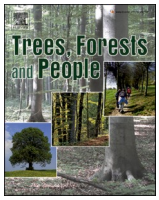
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Integrating phenotypic and genetic diversity, and species distribution modeling to set long-term conservation strategies for the endangered *Afzelia africana* in Benin (West Africa)

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ABSTRACT

Afzelia africana is one of the most threatened multipurpose species in sub-Saharan Africa. Understanding its potentially suitable habitats, coupled with its phenotypic and genetic diversity is valuable for establishing sustainable and efficient conservation strategies for the species. This study combines phenotypic and genetic data with best-fit habitat models to identify conservation opportunities for *A. africana* across Benin. Natural populations were sampled for phenotypic and genetic diversity. Occurrence data were collected in the field and supplemented with available data from GBIF. Current and future climate data under two Shared Socioeconomic Pathways (SSP2-4.5 and SSP5-8.5) were used to model the current and potential future distribution of the species using MaxEnt. The results showed a large natural variation in phenotypic diversity, with populations from the Sudano–Guinean zone exhibiting intermediate diversity ($H' = 0.45$), while those from the Guinean and Sudanian zones exhibited high levels of diversity ($H' > 0.60$). Currently, 55.40 % of the country was predicted to be potentially suitable for the conservation of *A. africana*. Under the SSP5-8.5 and SSP2-4.5 scenarios, a significant increase respective of 70.27 % and 68.85 % in suitable habitat is predicted by 2041–2060. Nevertheless which will negatively affect both phenotypic and genetic diversity. However, individuals from the Sudano–Guinean subgroup are the most vulnerable to future climate conditions. This integrated approach not only helps to identify potential conservation areas but also reveals a crucial interplay in the phenotypic diversity and genetic dynamics of the species.

1. Introduction

Rapidly changing global climate poses a serious threat to biological diversity (Sang *et al.,* 2022). Conserving biodiversity in the context of climate change is one of the greatest challenges of our time (Manda *et al.,* 2022). Climate change is an ecologically important factor with profound effects on the geographic distribution of species, especially in tropical areas (Assogba *et al.,* 2022, Biaou *et al.,* 2023a). It has far-reaching effects on phenology, tree physiology (Thuiller *et al.,* 2005), phenotypic traits (Hounkpèvi *et al.,* 2016, Houehanou *et al.,* 2019b), and genetic variation (Leal *et al.,* 2021, Tobón-Niedfeldt *et al.,* 2022). To mitigate the risk of population decline or potential extinction, several species use different strategies to adapt to changing environmental conditions (Aitken *et al.,* 2008). These strategies include, but are not limited to: (i) shifting their range to match their ecological niche, (ii) using phenotypic plasticity as a means to tolerate and adapt to environmental changes, and (iii) genetic evolution as a mechanism to adapt to new local conditions (Waldvogel *et al.,* 2020). However, for many species, migration may be challenging in the face of rapid climate change (de Lafontaine *et al.,* 2018). Understanding and studying the evolutionary adaptive

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capacity of species in the future is, therefore, not only important for understanding the potential resilience of natural species to climate change, but can also contribute to monitoring approaches aimed at addressing global biodiversity loss (Waldvogel *et al.,* 2020). Furthermore, understanding species range shifts in response to climate change and the underlying environmental factors that govern such phenomena is crucial to facilitating informed decision-making and designing effective strategies for species conservation, as argued by Phillips *et al.* (2017) and Hounkpèvi *et al.* (2020).

Several studies have been conducted worlwide to examine biodiversity conservation in the context of climate and global change. Most of these studies use species distribution models (SDMs). These models examine the relationship between species occurrence and environmental factors to predict the current and future species distribution (Zeng *et al.,* 2016, Phillips *et al.,* 2017; Barlow *et al.,* 2021). Among SDMs, the maximum entropy algorithm (MaxEnt) is widely used because of its high predictive power (Elith *et al.,* 2006, Phillips *et al.,* 2006). Bioclimatic variables from the WorldClim database are often used to run MaxEnt (Coulibaly *et al.,* 2022). MaxEnt has been successfully used to identify the current and future potential habitat of several endangered species (Nguyen *et al.,* 2021, Pattanaik *et al.,* 2022).

Afzelia africana is a forest tree species belonging to the subfamily Caesalpinioideae and widely distributed in different vegetation types, ranging from the dense forests of the Guinean zone to the savannas and open forests of the Sudanian zone (White 1986). Among the selectively exploited species reported in Benin, such as *Afzelia africana* Sm. (Sinsin *et al.,* 2010), *Khaya senegalensis* (Desr.) A. Juss (Gaoue and Ticktin 2008), and *Pterocarpus erinaceus* Poir (Glèlè Kakaï *et al.,* 2009), *A. Africana* is the most threatened and is classified as an endangered species in Benin (Adomou *et al.,* 2009, Houehanou *et al.,* 2011). It is therefore, important to develop conservation strategies based on the remaining populations. Human pressure, which continues to exacerbate its populations due to the use of the species' parts (Adjanohoun *et al.,* 1989, Houehanou *et al.,* 2011), combined with the effects of climate change, calls for urgent action to ensure the management and conservation of the species.

According to the ecological gradient hypothesis, climate has been shown to significantly determine the natural variation of phenotypic traits at large scales in many West African countries (Okello *et al.,* 2018) and is worth considering in understanding the observed phenotypic differences. Although several efforts have been made in the promotion and sustainable management of this species by assessing the variation of phenotypic traits in relation to climatic conditions and human disturbances (Amahowe *et al.,* 2018, Houehanou *et al.,* 2019a), the genetic traits (Houehanou *et al.,* 2023), and assessing the local importance of its uses (Balima *et al.,* 2018), little is known about the impact of climate change on the distribution of its phenotypic and genetic diversity. Moreover, studying the effects of climate change on the distribution of genetic and phenotypic diversity is important for planning the long-term conservation strategies for this species. Integrating these traits into SDMs has proven effective in modeling the impacts of climate change on the geographic distribution of species (Ikeda *et al.,* 2017, Coulibaly *et al.,* 2022). However, determining how genetic diversity responds to climate change remains a challenge (Hansen *et al.,* 2012). This study aims to (i) explore the potential current and future impact of climate on the distribution of *A. africana* in Benin, (ii) determine the impact of climate change on the distribution of phenotypic and genetic diversity and (iii) identify suitable areas for future conservation of phenotypic and genetic diversity.

2. Method

2.1. Study area

The study was carried out in the Republic of Benin, located in West Africa between latitudes 6°10′N and 12°25′N and longitudes 0°45′E and 3°55′E with 114,869 km^2 of area. The country is split into three climatic zones from south northwards: Guinean zone, Sudano-Guinean zone and Sudanian zone. Each zone is divided into phytodistricts, which are mesoscale subdivisions based on differences in soils, natural vegetation and to some extent climatic conditions (White, 1986). The Guinean zone is characterized by a truly humid climate with a bimodal rainfall regime that lasts an average of 8 months. The temperature ranges from 25 to 29 °C and the average annual rainfall from 1000 to 1400 mm. The area is also characterized by a natural ecosystem of dense forests and has 422 inhabitants per km^2. The Guinean zone comprises four phytodistricts: the Plateau, the Ouémé Valley, the coastal zone and Pobè (Adomou *et al.,* 2006). The transitional zone, called the Sudano-Guinean zone, is characterized by a sub-humid climate with a unimodal rainfall pattern and an average season length of 6 months. The average annual rainfall varies from 1100 to 1300 mm and the temperature from 25 to 29 °C. The population density is 52 inhabitants per km^2. The Sudano-Guinean zone is divided into three phytodistricts: Zou, South-Borgou and Bassila (Adomou *et al.,* 2006). The Sudanian zone, also known as the dry zone, is characterized by a tropical climate with a unimodal regime and a rainy season that lasts an average of 6 months. The average annual rainfall ranges from 800 to 1100 mm and the temperature is between 24 and 31 °C. With a natural ecosystem of open forests and savannahs, this zone has 36 inhabitants per km^2. The Sudanian zone is divided into three phytodistricts: North-Borgou, Atacora chain and Mékrou–Pendjari (Adomou *et al.,* 2006).

2.2. Occurrence data

A total of 364 occurrences were recorded in the field in 2018, i.e. 156 in the Sudanian zone constituting the Sudanian subgroup (SZ), 75 in the Sudano-Guinean zone constituting the Sudano-Guinean subgroup (SGZ) and 133 in the Guinean zone constituting the Guinean subgroup (GZ) (Houehanou *et al.,* 2019b, 2023) and 3470 occurrences were obtained from GBIF in 2021 (Fig. 1). The dataset underwent rigorous quality control procedures to remove duplicates and observations without latitude or longitude. To minimize sampling bias associated with overrepresentation of occurrences in certain geographic areas, the data was thinned. Subsequently, a refined dataset comprising 3709 occurrences was retained for species distribution modeling (Fig. 1).

2.3. Environmental data

Environmental data included bioclimatic variables, obtained from the WorldClim database (http://www.worldclim.org, accessed on October 15, 2021). A total of 19 bioclimatic variables related to temperature and precipitation were used (Table 1). Data on bioclimatic variables were downloaded for current (1970–2000) and future (2041–2060) climate at a resolution of 30 arc-seconds (~1 km^2).

Some of the 19 bioclimatic variables, such as mean temperature of the wettest month (bio-8), mean temperature of the driest month (bio-9), precipitation of the warmest month (bio-18), and precipitation of the coldest month (bio-19), exhibit discontinuities in the Americas and sub-Saharan Africa (Escobar *et al.,* 2014, Booth 2022, Biaou *et al.,* 2023b). Therefore, these variables were excluded from our models to minimize the potential bias.

For future climate projections, the weighted average of three global climate models (GCMs) from the WorldClim database was used. These are HadGEM3-GC3.1, a projection model developed by the Met Office Center (Ridley *et al.,* 2018); MIROC6, the sixth version of a climate model developed by a Japanese community within CMIP6 (Tatebe *et al.,* 2019); and MPI-ESM1.2-HR, the latest version of the Max Planck Institute's Earth system model (Gutjahr *et al.,* 2019, Steger *et al.,* 2020). Climate projections were made for the period 2041–2060 (2050) horizon, considering two climate scenarios from the 6th Assessment Report of the IPCC: SSP 2–4.5 and SSP 5–8.5 (Beny *et al.,* 2023). Indeed, the use of multiple GCMs is strongly recommended for long-term projections to

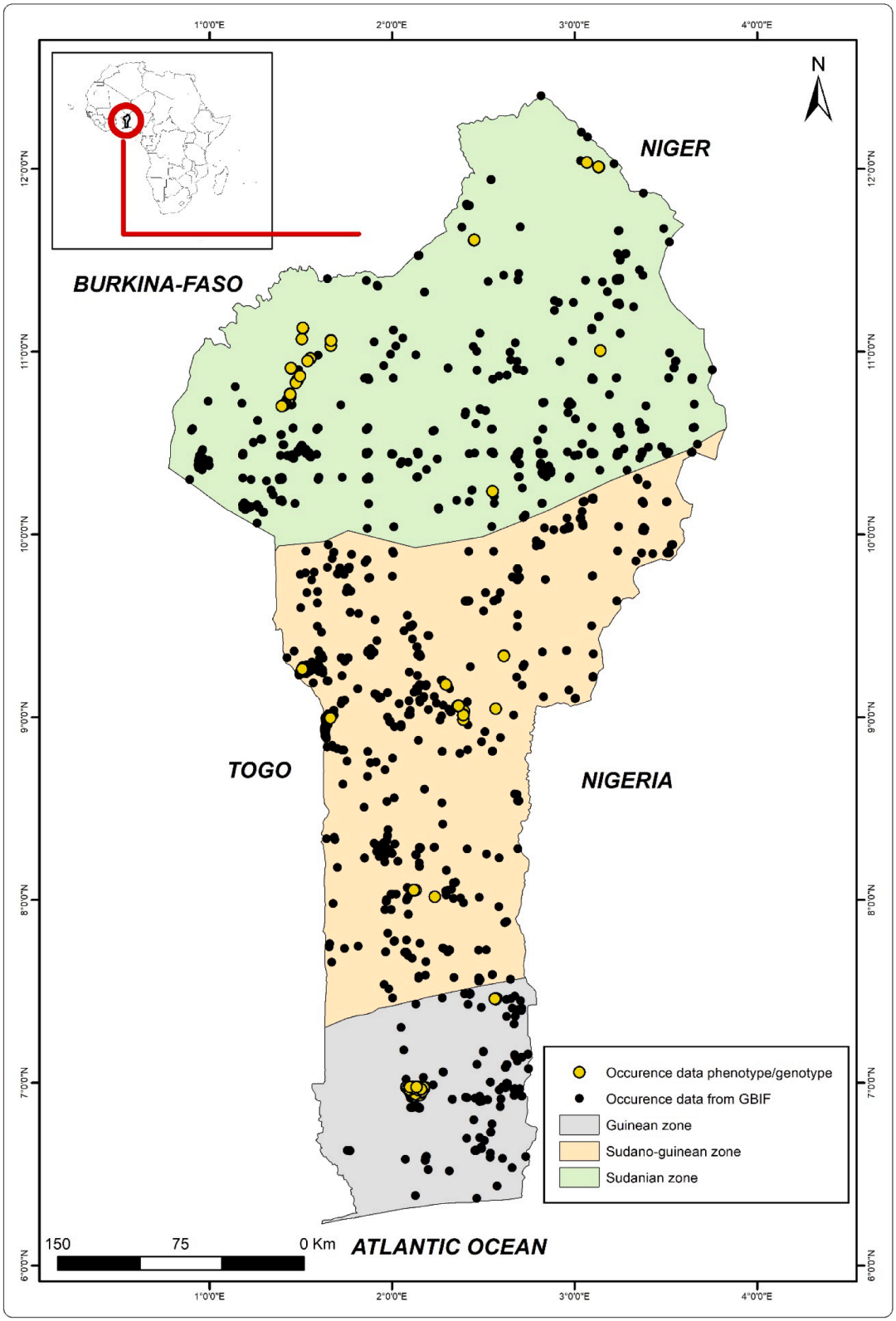


Fig. 1. Map of the study area showing the occurrence data points of *A. africana* across Benin.

effectively capture this variability (Buisson *et al.,* 2010). These SSPs (SSP 2–4.5 and SSP 5–8.5) have previously been used in previous studies of West African ecosystems (Coulibaly *et al.,* 2023).

2.4. Development and evaluation of SDM

Species distribution modeling (SDM) was used to assess the impact of climate change on the range of *Afzelia africana* in Benin. The MaxEnt algorithm (Phillips *et al.,* 2017a), known for evaluating the probability of species distribution based solely on presence occurrence data, was

Table 1
Display of bioclimatic and environmental variables.

Codes	Meaning	Units
Temperature		
bio 1	Average annual temperature	°C
bio 2	Average diurnal temperature difference	°C
bio 3	Isothermality	°C
bio 4	Seasonality of temperatures	°C
bio 5	Maximum temperature of the hottest month	°C
bio 6	Minimum temperature of coldest month	°C
bio 7	Annual temperature difference	°C
bio 8	Average temperature of the wettest quarter	°C
bio 9	Average temperature of the driest quarter	°C
bio 10	Average temperature of the warmest quarter	°C
bio 11	Average temperature of the coldest quarter	°C
Humidity		
bio 12	Total annual precipitation	mm
bio 13	Rainfall in wettest month	mm
bio 14	Precipitation in driest month	mm
bio 15	Seasonality of precipitation	mm
Bio 16	Precipitation of the wettest quarter	mm
bio 17	Precipitation of the driest quarter	mm
bio 18	Warmest quarter precipitation	mm
bio 19	Coldest quarter precipitation	mm
elev	Elevation	m
soil	Soil	-

used (Alsamadisi *et al.,* 2020). MaxEnt outperforms other SDM algorithms, including Generalized Linear Model (GLM), Generalized Additive Model (GAM), Boosted Regression Trees (BRT), and Multivariate Adaptive Regression Splines (MARS), as shown by Elith *et al.* (2006). The MaxEnt results indicate the level of environmental suitability, while also representing the potential ecological niche of the species (Tepa-Yotto *et al.,* 2021). The algorithm determines the most coherent distribution of sample points with respect to background locations, taking into account constraints derived from the data (Phillips *et al.,* 2006). For model calibration, 80 % of the occurrence points were used as training data, while the remaining 20 % were kept as test data (Phillips and Dudík 2008). Models were fitted using the default settings of Maxent 3.4.1 (hinge, product, linear, and quadratic, 10,000 background points, 1000 replicates; cross-validation, and clamping). The jackknife test was used to determine the relative importance of environmental variables in determining likely species distribution (Phillips *et al.,* 2006). Models outputs were generated using the Cloglog format (Rodríguez-Rodríguez *et al.,* 2020). The statistical value of the Area Under the Curve (AUC) was then used to assess the model performance according to the interpretation proposed by (Araújo *et al.,* 2005): $0.5 < AUC < 0.7$ (the model is not of good quality); $0.7 < AUC < .9$ (the model is good); $AUC > 0.9$ (the model is excellent). The Symmetric Dependence of Extremals Index (SEDI) and the True Skill statistic (TSS) were also used to assess the performance of the model. The SEDI has been reported to be more appropriate for most presence-background SDM initiatives (Wunderlich *et al.,* 2019) and the closer the SEDI value is to 1, the better the performance of the model. TSS values greater than 0.5 reflect good predictive ability of the model (Allouche *et al.,* 2006). We analyzed the multicollinearity of variables using the 'SDM' package (Naimi and Araújo, 2016) in R 3.6.3 (R. Core Team, 2020). The variables included those from the occurrence matrix and the bioclimatic data. The variance inflation factor (VIF) (Marquardt, 1970) was applied to assess collinearity, with a default threshold of $VIF < 10$ (Chatterjee and Hadi, 2006). Based on this analysis, six non-collinear and biologically relevant variables were selected for modeling the distribution of *A. africana*.

2.5. Mapping of the species' potential habitat suitability

Habitat mapping was carried out using ArcGIS 10.7.1. Two habitat classes were defined based on the threshold "10th percentile training presence cloglog". This threshold excludes areas with suitable habitat values below the lowest 10 % of presence records (Merow *et al.,* 2014). Thus, habitat classes with values below this threshold were considered unsuitable, while those with higher values were considered suitable. Habitat extent was then estimated in square kilometers (km^2) using ArcGIS 10.7.1 spatial analysis tools (ESRI, 2019).

2.6. Phenotypic and genetic diversity

2.6.1. Phenotypic diversity

The focus was on the natural populations sampled and used by Houehanou *et al.,* (2019a). A total of 100 individuals divided into 13 populations were sampled in the three climatic zones, i.e. 51 in the Sudanian zone, 7 in the Sudano-Guinean zone and 42 in the Guinean zone (see Houehanou *et al.,* 2019a). All individuals were recorded using a global positioning system (GPS). In each climatic zone, protected and disturbed populations of *Afzelia africana* were sampled assuming similar environmental conditions. Protected populations were located in areas without human disturbance, while disturbed populations were located in areas affected by human activities. Individuals were selected on the basis of the presence of fruits, with similar mean diameter at breast height (dbh) to avoid age-related effects on the trees. Measurements of the dbh, fruits (4 morphometric characters), and seeds (6 morphometric characters) were made on a total of 100 individuals, 672 fruits, and 2243 seeds. For detailed information on sampling and morphological data collection, see Houehanou *et al.* (2019a).

For each trait, phenotypic classes were defined and the Shannon-Weaver diversity index (H) was used to estimate the phenotypic diversity classes of the different traits (Martínez *et al.,* 2017). The classes were determined by K-means, which was used to evaluate distinct patterns and group similar datasets together. The resulting K-variable represents the number of clusters in the data, and was applied for each trait to highlight the different optimal classes. The classes would vary from 2 to 6 for the different traits. The Shannon-Weaver diversity index was calculated using the following equation Eq. (1):

$$H = -\sum_{i=1}^{n} PilnPi \quad (1)$$

where n is the number of phenotypic classes for a given trait and Pi is the proportion of the total number of entries in the i^{th} class.

H was estimated for each trait and population. In order to standardize H, it was divided by $Hmax = ln(n)$. The standardized phenotypic diversity index (H') is between 0 (when the population is uniform for the trait) and 1 (when the population has maximum diversity for the trait) (de Oliveira *et al.,* 2012). It was classified as high ($H' \geq 0.60$), intermediate ($0.40 \leq H' < 0.60$) or low ($0.10 \leq H' < 0.40$), as described by Eticha *et al.* (2005) and used by Avakoudjo *et al.* (2021). This index, analyzing phenotypic frequency is a measure of the regularity of the distribution of frequency classes for a morphological descriptor and a phenotypic diversity (Bekele *et al.,* 2006, Martínez *et al.,* 2017). An analysis of variance (ANOVA) followed by the Student Newman Keuls (SNK) test was performed to compare phenotypic diversities between populations and bioclimatic zones. All statistical analyses were performed with the R v3.6.1 (R. Core Team, 2020).

2.6.2. Genetic diversity

Genetic data and estimated genetic diversity parameters were obtained from Houehanou *et al.* (2023). DNA was extracted from silica-dried leaves and 264 samples were genotyped at 11 SSR (Houehanou *et al.,* 2019b, 2023). We estimated the genetic diversity parameters such as the number of alleles (Na), the effective number of alleles (Ne), the observed heterozygosity (Ho), the expected heterozygosity (He), and the fixation index using GenAlEx (Peakall and Smouse, 2006).

2.7. Assessing the impact of climate change on phenotypic and genetic diversity

First, a correlation analysis was conducted to identify phenotypic and genetic traits associated with the selected best performing environmental variables. Phenotypic and genetic traits were then combined with SDM outputs to derive current and future conservation areas. This was achieved by projected populations with phenotypic and genetic traits onto the maps resulting from the modelling in order to identify those falling within or outside a suitable habitat.

3. Results

3.1. Validation of SDM and contribution of environmental variables to the distribution of Afzelia africana

The variables retained from the multicollinearity analysis (Table 2) all contributed to the prediction of habitats suitable for the conservation of *A. africana*. The model of the Sudanian subgroup was characterized by the remarkable contribution of precipitation of the wettest month (bio-13, 39.7 %), temperature seasonality (bio-4, 23.8 %), and mean diurnal temperature deviation (bio-2, 10.2 %) (Table 2). Temperature seasonality (bio-4) is both the environmental variable with the highest gain when used in isolation and the one with the largest loss when omitted (Fig. 2).

Regarding the Sudano-Guinean subgroup model, the variables that contributed most to the prediction of habitats were: soil (55.5%), precipitation of the driest month (bio-14, 19.9 %) and seasonality of temperatures (bio-4, 14.2 %) (Table 2). However, the environmental variable with the highest gain when used in isolation is bio-3, while the one that decreases the gain the most when omitted is elevation (elev) (Fig. 2). As for the Guinean subgroup model, it was characterized by precipitation of the driest month (bio-14, 47.7 %), elevation (elev, 30.7 %), and isothermality (bio-3, 11 %) (Table 2). Elevation (elev) is both the environmental variable with the highest gain when used in isolation and the one that decreases the gain the most when omitted (Fig. 2).

According to the performance indices, the models of the Sudanian and Sudano-Guinean subgroups proved to be good models, while that of the Guinean subgroup was excellent (Table 3).

Table 2
Percentage contribution of variables included in MaxEnt species distribution modeling (SDM).

Code	Description of variables	Percent contribution (%)
	SZ	
bio-13	Rainfall in wettest month	39.7
bio-4	Seasonality of temperatures	23.8
bio-2	Average diurnal temperature difference	10.2
elev	Elevation	9.5
soil	Soil	8
bio-14	Precipitation in driest month	5.5
bio-6	Minimum temperature of coldest month	3.3
	SGZ	
soil	Soil	55.5
bio-14	Precipitation in driest month	19.9
bio-4	Seasonality of temperatures	14.2
bio-2	Average diurnal temperature difference	5.5
elev	Elevation	3.2
bio-3	Isothermality	1.7
bio-12	Total annual precipitation	0.1
	GZ	
bio-14	Precipitation in driest month	47.7
elev	Elevation	30.7
bio-3	Isothermality	11
bio-15	Seasonality of precipitation	6.4
bio-4	Seasonality of temperatures	2.6
bio-11	Average temperature of the coldest quarter	1.1
soil	Soil	0.6

3.2. Change in the suitable habitat under the climate scenarios

Overall, current and future climate conditions indicate suitable habitats for the cultivation of *A. africana* species in Benin (Fig. 3). The Sudanian subgroup (35,042.41 km^2) has more suitable habitats compared to the Sudano–Guinean subgroup (26,879.24 km^2) and the Guinean subgroup (1710.31 km^2), according to current projections (Fig. 3.a; Table 4). Two typical habitat types have been identified following the expansion of suitable habitats beyond their original climatic zone. An area of about 49.49 km^2 located south of the Sudanian zone, with climatic conditions suitable to the Sudanian and Sudano–Guinean subgroups. Then an area of about 83.88 km^2 in the Guinean zone, which presents suitable conditions for the Sudano-Guinean and Guinean subgroups.

Under the SSP 2–4.5 climate scenario, climate projections for 2041–2060 indicate a loss of suitable habitat for the Sudano-Guinean subgroup (-21.97 %), while a gain is observed for the Sudanese (+99.15 %) and Guinean (+928.10 %) subgroups (Fig. 3.b; Table 4). These gains in suitable habitats have led to an extension of the area of the two typical habitats previously identified. In addition, a third type of habitat was observed, suitable for both the Sudano–Guinean and Guinean subgroups. However, these typical habitats converge towards the Sudano–Guinean zone.Similar trendswere observed under the SSP 5–8.5 scenario, with large gains and high losses (Fig. 3.c; Table 4). In this scenario, typical habitats converge completely towards the Sudano-Guinean zone.

Less suitable habitat is found in protected areas compared to unprotected areas. However, protected areas contain typical suitable habitats in the pair of subgroups ZS-ZSG and ZSG-ZG under current projections and then in the pair of ZS-ZSG, ZSG-ZG, and ZS-ZG under the two future climate scenarios (Fig. 3; Table 4).

3.3. Phenotypic diversity of Afzelia africana individuals between populations

The assessment of diversity across climatic zones revealed a large variation for all studied traits. Individuals from the Sudano-Guinean zone exhibited intermediate diversity (H'= 0.45) while individuals from the Guinean and Sudanian zones displayed high levels of diversity ($H' > 0.60$). The overall mean value of diversity for all traits was 0.93. A remarkable diversity (H'= 1) was observed for the descriptor total seed weight in the Guinean zone (Table 5). In contrast, low diversity was observed for seed weight in the Sudano-Guinean zone (H'= 0.36) (Table 3). Phenotypic diversity (H') for individual descriptors ranged from 0.87 (for seed thickness) to 0.98 (for seed rate). For all descriptors, a low diversity (H'= 0) was observed for fruit width and fruit weight in the Sudano-Guinean zone (Table 5).

On a population basis, high phenotypic diversity indices were obtained in the Azalime, Batia1, Koto1 and Konkombri populations with H' higher than 0.60. The populations of Koto3 and Tchatigou2 have a low phenotypic diversity index with H'= 0.35 and H'= 0.31 respectively. The other remaining populations have an intermediate diversity index ($0.40 < H' < 0$ (Table 4). On the population side, monomorphism is observed for the same characters (fruit width, fruit weight) in Batia2, Koto3, Parakou, Pendjari3 and Tchatingou2 (Table 6). A high diversity (H'= 1) was observed for the fruit weight descriptor in Ouedeme (Table 6). However, low diversity was observed for seed length in the Adakplame, Koto2, Koto3 and Ouedeme populations (Table 6).

3.4. Genetic diversity of Afzelia africana populations

Genetic diversity was analyzed across three climatic zones, revealing a total of 149 alleles with an average of 13.54 alleles per locus. Genetic diversity parameters, such as allelic richness (Na) and observed heterozygosity (Ho) and expected heterozygosity (He) showed a significant variation among the populations of different zones. Most of the

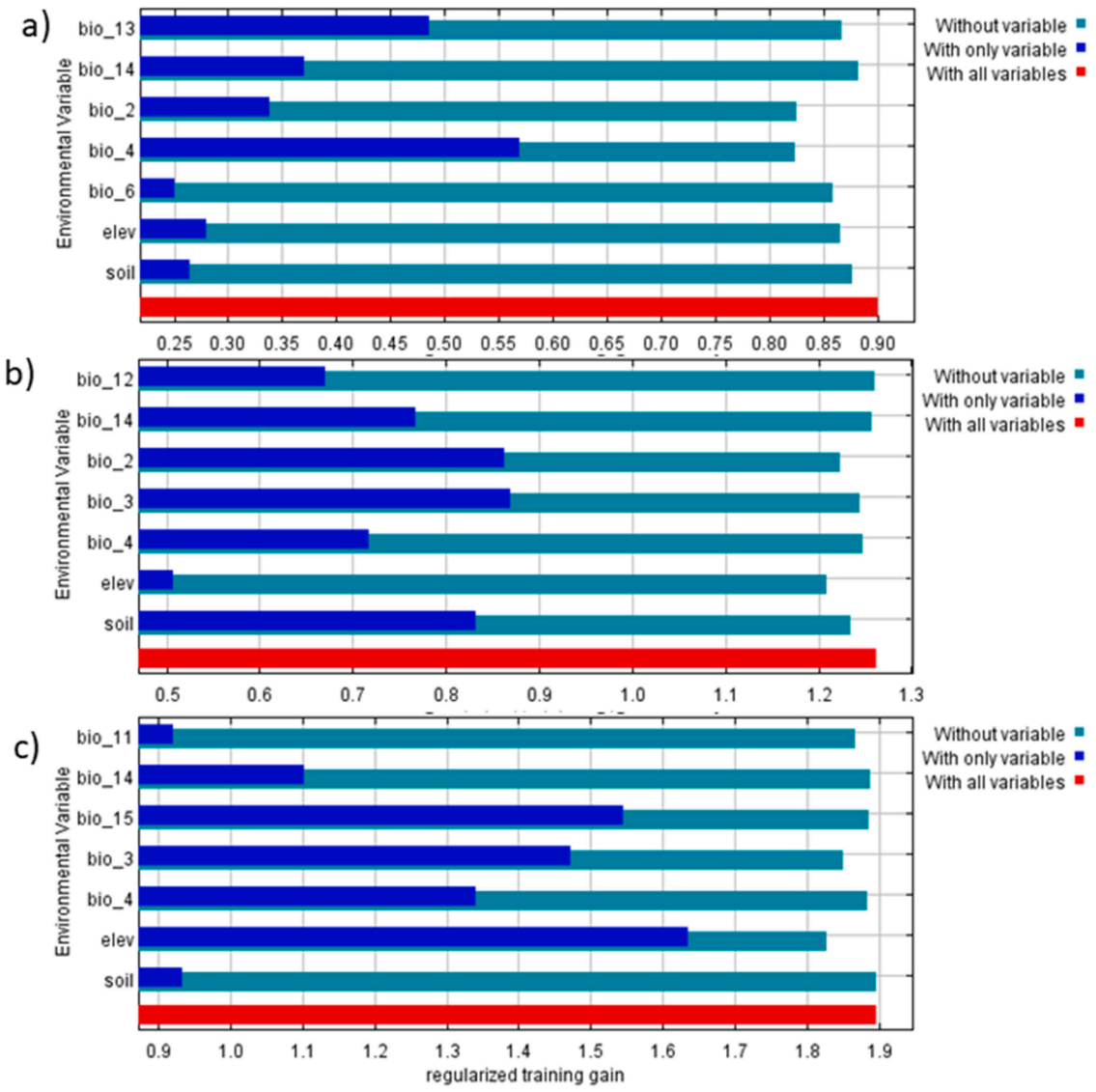


Fig. 2. Jackknife test results of the relative contribution of the environmental variables to the distribution of *Afzelia africana* with respect to the training gain for SZ subgroup (a), SGZ subgroup (b) and GZ subgroup (c). Blue bars represent the relative gain achieved by Maxent when the model is created with only each variable. Lighter blue bars represent the relative gain obtained by omitting each variable in turn. Red bars represent the gain achieved by Maxent when all variables are considered.

Table 3
Distribution model performance.

	AUC	TSS	SEDI
SZ	0.86	0.56	0.73
SGZ	0.89	0.60	0.77
GZ	0.95	0.81	0.92

populations showed a negative value of the fixation index (Fis). Similarly, Ho was higher than the He for most populations (see Houehanou *et al.,* 2023). The mean values of He are the highest in the Koko population (0.75) and the lowest in Banikoara–Sampèto population (0.49) (see Houehanou *et al.,* 2023). The Sudanian zone stands out with the highest values for the Na= 11.36, the average number of alleles per locus (Ne= 5.66), the Ho and He= 0.79, indicating a high genetic diversity in this zone (Table 7). However, it also shows an excess of heterozygosity (Fis= -0.02), compared to the expected genetic equilibrium (Table 7). The Sudano-Guinean zone shows similar values to Sudanian for Na= 10.64 and Ne= 5, indicating notable genetic diversity as well (Table 7). However, it displays a more negative Fis= -0.20 than Sudanian, indicating even higher heterozygosity compared to the genetic equilibrium. The Guinean zone presents moderate values with an average Na= 10.27 and He= 0.75, indicating significant genetic diversity (Table 7). Additionally, the Fis= -0.02 in the Guinean zone is close to zero, suggesting a balanced heterozygosity compared to the expected genetic equilibrium. The detailed distribution of the genetic diversity is presented in Table 7, adapted from Houehanou *et al.* (2023) and was used to assess the impact of climate change.

3.5. *Correlation between genetic and phenotypic characteristic and environmental variables*

Of all the phenotypic traits, only one showed a correlation with an environmental variable for all subgroups (Fig. 4). This was the expected heterozygosity (He), which showed a significant negative correlation with temperature seasonality (bio-4) (Fig. 5). For morphological traits, specific correlations were observed according to the subgroups. For the Sudanian subgroup, two traits showed a correlation with environmental variables (Fig. 4). Mean seed weight (weightseed) is positively and

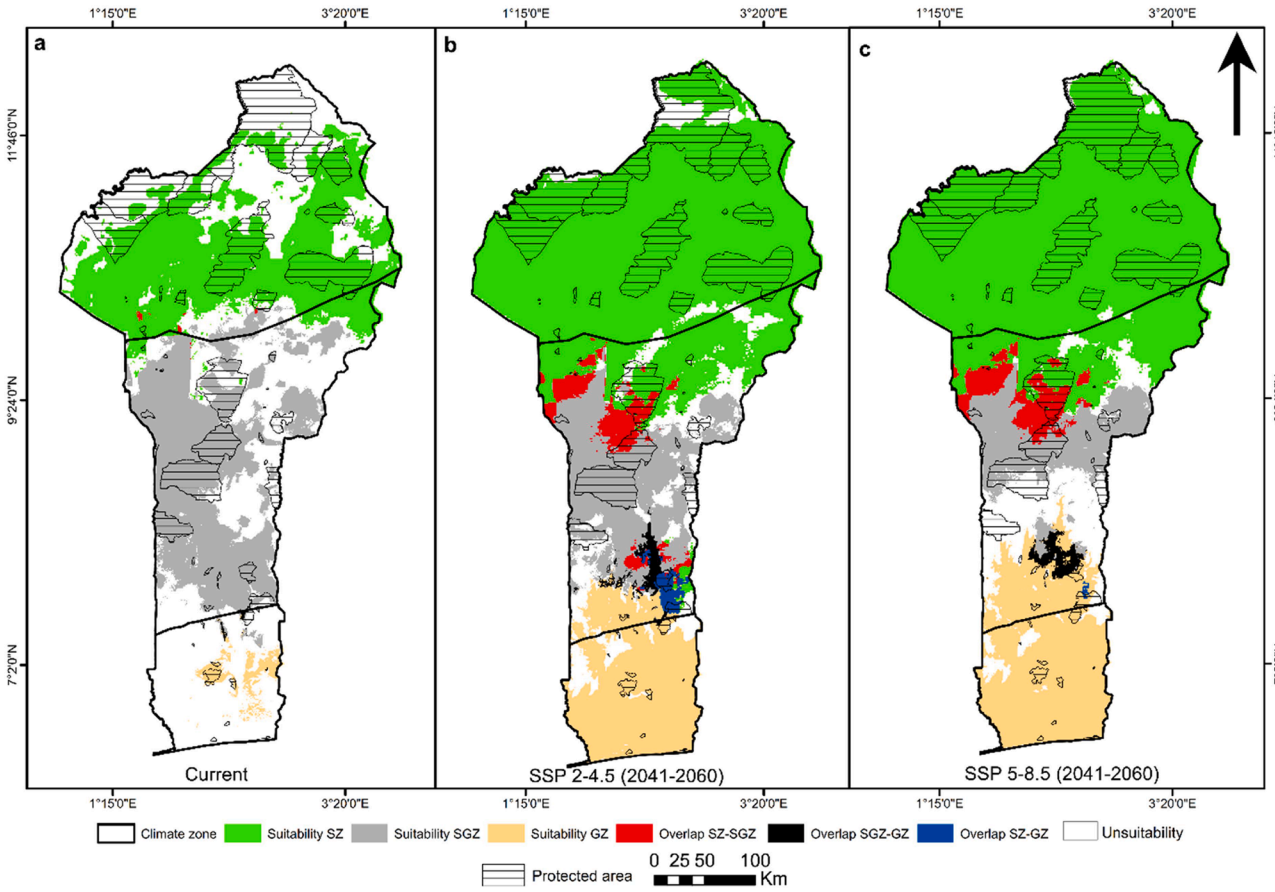


Fig. 3. Projections of the populations in potentially suitable habitats under current and future climate under the SSP2–4.5 and SSP5–8.5 scenarios.

Table 4
Dynamic of the suitable areas for *Afzelia africana* under the current and future climates at 2050-time horizon.

Subgroups	Scenarios	Suitable habitat	
		Area in Km^2 (Protected area)	Tendency in % (Protected area)
Sudanian (SZ)	Current	35,042.41 (10,197.25*)	
	SSP 2–4.5	69,787.88 (30,371.01*)	+99.15 (+197.84*)
	SSP 5–8.5	70,936.54 (21,875.82*)	+102.43 (+114.53*)
Sudano-guinean (SGZ)	Current	26,879.24 (5361.59*)	
	SSP 2–4.5	20,973.27 (4517.76*)	-21.97 (-15.74*)
	SSP 5–8.5	15,859.10 (3586.69*)	-40.10 (-33.10*)
Guinean (GZ)	Current	1710.31 (213.89*)	
	SSP 2–4.5	17,583.69 (801.89*)	+928.10 (+274.91*)
	SSP 5–8.5	20,648.66 (904.22*)	+1107.31 (+322.75*)
Overlap of SZ-SGZ	Current	49.49 (1.68*)	=
	SSP 2–4.5	1917.49 (485.66*)	+3774.50 (+28,808.33*)
	SSP 5–8.5	197,872 (577.09*)	+399,722.19 (+34,250.60*)
Overlap of SGZ-GZ	Current	83.88 (10.07*)	
	SSP 2–4.5	1755.60 (253.32*)	+1992.99 (+2415.60*)
	SSP 5–8.5	1524.09 (159.37*)	1716.99 (+1482.62*)
Overlap of SZ-GZ	Current	0 (0*)	
	SSP 2–4.5	411.01 (146.79*)	+
	SSP 5–8.5	36.91 (10.07*)	+

* Suitable areas and tendency of protected area

Table 5
Phenotypic diversity index (*H'*) for each trait across climatic zones.

Morphological traits	*H'* index			
	Guinean	Sudanian	Sudano-Guinean	Overall
Lengthfr	0.88	0.92	0.40	0.96
Widthfr	0.86	0.24	0.00	0.93
Thickfr	0.61	0.64	0.79	0.85
Weigtfr	0.79	0.24	0.00	0.95
Weigttotseed	1.00	0.81	0.40	0.95
Seedrate	0.76	0.91	0.68	0.98
Lengthseed	0.82	0.83	0.40	0.90
Widthseed	0.90	0.96	0.79	0.94
Thickseed	0.81	0.83	0.68	0.87
Weightseed	0.80	0.92	0.36	0.95
Grand diversity mean	0.82	0.73	0.45	0.93

Legend: Lengthfr = length of fruit, Lengthseed = length of seeds, Seedrate = seed rate, Thickfr = thickness of fruit, Thickseed = thickness of seeds, Weightseed = seed weight, Weigtfr = fruit weight, Weigttotseed = total seed weight, Widthfr = width of fruit, Widthseed = width of seeds

significantly correlated with rainfall in the wettest month (bio-13) and temperature seasonality (bio-4). Similarly, the weighted fraction (weightfr) is positively and significantly correlated with temperature seasonality (bio-4). For the Sudano-Guinean subgroup, the weighted fraction (weightfr) is positively and significantly correlated with precipitation of the wettest month (bio-13) and mean diurnal temperature variation (bio-2), but significantly negatively correlated with the soil variable. Mean seed weight (weightseed) is positively and significantly correlated with temperature seasonality (bio-4), but significantly negatively correlated with isothermality (bio-3) and precipitation of the driest month (bio-14). Finally, seed length (lengthseed) is significantly

Table 6
Estimated phenotypic diversity index (*H'*) for each trait across populations of *A. africana*.

Morphological traits	*H'* index												
	Ada	Aza	Bat1	Bat2	Kon	Kot1	Kot2	Kot3	Oue	Par	Pen3	Tch1	Tch2
Lengthfr	0.42	0.91	0.80	0.79	0.88	0.85	0.50	0.42	0.65	0.40	0.77	0.83	0.83
Widthfr	0.00	0.47	0.47	0.00	0.00	0.72	0.47	0.00	0.00	0.00	0.00	0.72	0.00
Thickfr	0.36	0.49	0.68	0.38	0.36	0.44	0.50	0.00	0.41	0.79	0.62	0.49	0.00
Weigtfr	0.97	0.88	0.47	0.00	0.47	0.72	0.47	0.00	1.00	0.00	0.00	0.00	0.00
Weigttotseed	0.42	0.97	0.59	0.58	0.64	0.59	0.66	0.62	0.86	0.40	0.68	0.83	0.00
Seedrate	0.42	0.38	0.68	0.71	0.93	0.42	0.80	0.25	0.35	0.68	0.83	0.59	0.77
Lengthseed	0.31	0.68	0.59	0.66	0.80	0.59	0.31	0.37	0.35	0.40	0.68	0.31	0.40
Widthseed	0.49	0.65	0.95	0.70	0.74	0.92	0.68	0.78	0.50	0.79	0.65	0.49	0.33
Thickseed	0.66	0.68	0.80	0.58	0.64	0.80	0.59	0.62	0.65	0.68	0.68	0.59	0.43
Weightseed	0.53	0.57	0.73	0.52	0.74	0.61	0.45	0.44	0.58	0.36	0.52	0.59	0.36
Grand diversity mean	0.46	0.67	0.67	0.49	0.62	0.67	0.54	0.35	0.53	0.45	0.54	0.54	0.31

Legend: Adm: Adakplame, Aza: Azalime, Bat1: Batia1, Bat2: Batia2, Kon: Konkombri, Kot1: Koto1, Kot2: Koto2, Kot3: Koto3, Oue: Ouedeme, Par: Parakou, Pen3: Pendjari3, Tch1: Tchatingou1, Tch2: Tchatingou2, Lengthfr = length of fruit, Lengthseed = length of seeds, Seedrate = seed rate, Thickfr = thickness of fruit, Thickseed = thickness of seeds, Weightseed = seed weight, Weigtfr = fruit weight, Weigttotseed = total seed weight, Widthfr = width of fruit, Widthseed = width of seeds

Table 7
Mean values of genetic diversity parameters among populations, climatic zones and adapted from Houehanou *et al.* (2023).

Populations		Code	*N*	*Na*	*Ne*	F_{IS}	H_O	H_E
Pendjari1		Pop1	8	5.45	3.90	-0.15	0.78	0.69
Tchatingou1		Pop2	9	5.82	4.20	-0.08	0.77	0.72
Konkombri		Pop3	8	5.27	3.81	-0.26	0.88	0.70
Batia1		Pop4	10	5.36	3.67	-0.39	0.89	0.66
Batia2		Pop5	10	5.09	3.77	-0.35	0.90	0.69
Tchatingou3		Pop6	19	7.64	4.76	-0.16	0.83	0.72
Pendjari2		Pop7	17	6.00	4.05	-0.06	0.75	0.71
Forêt classée de Ouènou-Bénou		Pop8	10	4.64	3.42	-0.10	0.70	0.65
Forêt classée de Sota		Pop9	6	3.73	2.87	-0.10	0.64	0.59
Karimama-Mamassigouma		Pop11	4	3.36	2.56	-0.28	0.74	0.58
Banikoara-Sampèto		Pop12	4	3.00	2.44	0.02	0.48	0.49
Parakou		Pop13	3	3.64	3.09	-0.21	0.79	0.63
Glazoué-Ouèdèmè		Pop14	4	3.73	3.28	-0.40	0.89	0.65
Bassila		Pop15	8	2.55	2.10	-0.61	0.82	0.52
Alafarou		Pop16	7	4.91	3.51	-0.32	0.88	0.67
Tchatchou		Pop17	10	5.18	3.88	-0.45	0.93	0.68
Beterou		Pop18	10	5.36	3.81	-0.32	0.88	0.69
Penelan		Pop19	10	5.45	4.10	-0.36	0.94	0.70
Koko		Pop20	20	7.82	4.85	-0.18	0.87	0.75
Adakplame		Pop21	5	3.73	3.03	-0.49	0.93	0.63
Azalime		Pop22	16	6.36	3.90	-0.06	0.70	0.67
Koto1		Pop23	15	5.82	3.97	-0.15	0.77	0.66
Koto3		Pop24	12	6.55	4.52	-0.09	0.80	0.74
Sud-Ouest Lama		Pop25	12	5.27	3.74	-0.11	0.76	0.70
Koto2		Pop26	14	5.18	3.54	0.09	0.60	0.67
Sud-Est Lama		Pop27	13	6.09	4.14	-0.16	0.81	0.71
Total			264					
Mean				5.12	3.65	-0.22	0.80	0.66
Climatic zones								
Guinean	Mean		79.27	10.27	4.98	-0.02	0.75	0.75
	Standard error (SE)		0.95	1.61	0.76	0.05	0.04	0.04
Sudanian	Mean		96.64	11.36	5.66	-0.02	0.79	0.79
	Standard error (SE)		1.56	1.83	0.75	0.04	0.03	0.03
Sudano-Guinean	Mean		68.73	10.64	5.00	-0.20	0.75	0.75
	Standard error (SE)		0.82	1.72	0.71	0.05	0.04	0.04

Legend: *N: Sample size, Na*: Allelic richness, *Ne*: Average number of alleles per locus, F_{IS}: fixation index, H_O : Observed Heterozygosity H_E : expected heterozygosis, *SE: Standard error*

negatively correlated with precipitation of the driest month (bio-14) and precipitation of the wettest month (bio-13). For the Guinean subgroup, seed length (lengthseed) is positively and significantly correlated with mean temperature of the coldest quarter (bio-11), but negatively and significantly correlated with isothermality (bio-3) and precipitation of the driest month (bio-14). Mean seed weight (weighted) is positively and significantly correlated with temperature seasonality (bio-4), mean temperature of the coldest quarter (bio-11), and precipitation seasonality (bio-15), but negatively and significantly correlated with isothermality (bio-3) and precipitation of the driest month (bio-14). Finally, seed width (widthseed) is positively and significantly correlated with the mean temperature of the coldest quarter (bio-11) and weighted fraction (weightfr) is positively and significantly correlated with elevation (elev), but negatively and significantly correlated with the soil variable.

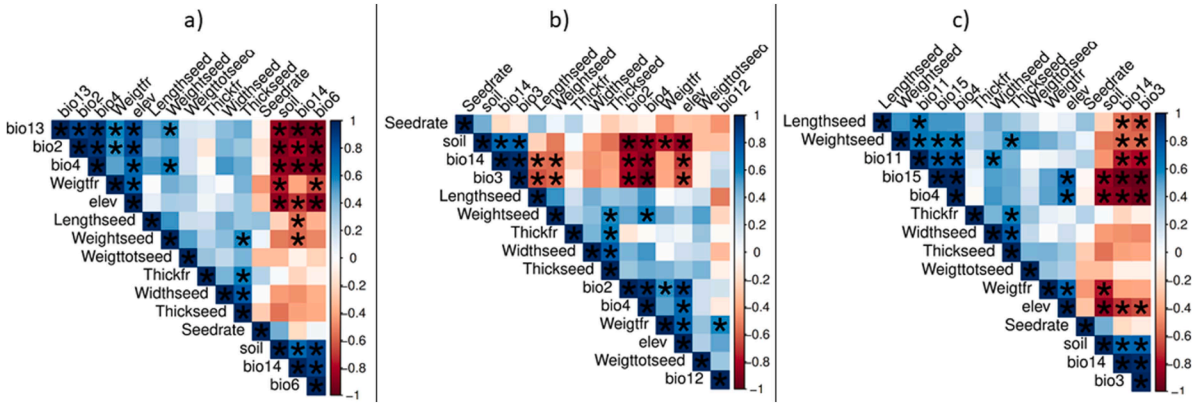


Fig. 4. Correlogram of environmental bioclimatic variables and phenotypic diversity parameters. Positive correlations are displayed in blue, and negative correlations are shown in red. The intensity of the color and the size of the circles are proportional to the correlation coefficients. On the right side of the correlogram, the color legend represents the correlation coefficients and their corresponding colors. A combination of the correlogram with a significance test using p-value > 0.05 was performed, and non-significant correlations are marked with a star. ZS (a), ZSG (b) and ZG (b).

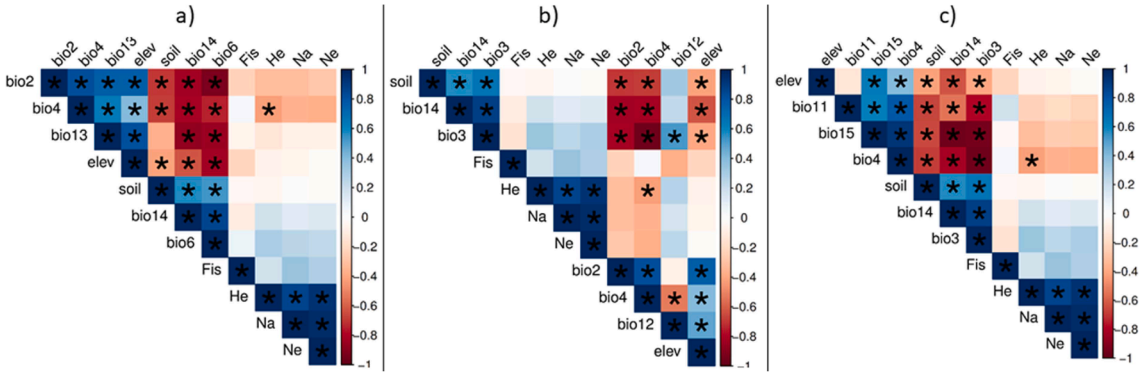


Fig. 5. Correlogram of environmentally bioclimatic variables and genetic diversity parameters. Positive correlations are displayed in blue, and negative correlations are shown in red. The intensity of the color and the size of the circles are proportional to the correlation coefficients. On the right side of the correlogram, the color legend represents the correlation coefficients and their corresponding colors. A combination of the correlogram with a significance test using p-value > 0.05 was performed, and non-significant correlations are marked with a star. ZS (a), ZSG (b) and ZG (b).

3.6. Impact of climate change on the distribution of genetic and phenotypic diversities

Populations with low and high phenotypic diversity are found in suitable habitats in the Sudanian zone and unsuitable habitats in the Guinean zone under current climates conditions (Fig. 6.a). Populations with intermediate phenotypic diversity, identified in the three climatic zones, are present in both suitable and unsuitable habitats in the Sudanian and Sudano-Guinean zones. In the Guinean zone, however, they are found exclusively in unsuitable habitats.

Climate projections under the SSP 2–4.5 scenario for 2041–2060 indicate that climatic conditions will become suitable for all three types of phenotypic diversity in the Sudanian and Guinean zones (Fig. 6.b). In the Sudano–Guinean zone, populations with intermediate phenotypic diversity in Parakou will remain in unsuitable habitats, while those in Ouedeme will be in suitable habitats.

Under the SSP 5–8.5 scenario, similar trends will be observed, with the exception of the Ouedeme population with intermediate phenotypic diversity, which this time will be located in a habitat typically suitable for two distinct subgroups: the Sudano-Guinean subgroup and the Guinean subgroup (Fig. 6.c).

Populations characterized by a lack of heterozygosity, currently located in unsuitable habitats, will be found in suitable habitats under both future climate scenarios (Fig. 7). As for populations characterized by an excess of heterozygosity, their wide distribution will allow them to occupy different types of habitat, with a majority in suitable habitats according to current and future projections.

4. Discussion

4.1. Performance of the model and key environmental factors affecting the prediction of Afzelia africana distribution

The results of this study demonstrate a strong predictive capacity of the models, as evidenced by the high performance indices (AUC, TSS, and SEDI). This is particularly true for the Guinean subgroup, whose values (AUC: 0.95; TSS: 0.81; SEDI: 0.92) indicate excellent accuracy.

A critical step in the study was the analysis of multicollinearity, which enabled the selection of the most relevant variables while minimizing redundancies. This approach highlighted the significance of edaphic and topographic factors, such as soil (in the Sudano–Guinean model) and altitude (in the Guinean model), alongside to climatic variables. These results align with the conclusions of Dimobe *et al.* (2020) and Biaou *et al.* (2023), who also emphasized the key role of climatic and edaphic variables in the distribution of woody species in West Africa. Nevertheless, climatic variables remain essential to explain the distribution of *Afzelia africana*. Seasonality of temperature (bio-4) and precipitation of the driest month (bio-14) were found to be determinants, reflecting the species' sensitivity to extreme thermal fluctuations and water deficits. These factors directly influence vital processes such as seed viability and seedling survival. By combining climatic, edaphic and topographic variables, this study captures the complexity of the

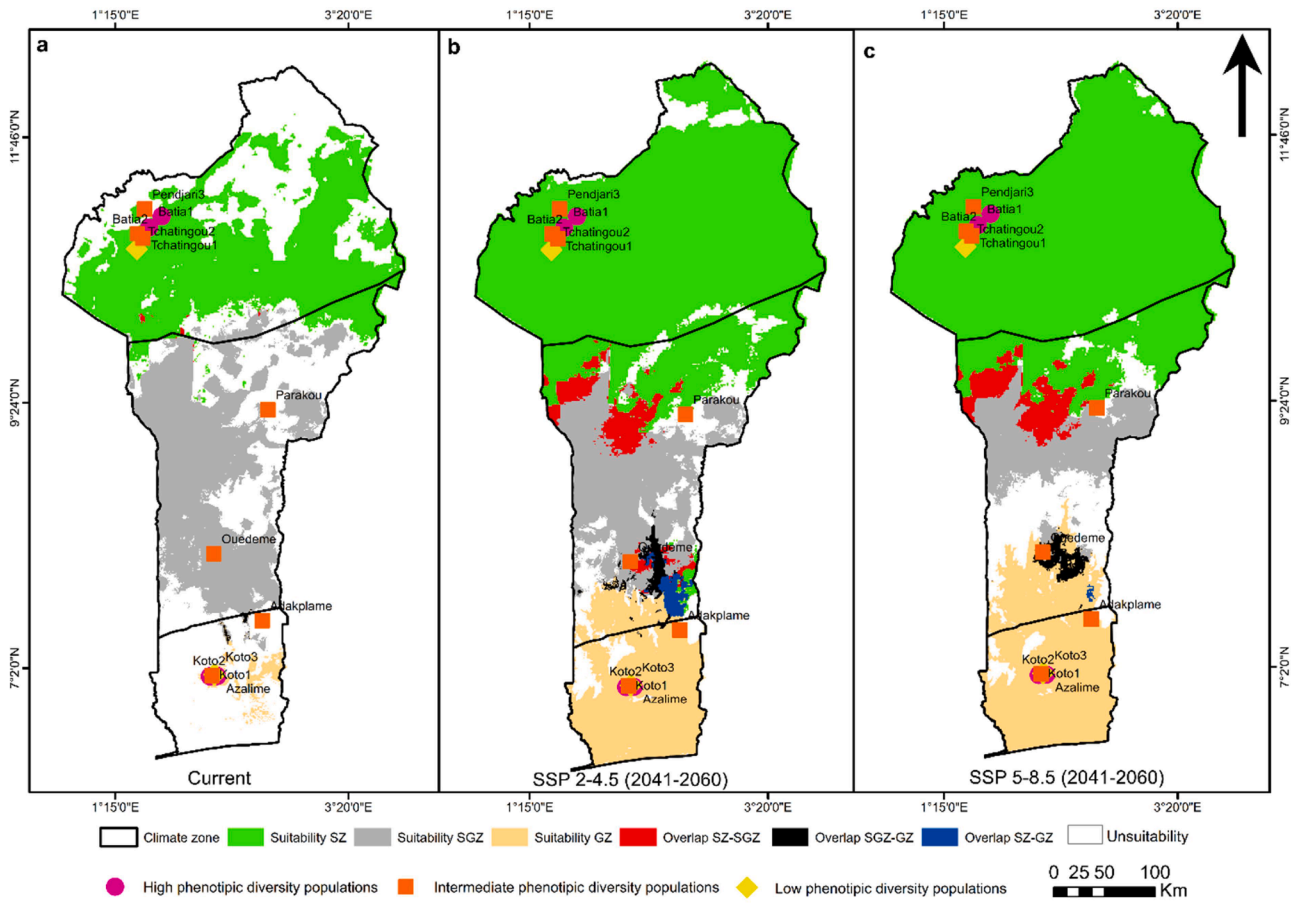


Fig. 6. Projections of the phenotypic diversity of populations in predicted suitable habitats under current and future climate under the SSP2–4.5 and SSP5–8.5 scenarios.

ecological habitats of *Afzelia africana*.

4.2. Impact of f climate change on the distribution of suitable habitats of *Afzelia africana*

The results of this study reveal intricate dynamics in the distribution of *A. africana* in Benin, influenced by climate change and differing management practices between protected and unprotected areas. While the Sudanian and Guinean zones show an increasing potential to support this species, the Sudano–Guinean zone is experiencing a decline in suitable habitats. Interestingly, unprotected areas, despite being more constrained, offer larger expanses of potentially suitable habitats. In contrast, protected areas, though characterized by high-quality habitats, occupy only a limited portion of the territory and are often subject to anthropogenic pressures (Lindsey *et al.,* 2013, Watson *et al.,* 2014, Gouwakinnou *et al.,* 2019, Suarez *et al.,* 2023).

Many studies have highlighted that climate change is causing species to shift their climate-adapted habitats towards higher latitudes and altitudes, as demonstrated by the work of Aguirre-Gutiérrez *et al.* (2017) and Lenoir *et al.* (2020). The impact of future climate change on the geographic distribution of *Afzelia africana*, as explored in this study, shows variations depending on the new emission scenarios used, similar to previous studies using older emission scenarios (Gbètoho *et al.,* 2017, Balima *et al.,* 2022). The lowest emission scenario (SSP2–4.5) shows a larger spatial coverage of potentially unsuitable areas compared to the highest emission scenario (SSP5–8.5). This suggests that, without the mitigation measures outlined in SSP5–8.5, the negative impacts of climate change on the species' range would be comparatively less severe, in contrast to the situation under the SSP2–4.5 scenario, which would significantly affect the species' distribution range. A possible explanation for these contrasting results may lie in the evolutionary ecological niche hypothesis, which assumes that species maintain constant environmental preferences over time. Species may evolve or adapt to new climatic conditions (Biaou *et al.,* 2023a). The result is in line with the findings of Harris *et al.* (2014), who state that emission scenarios are the main source of uncertainty in the model. In addition, some unanticipated impacts of climate change can be observed. It is plausible that specific factors associated with the lowest emission scenario (SSP2–4.5) could have unforeseen repercussions in regions that may not be suitable. For example, changes in precipitation patterns or other climate variables could create conditions that favor the presence of the species in these regions. The projected habitat loss (Gbètoho *et al.,* 2017, Dimobe *et al.,* 2020a) and potential range expansion (Adjahossou *et al.,* 2016, Hounkpèvi *et al.,* 2016) of woody vegetation in response to impeding climate change highlights the uncertainties facing the West African region regarding future climate trends. According to most climate projections, West African countries are expected to experience an increase in precipitation (Heubes *et al.,* 2013, Platts *et al.,* 2015). Conversely, some authors (Fandohan *et al.,* 2013) have reported a decrease in precipitation in West Africa. Climate projections for West Africa (IPCC 2023) show considerable variability, which poses a major challenge for regional ecological simulations and hinders accurate conclusions on the impact of future climate change on plant biodiversity and ecosystems. The effects of climate change, such as habitat loss or range expansion, species turnover, and greening or drying of the Sahel, remain uncertain (Balima *et al.,* 2022). However, certain species will be more vulnerable to the effects of climate change than others, with the ability to adapt, expand their spatial extent, or shift their geographic range (Balima *et al.,*

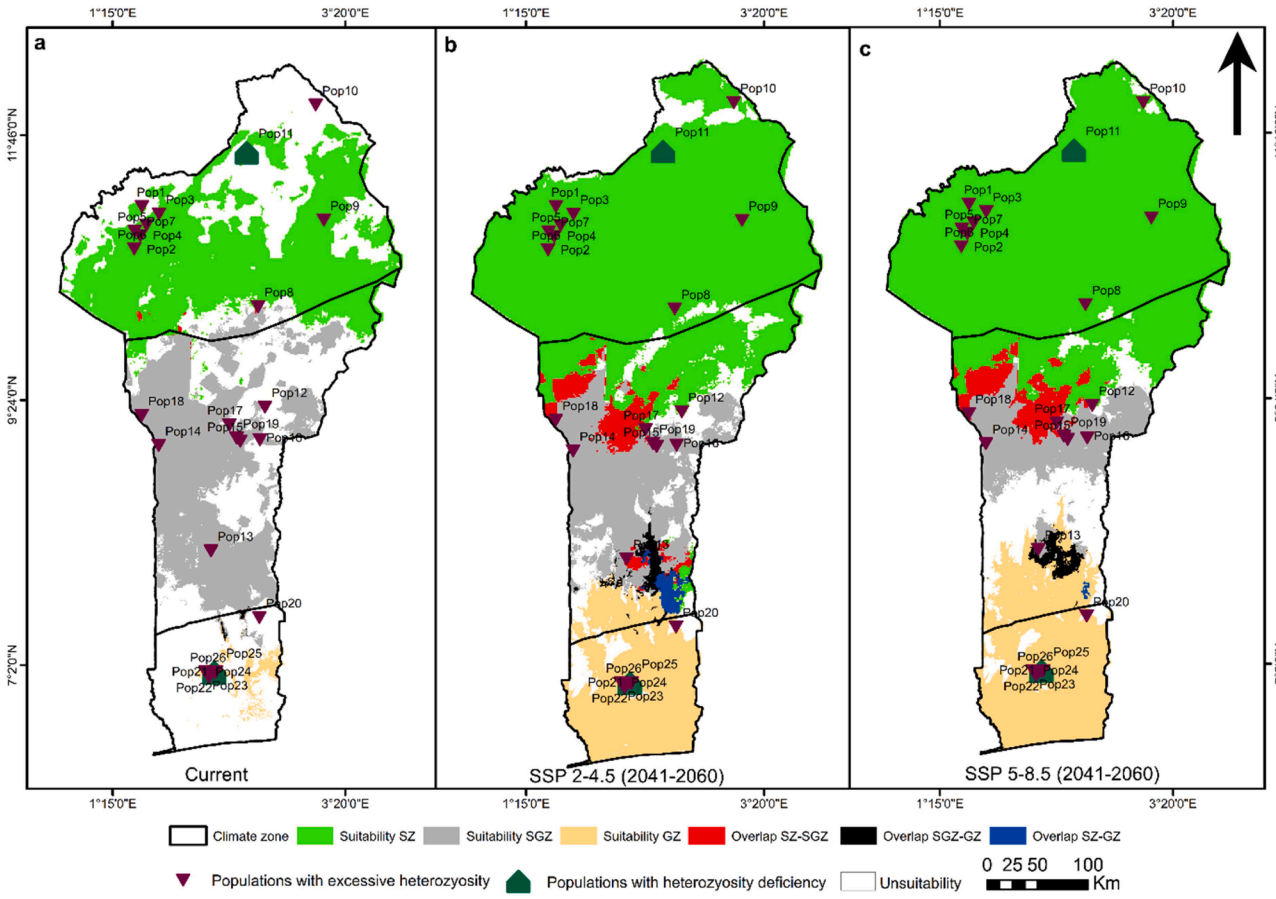


Fig. 7. Projections of genetic diversity of populations in predicted suitable habitats under current and future climate under the SSP2–4.5 and SSP5–8.5 scenarios.

2022). Climate change in Benin is likely to significantly affect the distribution of suitable habitats for *Afzelia africana*. Variations in temperature and precipitation could lead to a desynchronisation of phenological events such as flowering and fruiting, thereby disrupting reproductive processes. These changes may also affect interactions with pollinators, which are crucial for the reproduction of *Afzelia africana*.

4.3. Impact of climate change on the species phenotypic and genetic diversity distributions

This study highlights the differences within populations of *Afzelia africana* in terms of phenotypic diversity and genetic diversity when exposed to climate change. This heterogeneity is likely a consequence of the species' adaptability to different habitats, contributing to its ability to survive and thrive under changing climatic conditions (Hounkpèvi *et al.,* 2016). Species adaptations may explain the correlations identified for morphological traits with specific environmental conditions or the result phenotypic plasticity of the species (Dauphin *et al.,* 2020). For example, heavier fruits may be favored in environments with higher temperatures, which can be explained by the need for a greater energy and nutrient reserves in fruits to support embryo development under more demanding environmental conditions (Rajametov *et al.,* 2021). Conversely, longer seeds may confer advantages in cooler environments, possibly related to seed dispersal strategies. Plants with longer seeds may benefit from better wind dispersal or other mechanisms in environments with shorter growing seasons due to colder temperatures. Similar observations were made by Tamme *et al.* (2014), who predicted maximum species dispersal distances based on simple plant traits and found significant variation in seed size based on temperature. The negative correlation between fruit weight and precipitation suggests that water availability may influence fruit size (Rahmati *et al.,* 2015). Similarly, environmental variables may influence seed production, which could be crucial for the species' survival and reproduction of the species (Moreira *et al.,* 2020). Regarding genetic diversity, the negative correlation between expected heterozygosity and temperature seasonality (bio4) could be related to selection mechanisms or species dispersal processes (Liu *et al.,* 2016).

There is considerable variation in the morphological diversity of the traits measured. This study also found a high level of natural variation in the population of *Azelia africana* in different climatic zones. The populations of Azalime, Batia1, Konkombri, Ouedeme and Koto1 are known to have levels of diversity due to their occupation of suitable ecological niches that provide environmental conditions conducive to their survival and reproductive success. Furthermore, the level of phenotypic diversity of Azalime, Batia1, Konkombri, Ouedeme and Koto1 includes a wide range of observable traits within the population. This increased phenotypic diversity may confer greater adaptability and flexibility in response to environmental changes, thereby maintaining their high ecological status under different climate scenarios. In contrast, the Koto3 and Tchatingou2 populations exhibit a low phenotypic diversity status, which may be the result of selective logging. Most populations occupying a suitable habitat within the SSP2–4.5 are also found in a suitable habitat within the SSP5–8.5. This means that populations that occupy suitable ecological niches, whether greenhouse gas emissions decrease or increase, show a certain degree of resilience to climate change. This resilience can be attributed to their adaptation to the prevailing environmental conditions, enabling them to effectively cope effectively with a certain degree of climate variability.

Regarding the impact of climate change on genetic diversity, the Bassila population has a lower genetic diversity (*Na* and *Ne*) than the other populations, and if it is currently located in a suitable habitat, it will no longer be there under the two scenarios (SSP2–4.5 and

SSP5–8.5). This suggests that climate change may affect the availability and quality of suitable habitat. Populations rely on the specific environmental conditions of their habitat for their survival and reproduction (Auffret *et al.,* 2017). If these conditions change due to climate change, some populations may find themselves in less suitable habitats, which may lead to a reduction in their genetic diversity (Knowlton and Graham, 2010). Indeed, climate change can result in modifications of landscapes and habitats that affects the dispersal of individuals and the possibility of genetic exchange between populations (Knowlton and Graham, 2010). Geographical barriers exacerbated by climate change may also have contributed to the observed genetic differentiation (Le Corre *et al.,* 1997).

It should be noted that individuals in the Sudanian zone are less genetically diversified than those in the Sudano–Guinean zone. This is due to the fact that the Sudanian climate is more stable than that of the transition zone. Species from the Sudano–Guinean zone will be more subject to continuous adaptation to climatic fluctuations. Some populations, such as Adakplame, may have undergone positive selection pressure, where specific traits or genetic combinations have given them an advantage in their habitat. This phenomenon could explain their occupation of a suitable ecological niche in both the SSP2–4.5 and SSP5–8.5 scenarios. Conversely, populations such as Glazoué-Ouèdémè under the SSP5–8.5 scenario, which no longer benefit from a suitable habitat, may experience genetic diversity. This could be attributed to various factors such as geographical isolation, genetic drift, or distinct selective pressures in their current environment (Méndez-Cea *et al.,* 2023). These mechanisms can lead to genetic changes that make them less adapted to their original habitat (Wasserman *et al.,* 2012). Furthermore, the existence of a suitable ecological niche despite the scarcity of heterozygotes in Koto2 could indicate a recent decrease in genetic variability. This result could be due to events such as demographic bottlenecks or abrupt environmental changes that have reduced the genetic diversity of the population. Koto2 may be proactively adapting to its environment. In other words, the observed lack of heterozygotes may be due to selective pressures favoring certain alleles that confer an advantage in the current habitat (Méndez-Cea *et al.,* 2023). Therefore, Koto2 may be able to maintain its suitable status despite different climate scenarios.

4.4. Implications for the long-term conservation and sustainable management of Afzelia africana

This study has shown that the creation of genetic reserves and the promotion of reproduction among genetically distinct individuals can contribute to the preservation of genetic diversity in *Afzelia africana* populations, particularly in the Azalime, Batia1, Konkombri, and Koto1 populations. Given the high phenotypic diversity status of the Azalime, Batia1, Konkombri and Koto1 populations, it is worth considering using their seeds in the future reforestation schemes, especially as their habitat is conserved in both scenarios. Furthermore, this study has identified populations with high genetic diversity and resilience, providing valuable insights into the adaptive traits of the species. The knowledge gained from this study can be used to direct conservation and management efforts towards individuals or populations with suitable adaptive traits, such as the Adakplame population. The identification of populations with low levels of genetic diversity, such as the Bassila population observed in this study, highlights priority areas for conservation. This population may require tailored protection and management measures to prevent further loss of genetic diversity and ensure long-term viability. Given the potential impact of climate change on habitat availability and quality, it is of utmost importance to conserve habitats that are suitable to *Afzelia africana*. The results of this study highlight the importance of conserving currently suitable habitats to maintain genetically diverse and healthy populations. However, it should be noted that phenotypic and genotypic diversity manifests itself among populations, highlighting the importance of integrating intraspecific diversity into species conservation and management, particularly in the context of climate change.

Furthermore, research conducted by Habou *et al.* (2021) shows that changes in climate variables, particularly precipitation and temperature, have a significant impact on biodiversity and the distribution of habitats suitable to species. However, it is important to note that the accuracy of predictive models is limited due to uncertainties associated with parameters of ecological interactions, as well as species-specific dispersal constraints. Furthermore, it is evident that the majority of models in the subregion have not adequately considered the impacts of intraspecific diversity on population distributions, as noted by Biaou *et al.* (2023). Nevertheless, it is widely accepted that genetic diversity plays a crucial role in the adaptation of species to their respective environments and defines the variability of species populations, as noted by Maguire *et al.* (2018). Therefore, it is important to consider this parameter and identify ecotypes in order to improve the modelling of species habitats. The integration of the phenotypic, genetic, and habitat distribution modeling approaches for the studied species provides a holistic perspective of its biology and ecology, thereby improving the understanding of its adaptation to the environment. As a result, the combined results of the three methods strengthen the basis for conservation by identifying genetically distinct populations with specific adaptations and key habitats. This approach refines conservation strategies to ensure the long-term viability of the species, while providing invaluable insights to guide management and conservation efforts.

5. Conclusion

The present study assessed the phenotypic and genetic diversity variation of *Afzelia africana* populations in relation to habitat suitability across climatic zones in Benin and provided useful information for the sustainable management and conservation of its populations. The results showed that the genetic and phenotypic diversity variation between populations from different climatic zones is affected by a variation in the suitability of *Afzelia africana* habitats. The former is caused by global climate change under the two scenarios used. Thus, the climate change factor threatens the genetic and phenotypic diversity of *Afzelia africana*. We suggest that the populations with high genetic diversity level and located in suitable areas need to be maintained for forest conservation. Seeds should be collected from these populations to establish seed orchards as genetic resources. During the seed collection process, it is crucial to gather seeds from a diverse range of distantly related mother plants that are minimally related genetically. This approach helps prevent future inbreeding depression when the seeds are used for planting. Thus, this research lays the foundation for future investigations aimed at developing appropriate strategies for the species domestication. Finally, innovative approaches and assessment tools are essential to better understand the relationship between climate change and the genetic and phenotypic diversity of plant species. It is also crucial to integrate intraspecific diversity into conservation and management efforts to ensure the species' long-term sustainability.

CRediT authorship contribution statement

Dowo Michée Adjacou: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Rodrigue Idohou:** Writing – review & editing, Writing – original draft. **Alain Sèakpo Yaoitcha:** Writing – review & editing. **Jacques Kadjobgé Idohou Ayena:** Writing – review & editing, Formal analysis. **Thierry Dehouegnon Houehanou:** Writing – review & editing, Writing – original draft, Supervision, Resources, Funding acquisition. **Gérard Nounagnon Gouwakinnou:** Writing – review & editing.

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.

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Data availability

Data will be made available on request.

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