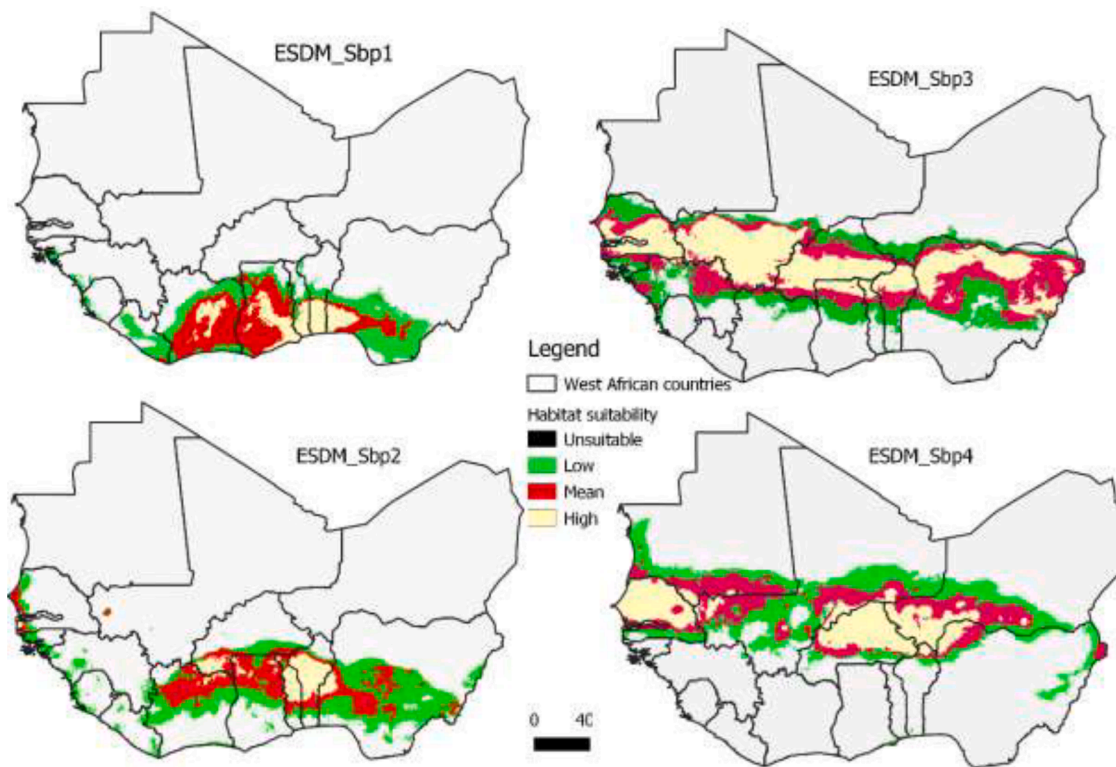
Fig. 5. Potentially suitable habitats for *Adansonia digitata* subpopulations in West Africa.
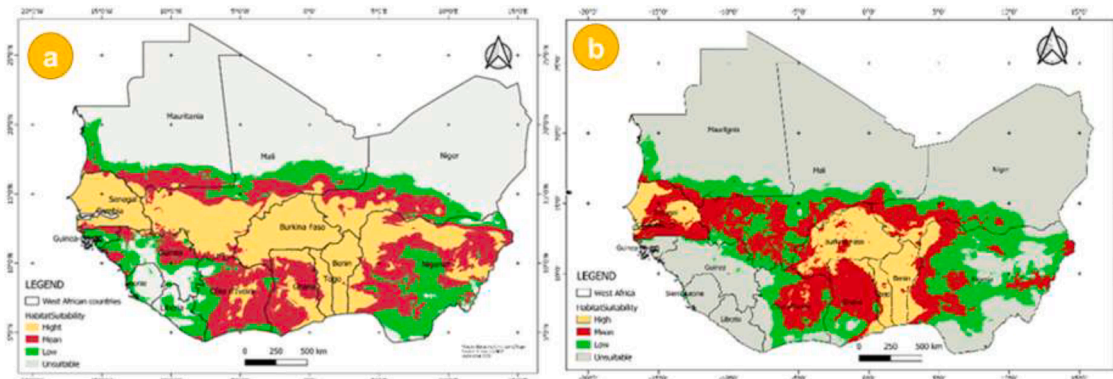

Fig. 6. Global habitat suitability for Adansonia digitata in West Africa: subpopulations (a), and species level (b) (The highly suitable habitats are highlighted in orange, while moderately suitable habitats are marked in red. The habitats that are considered poor or unsuitable are colored in gray).

difference was mostly high between Sbp1 and Sbp4, and between Sbp2 and Sbp4, followed by Sbp1 and Sbp3 with *D* index values of 0.15, 0.17, and 0.22.

In general, habitat suitability depends on the occurrence data used. The habitat appears to be more extensive and more accurate when using subpopulations than when building the model at the species level (Fig. 6). When considering the habitat suitability elaborated at the species level, there is no highly suitable habitat for the species in Mali. In contrast, the models from the subpopulations show highly suitable habitats in the southern part of the country. Liberia also appears to be entirely unsuitable for the model at the species level and poorly suitable at the subpopulation level. For the two global models, unsuitable habitats are mainly found in the northern part of West Africa (Fig. 6). Specifically, for the species level model, the species is absent in Liberia and almost absent in Sierra Leone (Fig. 6b).

Based on the combination of subpopulation maps, 47.63% of West African habitats are not suitable for the cultivation and conservation of

A. digitata. In comparison, the highly suitable habitats represent 15.8% (Fig. 7). Low- and moderately suitable habitats account for 37 % of the total habitats in the study area. Considering the model generated with the global sample at the species level, the unsuitable habitats rate increased (56.88%), while the highly suitable habitat decreased (9.25%, less than half).

4. Discussion

The splitting of *A. digitata* occurrences based on environmental variables highlights statistically significant differences in climatic conditions along latitudes. This result suggests that environmental constraints vary throughout the range of the species. Local variations in environmental constraints could lead to morphological and adaptive genetic variations within the species, as previously demonstrated in studies by Assogbadjo et al., (2006), De Smedt et al., (2010), and Munthali et al., (2012). Local adaptation may also result in biological
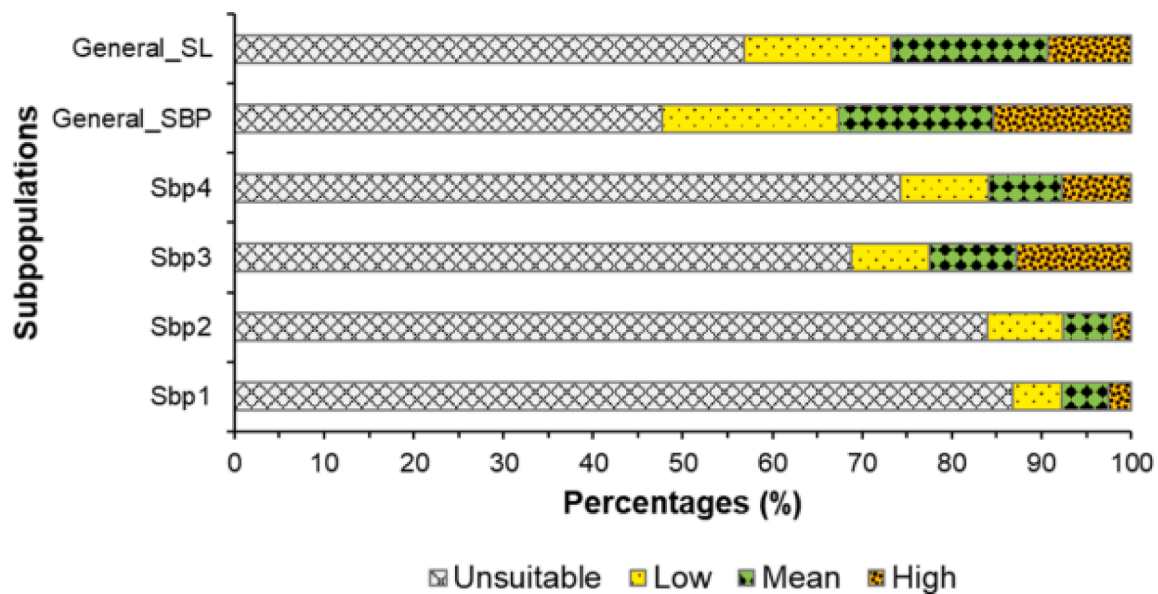
Fig. 7. Trends in habitat suitability for Adansonia digitata in West Africa at subpopulation (SBP) and species (SL) levels.

responses, as reported by Assogbadjo et al. (2011), who showed morphology and biology disparities of the species in different climatic zones in Benin. Adaptation to local climatic variables may affect the species' genetic diversity, as highlighted by Chládová et al. (2019) in Kenya, who reported genetic differences between populations across coastal and inland zones.

Niche subpopulation models confirmed statistical discrimination based on environmental variables, as no overlapping was observed between models. Furthermore, the range and contribution of environmental variables in niche models differed from one population to another. This difference highlighted the contribution of local conditions to the model and consequently the local adaptation of the target species. Hällfors et al. (2016) addressed the implication of local adaptation on genetic diversity, species distribution, and conservation. This is consistent with Smith et al. (2019), who analyzed the accuracy of models built at the species level and with subpopulations. Global models at the West African extent using samples of subpopulations and species-level samples clearly show bias with the global model at the species level. The bias induced by global models on the species distribution of *A. digitata* was discussed earlier by Moyo et al. (2019) in Zimbabwe. Therefore, considering local adaptative constraints, genetic diversity, or splitting species occurrences into subpopulations or ecotypes will help avoid model bias (Prasad and Potter, 2017; Moyo et al., 2019) and hence bestow plant conservation and valorization policies.

The main environmental factors shifting the distribution of *A. digitata* at the species-level, considering West Africa globally, are annual precipitation and isothermality. Sanchez et al. (2010) also reported annual temperature as a critical factor in the distribution of *A. digitata* using a single model at a coarse African scale. In contrast, the trend changed using subpopulations. In this case, we reported the precipitation of the coldest quarter and the minimum temperature of the coldest month. In both cases, soil was positioned as the third most important factor.

The extent of suitable habitat is more critical in the two current models at the West African extent than in the previous study by Sanchez et al. (2010). This difference may be explained by the number of occurrences used, as the size of occurrences can influence the accuracy of species distribution models (Benkendorf and Hawkins, 2020). In this study, more than 2000 occurrences were used, compared to 450 in a previous study conducted on an African scale. Moreover, the methodology used in this study involved forecasting habitat suitability based on subsamples below the species level rather than at the species level as done in previous studies to reduce bias and increase the accuracy of

niche models (Smith et al., 2019). The findings of this study also differ from those of Birhane et al. (2020) and Moyo et al. (2019), which were conducted at the country scale and identified temperature annual range and altitude as key factors determining the distribution of *A. digitata*, respectively. These studies (Moyo et al., 2019; Birhane et al., 2020) confirm that factors governing the distribution of the baobab are geographically and scale-dependent.

Local management shapes the occurrence and abundance of *A. digitata* (Dhillion and Gustad, 2004). The species is highly valued and sometimes planted, and its abundance in suitable habitats will depend mainly on the beliefs of the local population. The majority of species occurrences was found in areas predicted to be highly suitable. Within highly suitable habitats, the species is sometimes found in natural stands established by natural regeneration and sometimes by the local population for their use, reflecting the importance of the species (Assogbadjo and Loo, 2011; Kebenzikato et al., 2015). In the area where it is predicted to occur moderately (mean suitable habitat), its limited presence could be explained by less favorable environmental conditions for its growth. In a constrained environment, species growth could be handicapped if not carefully supported. Rarely, occurrences fell in unsuitable habitats where the environment is unfavorable to its growth, although people plant it. In other countries, the limitation of field surveys/scholars leads to low occurrence data.

Overall, the species' habitat suitability is moderately different from previous studies. According to Bonnet et al. (2008), the species range is more extensive than that reported by Assogbadjo and Loo (2011) and Sanchez et al. (2010). However, all these previous studies did not report Liberia as a suitable habitat, as the finding of this study is based on subpopulations. Consequently, the state reported (Sidibé et al., 2002; Bonnet et al., 2008; Sanchez et al., 2010; Assogbadjo and Loo, 2011) can be explained mainly by the existence of microclimate features limiting the installation and growth of the species, although the species could be successfully introduced in these areas. The implication of human behaviors on the distribution of the baobab was evoked by Sidibé et al. (2002), justifying its presence in forest areas, even though it is known to be confined to savannas, especially the driest areas.

Evaluation metrics used in this study were selected to reduce bias, especially those that could be induced by AUC, Kappa, or TSS (Allouche et al., 2006; Wunderlich et al., 2019). The findings of Guo et al. (2015)) report no significant difference between the three metric values (AUC, Kappa, TSS). However, in the present study, which employed all four metrics (AUC, Kappa, TSS, and SEDI), there was no significant difference

observed when considering the trend.

5. Conclusion

Four potential subpopulations of *A. digitata* were discriminated in West Africa based on environmental variables. No overlapping niche model of subpopulations was observed, indicating that each subpopulation has distinct environmental requirements. Moreover, the range and contribution of environmental variables in niche models differed from one subpopulation to another, supporting the general model accuracy. The realized habitat suitability results for *A. digitata* will benefit conservation policy. Parts of West Africa were found to be favorable for restrictive subpopulation development and may be more vulnerable to climate threats. More studies are needed to assess the impact of future climate factors based on splitting occurrences of *A. digitata* (Fig. 1).

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CRediT authorship contribution statement

WA: project conception and funding acquisition; methodology; data collection and analysis; original draft and revision. GNG: project supervision; methodology; original draft and revision. KD: methodology; original draft and revision. KB: project supervision; methodology; original draft and revision. AKN: project supervision; methodology; original draft and revision. KA: project administration and resources; project supervision; methodology; original draft and revision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2023.100397.

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