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# Climate change-induced shifts in the ecological niches of Parkia biglobosa (Jacq.) and Vitellaria paradoxa CF Gaertn, two species of agroforestry parks in Benin, West Africa

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ABSTRACT

Understanding the effects of climate change on species distribution patterns is fundamental to biogeography and evolutionary ecology, especiallyfor socio-economically important agroforestry species such as *Parkia biglobosa* R. Br. ex Benth and *Vitellaria paradoxa* CF Gaertn. However, gaps remain regarding the evolution of ecological niches of these widespread species. This study examines the effects of climate change on *P. biglobosa* and V. *paradoxa*, two key species of agroforestry parklands in Benin. By integrating intraspecific variation into niche modeling, three homogeneous subgroups (North, Center, and South) were identified and analyzed under current and future climate conditions. Maximum Entropy Modeling (MaxEnt), was used, chosen for its predictive power and flexibility in correcting for data bias. Climate projections were based on common socio-economic scenarios (SSP2-4.5 and SSP5-8.5), representing a moderate mitigation scenario and a high emissions scenario, respectively. The results showed significant climate change effects across subgroups for both species, mediated by temperature and humidity. Under the SSP2-4.5 scenario, the northern subgroup of *P. biglobosa* exhibited habitat shifts towards the central and southern subgroup regions, while the central and southern subgroups showed predictive habitat loss. For V. *paradoxa*, this scenario predicted significant habitat loss for the northern and central subgroups, while the southern subgroup demonstrated habitat expansion along altitudinal gradients. The more severe SSP-5–8.5 scenario predicted extensive habitat loss for both species. The Sudano-Guinean and Guineo-Congo zones remain climatically suitable for both species under future projections. The most pronounced interspecific niche overlap occurred between the northern and southern subgroups, indicating considerable ecological similarity. These results highlight the need for climate-adaptive management strategies in agroforestry systems with particular emphasis on subgroups facing imminent habitat loss. Future research directions should explore adaptive management approaches while maintaining essential ecosystem services and supporting local livelihoods.

## 1. Introduction

Understanding species distribution and abundance patterns is fundamental to biodiversity conservation strategies in the context of accelerating climate change (Agbo et al., 2019; Noulekoun et al., 2017; Zhang et al., 2019). Climate change affects species' distribution ranges, phenological patterns, physiological processes, and genetic composition, posing important challenges for biodiversity conservation (Prasad and Potter, 2017; Thuiller et al., 2005). In addition, ecological factors impose long-term constraints on population distributions, raising critical questions about species' responses to climate change. To address these challenges, researchers have developed various ecological tools including modelling tools for plant population dynamics. Some of these modeling tools include species distribution models (SDMs), dynamic global vegetation models (DGVMs), population viability analyses (PVAs), metapopulation models, landscape models, niche mappers, Bayesian belief networks (BBNs), ecohydrological models, agent-based models (ABMs), and ecosystem models (Elith and Leathwick, 2009;

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Guisan and Thuiller, 2005; Hanski, 1999). Among these methods, Species Distribution Modeling (SDM) has emerged as the dominant analytical framework (Steen et al., 2024; Toffa et al., 2022) integrating species occurrence data with environmental variables to assess spatial distributions (Zhang et al., 2019).

The SDM framework encompasses multiple algorithmic approaches, including MaxEnt (maximum entropy Modeling), Bioclim, GLM (generalized linear model), GAM (generalized additive model), GARP (genetic algorithm for rule-set production), random forest, and ANN (artificial neural network), each optimized for specific data types and research objectives (Elith and Leathwick, 2009; Guisan and Thuiller, 2005). In particular, the MaxEnt algorithm has demonstrated superior predictive capabilities (Phillips et al., 2017; Zeng et al., 2016). This methodology, based on Hutchison's (1957) fundamental ecological niche concept, has successfully characterized habitat distributions across a range of species. Recent applications include assessments of *Detarium senegalensis* J.F.G.mel. in Togo (Kore et al., 2023); *Balanites aegyptiaca* (L.) Delile. in Niger (Habou Abdou et al., 2021); *V. paradoxa* C.F.Gaertn in Burkina (Dimobe et al., 2020); *Cesalpinia bonduc* (L.) Roxb in Benin (Wouyou et al., 2022), *Xylosandrus ambrosia* beetles in France (Urvois et al., 2021); nesting birds in Belgium (Thomas, 2020); *Tamarindus indica* L. in Togo (Samarou et al., 2023); *Pterocarpus santalinus* Poir., China (Zhang et al., 2024), *Prosopis africana* Guill. & Perr. Taub in Benin (Tessi, 2024), *Adansonia digitata* L. in Malawi (Kokou et al., 2024), *Annona senegalensis* Pers. in Burkina Faso (Dao et al., 2024). Despite these advances, a critical limitation remains that most studies have not adequately addressed the heterogeneity in climatic conditions across species ranges, a factor that influences projections of climate change impacts on species niche distributions (Biaou et al., 2023; Chardon et al., 2020).

Identifying homogeneous and distinct subgroups within a species' range enables allows for a more accurate characterization of the niche requirements of different population segments (Austin and Van Niel, 2011; Smith et al., 2019). This approach is particularly relevant given that individuals within species populations experience differential exposure to climatic factors across their range (Hällfors et al., 2016). Recent investigations have shown that dividing populations into homogeneous subgroups significantly improve the accuracy of species niche modeling accuracy and provides deeper insights into local adaptation strategies (Atakpama et al., 2023; Biaou et al., 2023; Deguenonvo et al., 2024; Sinadouwirou et al., 2022; Yamontche et al., 2024). Furthermore, this methodological framework facilitates the empirical testing of niche conservatism hypotheses both within species populations and across species (Datta et al., 2019), thereby advancing our understanding of evolutionary responses to environmental heterogeneity. The niche conservatism hypothesis was first proposed and documented by Peterson et al. (1999) to help understand intraspecific and interspecific variation following species niche evolution and to ensure better conservation policy (Martínez-Meyer and Peterson, 2006). To empirically evaluate this hypothesis, researchers have adopted different methodological approaches, with the niche similarity test developed by Warren et al. (2019) emerging as a particularly robust framework. The principle of niche conservatism has been supported by recent scientific investigations across both plant and animal taxa (Ashraf et al., 2023; Grossman, 2021). Recent research integrating this approach into SDM models has also demonstrated its role in local adaptation of species (Atakpama et al., 2022; Biaou et al., 2023; Jinga et al., 2021; Sinadouwirou et al., 2022). This methodological framework is particularly relevant for assessing the ecological niches of dominant species in systems where it can directly inform conservation strategies. Two species in particular stand out in Benin and were the focus of our study: *V. paradoxa* C.F. Gaertn. and *P. biglobosa* (Jacq.) G. Don. Indeed, they are recognized for their socio-economic importance in Benin (Natta et al., 2012; Vodouhe et al., 2011). Moreover, they have been extensively studied in the country and are considered the most dominant species in agroforestry parks in the Sudanian zone (Avaligbé et al., 2021; Azongnide et al., 2019; Kakpo et al., 2023).

Studies of agroforestry parks in Benin show that these two species are the most valued by rural populations and contribute significantly to poverty reduction through trade in their fruits, nuts and butter (Houndonougbo et al., 2020; Schreckenberg et al., 2006; Vodouhe et al., 2011). They are also recognized for their role in honey production in the northwest of Benin, with a strong interest in beekeeping (Ahouandjinou et al., 2021). Furthermore, Saïdou et al. (2012) demonstrated the contribution of V. *paradoxa* and *P. biglobosa* parks to carbon sequestration in the Sudanean zone. According to Kakpo et al. (2023), cation exchange capacity, isothermality, and potential evapotranspiration are the environmental factors on which these two species depend in central Benin.

Although several studies have recommended the rejuvenation of ageing V. *paradoxa* and *P. biglobosa* tree populations in agroforestry systems (Dotchamou et al., 2016; Koura et al., 2013; Zinsouklan et al., 2014), information on restoration strategies that integrate climate data is lacking. Where such information is available, it often does not take into account potential changes in species niches within populations, which may require differentiated conservation and restoration strategies within species in response to climate gradients. Accounting for variation in environmental conditions in species distributions allows for a deeper understanding of species-environment interactions, contributing to more nuanced and realistic ecosystem modeling (Biaou et al., 2023). This is particularly important to maintain the ecosystem services provided by V. *paradoxa* and *P. biglobosa*, and to ensure their continued role as economic and ecological keystones for local communities. Within this framework, three hypotheses were proposed to study the evolution of the ecological niches of these species under current and future climatic conditions. The first hypothesis proposes that niche differentiation of *P. biglobosa* and V. *paradoxa* is a function of bioclimatic variables and the ecology of both species along the climatic gradient in Benin. The second hypothesis propose that the impact of climate change on *P. biglobosa* and V. *paradoxa* is a function of the distribution of subgroups of individuals and climatic zones according to climate scenarios. Finally, the third hypothesis proposes that the degree of niche conservatism of *P. biglobosa* and V. *paradoxa* is a function of their tolerance to climatic variation along the ecological gradient in Benin.

This study therefore aims to analyze the impact of climate change on the niches of V. *paradoxa* and *P. biglobosa* in Benin and to assess the level of niche conservatism, both intraspecific and interspecific, of these two species.

## 2. Material and methods

### 2.1. Study area

The study carried out in the Republic of Benin. Benin is located in a corridor of savannah ecosystems that interrupts the West African block of evergreen forests known as the Dahomey Gap, resulting from changes during the Holocene (Jenik, 1994; Salzmann and Hoelzmann, 2005). The country is divided into three contrasting chronological regions: the GCZ- Guineo-Congolean zone (6°25 - 7°30 N with humid climate), the SGZ- Sudano-Guinean zone (7°30′ N and 9°45′ N) and the SZ-Sudanean zone (9°45 'N - 12°30′ N) (White, 1983; Adomou, 2005) (Fig. 1). The GCZ has a subequatorial humid climate with two rainy seasons and two dry seasons, annual rainfall of 1200 mm, temperatures ranging from 25 to 29 °C, and relative humidity of 69 to 97 %. The SGZ is a transitional area with a sub-humid climate and rainfall ranging from 900 to 1110 mm, with similar temperatures, and humidity ranging from 31 to 98 %. The SZ has a dry tropical climate with rainfall below 1000 mm, temperatures between 24 and 31 °C, and humidity between 18 and 99 % (Adomou, 2005; Salzmann and Hoelzmann, 2005; White, 1983). The SZ is characterized by a mosaic of savannas, the SGZ by dense semi-deciduous forests, and the GCZ is dominated by dense moist forests (Adomou, 2005; Salzmann and Hoelzmann, 2005).

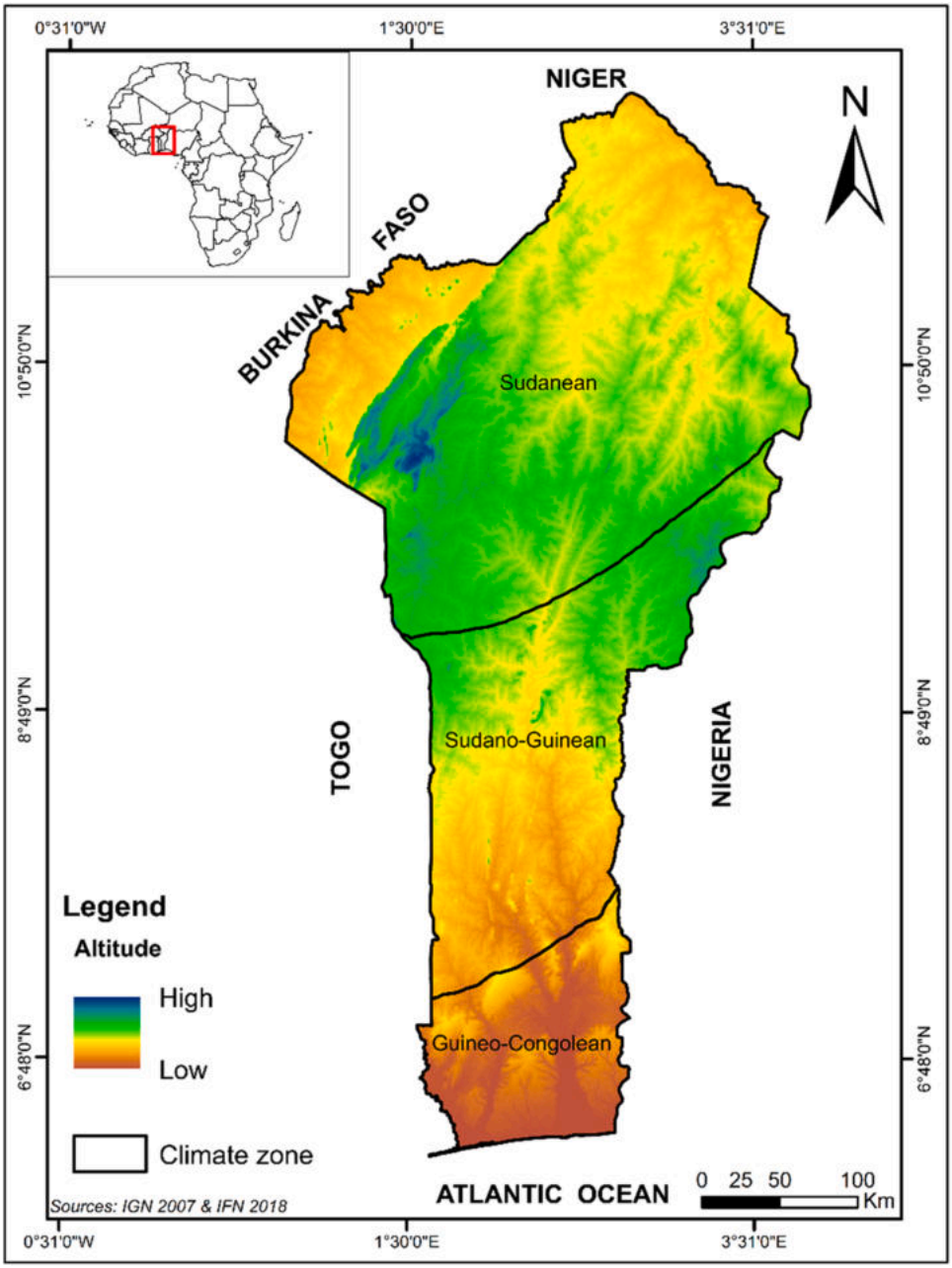



**Fig. 1.** Geographic map of the study area.

### 2.2. Study species

*V. paradoxa* CF. Gaertn (Sapotaceaeis a wood-producing species classified as vulnerable in the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN) and in the Red List of Benin (Arbonnier, 2004; Neuenschwander et al., 2011). It is present from the altitude of Atcherigbé uplands to Malanville, covering a range of habitats, from natural o anthropized areas (Gnangle, 2005). One of the main threats to this species is the progressive destruction of young trees in agricultural areas (Djossa et al., 2008). Indeed, a significant difference in the dendrometric and production parameters of V. *paradoxa* parks has been observed (Glèlè Kakaï et al., 2011). Its ecological optimum is influenced by several environmental variables, including the aridity index, isothermality, and temperature seasonality (Avaligbé et al., 2021). In addition, the variation of climatic factors along the ecological gradient in Benin has caused flower abortion, leading to a significant reduction in the nut yield of this species (Avaligbé et al., 2021). In addition to its ecological role, V. *paradoxa* occupies an important place in traditional medicine, particularly for the treatment of infectious diseases (Odounharo et al., 2022). Some studies have also shown that small fruit trees are widespread and provide better yields of fruit, nuts, and butter (Merinosy et al., 2022).

*P. biglobosa* (Jacq.) G. Don (Mimosaceae), another important agroforestry species, is not only vulnerable but also semi-domesticated due to constraints that limit its domestication (Arbonnier, 2004; Neuenschwander et al., 2011). It is mainly found in the agroforestry parklands of the Sudanean and Sudano-Guinean savannas (Boffa, 1999; Natta, 2003; Sina, 2006; Teklehaimanot, 2004). The work of Gnangle et al. (2011) showed a differentiation of dendrometric and production parameters of this species between Bohicon and Malanville in Benin. However, despite its socio-economic importance, this species suffers from insufficient regeneration and heavy exploitation, especially in the Pobè and Plateau phytodistricts (Fachola et al., 2019). The Donga department also shows alarming signs of insufficient regeneration (Koura et al., 2013).

Nevertheless, according to the projection by Ayihouenou et al. (2016), environmental conditions in Benin should remain favorable for the cultivation and preservation of this species until 2050. In addition to its ecological role, *P. biglobosa* is widely used in food and traditional medicine, for both humans and animals (Dedehou et al., 2016; Odounharo et al., 2022; Zinsouklan et al., 2014).

### 2.3. Data collection

#### 2.3.1. Occurrence data

Occurrence data were obtained from two main sources: the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org), accessed in December 2023, and field surveys. Field sampling was carried out in eight communes strategically distributed between two ecological zones: the Sudanean zone (Bembèrèkè, Boukounbé, Gogounou, and Kouandé) and the Sudano-Guinean zone (Bassila, Tchaourou, Ouèssè, and Savalou). Field locations were recorded using Global Positioning System (GPS) equipment and the Locus Maps application. After data preprocessing using ENMTools (Warren et al., 2010), the final dataset comprised 2384 occurrence points for *P. biglobosa* (75.82 % from GBIF, 24.18 % from field surveys) and 18,859 occurrence points for V. *paradoxa* (79.43 % from GBIF, 20.57 % from field surveys). Pre-processing consisted of first removing duplicates for both data sources. This was followed by a detailed cleaning of the GBIF data based on the ecology of the two species.

#### 2.3.2. Environmental variables

Nineteen (19) bioclimatic variables related to humidity and temperature (Table A1, Supplementary data), spanning 1950 to 2000 with a resolution of 30 s (,≅ $1Km^2$), and elevation data were acquired from the WorldClim 2.1 database (www.worldclim.org) (Fick and Hijmans, 2017) in October 2023. Soil data were obtained from the Harmonized World Soil Database 1.2 (http://www.data.tpdc.ac.cn/en/data/844010ba-d359-4020-bf76-2b58806f9205/), accessed in October 2023, with incorporates edaphic conditions known to influence species distribution patterns (Pearson and Dawson, 2003; Soberon and Peterson, 2005). Following Biaou et al. (2023), several climatic variables were excluded due to documented discontinuities across Benin. These are 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). These discontinuities, which are particularly prevalent in the Americas and sub-Saharan Africa, have been supported by several studies (Booth, 2022; Escobar et al., 2014). Their inclusion in the models may introduce a bias and reduce the reliability of the estimates. In addition, their use may alter the accuracy of the models by affecting the spatial continuity of the predictions, which could lead to slight under- or overestimation of the predictions. For future climate projections, four global climate models (GCMs) from the WorldClim 2.1 database were used, which were consulted in October 2023. These were CanESM5, the latest coupled model from the Canadian Center for Climate Modeling and Analysis (Swart et al., 2019), HadGEM3-GC3.1: which belongs to a family of climate prediction models from the Met Office Center (Ridley et al., 2018). MIROC6: which is the sixth version of a climate model developed by a Japanese climate modeling community to contribute to CMIP6 (Coupled Model Intercomparison Project Phase 6) (Tatebe et al., 2019) and the MPI-ESM1.2-HR: the latest version of the Max Planck Institute's Earth System Model (Gutjahr et al., 2019; Mauritsen et al., 2019; Steger et al., 2020).

The weighted average of these four models was used for the projections for 2050 (2041–2060) of two climate scenarios (Shared Socioeconomic Pathways of the latest (6th) report of the Intergovernmental Panel on Climate Change (Beny et al., 2023). Of the four scenarios provided by WorldClim (SSP 1–2.6, SSP 2–4.5, SSP 3–7.0, SSP 5–8.5), SSP 2–4.5 and SSP 5–8.5 were used. SSP 2–4.5 is the scenario in which temperatures increase by 2.7 °C by the end of the century, with $CO_2$ emissions trending downwards by mid-century but not reaching zero by 2100 (Lepousez and Aboukrat, 2022). This scenario is considered realistic because it reflects current political and economic trends, with climate policies in place but still insufficient to meet the most ambitious targets of the Paris Agreement (Arias et al., 2021). SSP 5–8.5, on the other hand, corresponds to a scenario of strong economic growth based on heavy reliance on fossil fuels, with a global average temperature of 4.4 °C by 2100 and a doubling of $CO_2$ emissions by 2050 (Lepousez and Aboukrat, 2022; Riahi et al., 2017). This scenario is used to assess the most severe climate impacts in the absence of policy action to achieve significant emissions reductions. On the other hand, SSP 1–2.6 is very optimistic and requires the use of ambitious and rapid climate policies to limit warming to below 2 °C, which is unlikely in the current socioeconomic context, especially in West Africa (Riahi et al., 2017). While SSP 3–7.0, results in high emissions, it is based on assumptions of geopolitical fragmentation and international conflict, which complicates its use for projections targeting agricultural systems (O'Neill et al., 2017). Thus, the selection of SSP 2–4.5 and SSP 5–8.5 allows for the analysis of climate change impacts under moderate and extreme conditions, providing a comprehensive risk assessment for agroforestry systems in the region.

### 2.4. Data analysis

#### 2.4.1. Analysis of trends in climate variables

Environmental variables were extracted for each occurrence point, followed by cluster analysis using Principal Component Analysis (PCA) implemented in R software using the 'factoextra' package (Kassambara and Mundt, 2020). This analysis allowed the identification of distinct climatic subgroups within the population (Hansen and Jaumard, 1997). Statistical comparisons of climatic variable mean between paired subgroups were made using the Kruskal-Walli's test, a non-parametric method suitable for comparing multiple independent samples.

#### 2.4.2. Species distribution modeling

Species distributions for each subgroup were performed using the MaxEnt algorithm (Hijmans and Elith, 2021; Phillips et al., 2017) implemented in the R software through the 'dismo' package (Hijmans and Elith, 2021). MaxEnt, which assesses potential species distributions based on presence-only data (Alsamadisi et al., 2020; Merow et al., 2016), has demonstrated superior performance compared to alternative approaches such as GLM, GAM, boosted regression trees (BRT), and multivariate adaptive regression splines MARS) (Elith et al., 2006). The models were calibrated using 80 % of the occurrence points and the remaining 20 % were used for validation (Phillips and Dudík, 2008). A jackknife test was used to assess the relative importance of environmental variables in the species distributions (Phillips et al., 2006). Models were fitted to the Cloglog output format (Rodríguez-Rodríguez et al., 2020). The model included hinge, product, linear and quadratic features, with a maximum of 10,000 background points, 1000 replicates and clamping (Rodríguez-Rodríguez et al., 2020). Model performance was assessed using the area under the curve (AUC) (Phillips et al., 2006) and the symmetric extreme dependence index (SEDI) (Ferro and Stephenson, 2011; Toffa et al., 2022). AUC values were interpreted according to the scoring grid of Araújo et al. (2005), which assesses the ability of the model to discriminate events (Table A2, Supplementary data). As the AUC is generated directly by the model, it is an internal performance index. The SEDI was preferred to the true skill statistic (TSS) (Allouche et al., 2006) as an external performance index, as it is recognized as the optimal criterion for evaluating background-based species distribution models (Wunderlich et al., 2019). A SEDI close to 1 indicates good model performance.

Distribution maps for current (1950–2000) and future (2041–2060) scenarios were generated using ArcGIS 10.8, using the *minimum training presence Cloglog threshold* (Liu et al., 2005; Merow et al., 2014, 2019).

This threshold represents the lowest habitat suitability value at which species occurrences are observed, ensuring comprehensive inclusion of all occurrence points in the binary distribution zone.

#### 2.4.3. Niche conservatism analysis

The principal component analysis (PCA) approach, applied to species-specific environmental variables, was implemented using the R package "ecospat" (Di Cola et al., 2017).This method was used to evaluate Schoener's (1968) similarity index (D) and Hellinger's distance (I) (Warren et al., 2008) under current climate scenarios. Both indices range from 0 to 1, and quantify the degree of ecological niche overlap. Species occurrence patterns within their respective environmental spaces were visualized using kernel density estimation, providing a smoothed distribution profile. Current ecological differentiation between climate subgroups was assessed by calculating Euclidean distances between the central position of each subgroup and its respective niche centroid. For future climate scenarios, the R package "ENMTools" was used (Warren et al., 2019). For the degree of interspecific niche overlap, the intersection of potential niche layers per subgroup pair and the R package "ENMTools" were used (Warren et al., 2019).

This analysis facilitated the identification of potential patterns of interspecific niche overlap.

## 3. Results

### 3.1. Composition and characterization of subgroups

Both species exhibited three distinct homogeneous subgroups occupying differentiated niches (Fig. 2), categorized according to their geographical distribution as Northern (NSG), Central (CSG), and Southern (SSG) subgroups.

The distribution pattern of *P. biglobosa* showed that the NSG was predominantly restricted to the Sudanean Zone (SZ), while the CSG spanned both the SZ and Sudano-Guinean Zone (SGZ). The SSG spanned the SGZ and Guineo-Congolean Zone (GCZ) (Fig. 2.a). For V. *paradoxa*, the NSG was distributed across both the SZ and SGZ, while the CSG and SSG showed a similar distribution pattern (Fig. 2.b).

Principal component analysis revealed a clear distinction between the three subgroups of *P. biglobosa*, with distinct environmental associations. The NSG was mainly characterized by mean temperature of the warmest quarter (bio-10), seasonality of temperature (bio-4), and maximum temperature of the warmest month (bio-5). The CSG was characterised by annual precipitation (bio-12), precipitation of the wettest quarter (bio-16), and altitude. The SSG was defined by the precipitation of the driest quarter (bio-17) and the minimum

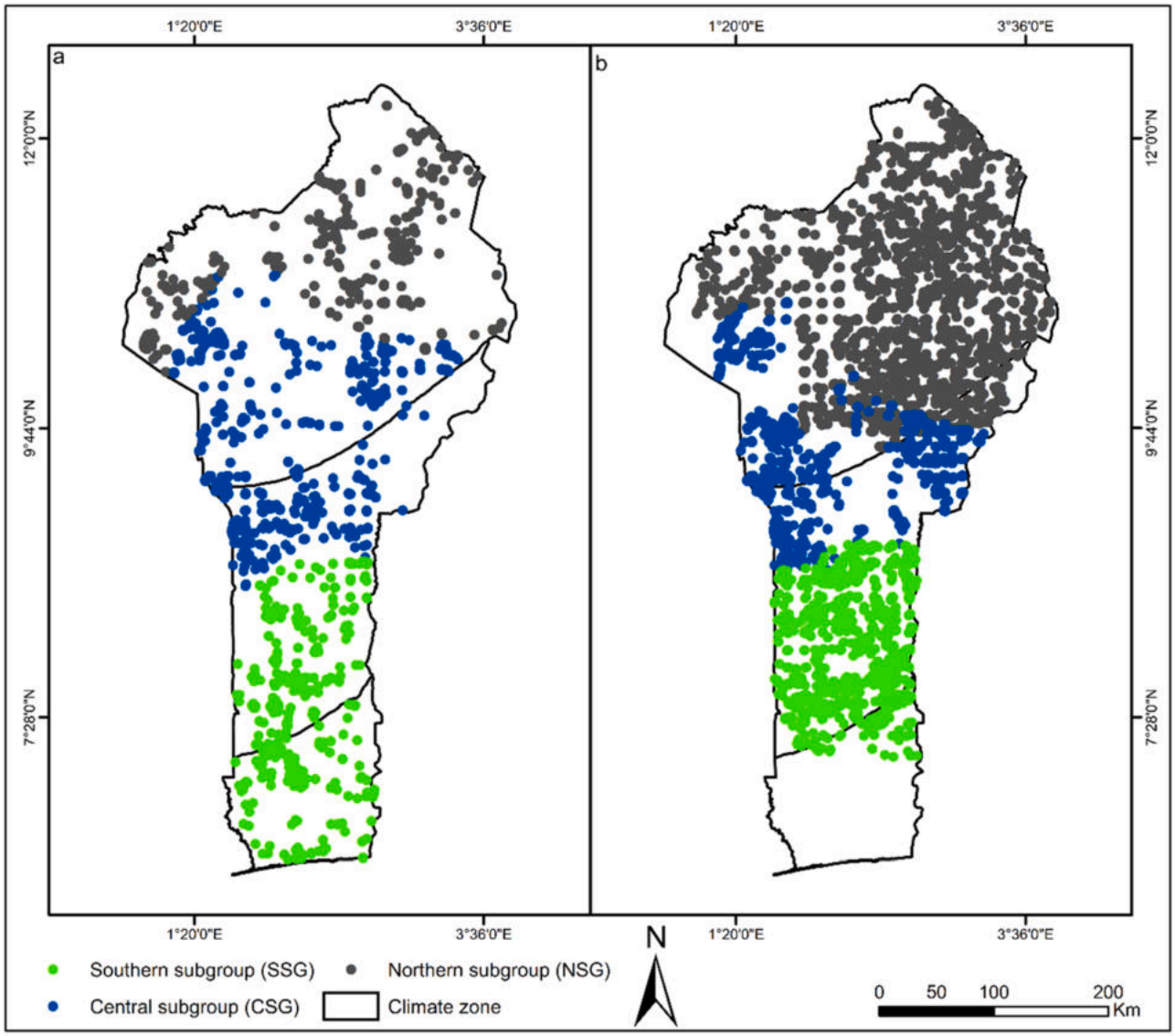



**Fig. 2.** Distribution of the subgroups of *P. biglobosa* (a) and *V. paradoxa* (b).

temperature of the coldest month (bio-6).

For V. *paradoxa,* the NSG was characterized by temperature seasonality (bio-4), annual temperature range (bio-7), and maximum temperature of the warmest month (bio-5). The CSG was distinguished by annual precipitation (bio-12), precipitation of the wettest quarter (bio-16), and elevation. The SSG was defined by a combination of precipitation of the driest quarter (bio-17), minimum temperature of the coldest month (bio-6), annual precipitation (bio-12), and isothermality (bio-3). Statistical analyses confirmed significant differences in climatic conditions among all subgroups ($p < 0.05$; Table A7, supplementary data), supporting the distinctiveness of these environmentally defined populations within each species.

### 3.2. Model validation

For *P. biglobosa*, the distribution of the northern subgroup (NSG) was predominantly influenced by three key variables: mean temperature of the warmest quarter (38.1 %), temperature seasonality (23.2 %), and precipitation of the driest month (11.3 %) (Table A3, supplementary data). The jackknife test revealed that temperature seasonality contributed substantial independent information, while the soil variable provided unique information not captured by other parameters (Fig. Aa, supplementary data). This model showed robust performance with an AUC of 0.92 and a SEDI of 0.85. The distribution of the central subgroup (CSG) was mainly shaped by the mean temperature of the coldest quarter (30.6 %), altitude (29.3 %), and isothermality (8.7 %) (Table A3, supplementary data). Jackknife analysis identified precipitation seasonality and precipitation in the driest quarter as significant contributors (Fig. Ab, supplementary data). Model performance metrics showed an AUC of 0.90 and SEDI of 0.81. The Southern Subgroup (SSG) distribution was most influenced by precipitation in the driest month (77.3 %), followed by minimum temperature in the coldest month (5.9 %) and precipitation in the wettest month (3.1 %) (Table A3, supplementary data). The jackknife test indicated that precipitation in the driest quarter provided substantial independent information, while precipitation in the wettest month contributed unique information when excluded from the model (Fig. Ac, supplementary data). This model achieved high performance metrics with an AUC of 0.93 and SEDI of 0.85.Fig. 3

For V. *paradoxa*, the northern subgroup (NSG) distribution was mainly determined by precipitation seasonality (67.29 %), followed by mean annual temperature (8 %), and total annual precipitation (6.50 %) (Table A4, supplementary data). Jackknife analysis identified precipitation in the driest quarter as a critical variable, showing influence both in isolation and when omitted from the model (Fig. Ad, supplementary data). This model gave an SEDI of 0.58 and an AUC of 0.76. The central subgroup (CSG) model achieved better discrimination (AUC = 0.87) and performance (SEDI = 0.81). The distribution was mainly influenced by the mean temperature of the coldest quarter (76.50 %), precipitation of the driest month (20.20 %), and precipitation of the wettest quarter (2.70 %) (Table A4, supplementary data). Jackknife test identified mean temperature of the coldest quarter as the most influential predictor (Fig. Ae, supplementary data). The southern subgroup (SSG) distribution was most influenced by precipitation in the driest month (84.00 %), with additional contributions from temperature seasonality (5.50 %) and precipitation in the driest quarter (2.70 %) (Table A4, supplementary data). Jackknife analysis indicated that precipitation in the driest quarter provided substantial independent information, while precipitation in the wettest quarter contributed unique information when excluded from the model (Fig. Af, supplementary data). This model showed robust performance with a SEDI of 0.80 and an AUC of 0.87.

### 3.3. Current distribution and future projections for P. biglobosa and V. paradoxa

In general, almost all of Benin is currently suitable for the conservation of *P. biglobosa* (Fig. 4.1a). However, according to future climate projections, the Sudanean zone could lose almost all of its potential niche area under the SSP 2–4.5 scenario (Fig. 4.1b). The losses would be even more pronounced under SSP 5–8.5 (Fig. 4.1c). Thus, two climate zones would no longer be able to contribute to the conservation of *P. biglobosa*. For V. *paradoxa*, the current climatic conditions in the Sudanean and Sudano-Guinean zones are potentially suitable for its conservation (Fig. 4.1d). However, according to future climate projections, conditions under the SSP 2–4.5 scenario will not be suitable in the Sudanean zone, nor in a significant part of the Guineo-Congolean zone (Fig. 4.1e). Under the SSP 5–8.5 scenario, an almost total loss of potential nesting area is expected in all climate zones (Fig. 4-1f).

Analysis of the current distribution of P. *biglobosa* revealed potential niches for all subgroups across climate zones (Fig. 4.2, Table A5, supplementary data). Current climatic conditions allow substantial niche

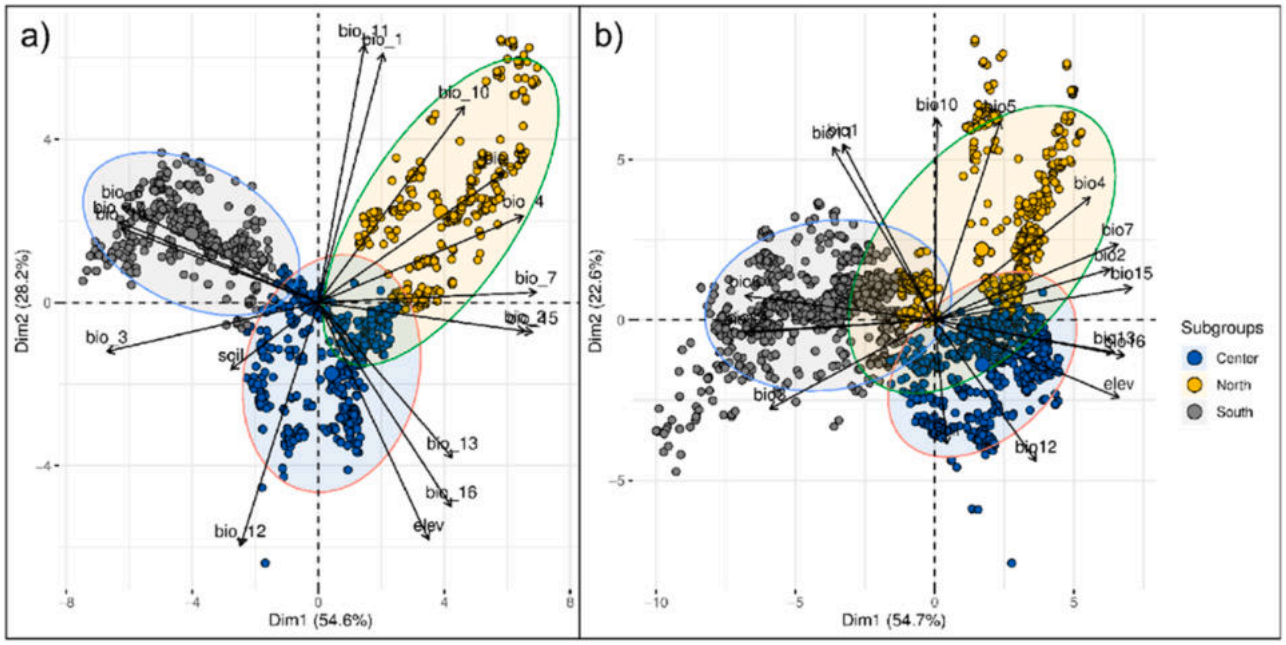



**Fig. 3.** Visualization and characterization of the subgroups of *P. biglobosa* (a) and *V. paradoxa* (b) in an axis system.

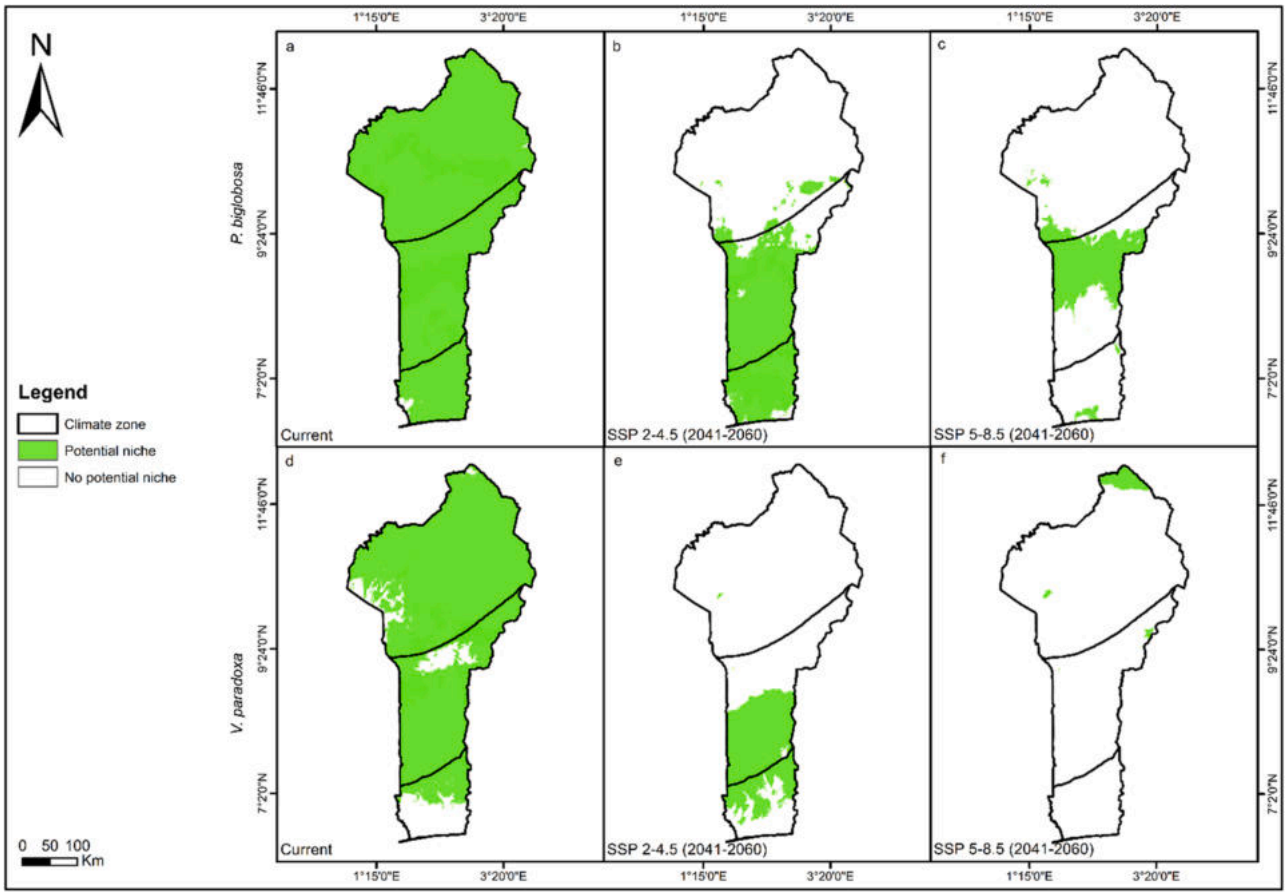



**Fig. 4.1.** General map of potential niches for the *P. biglobosa* model (a, b, and c) and the V. *paradoxa* model (d, e, and f).

overlap, particularly between NSG and CSG in the Sudanean Zone, with all three subgroups overlapping in the Sudano-Guinean zone. Projections for 2050 under the intermediate scenario (SSP 2–4.5) indicate a southward shift of suitable conditions towards the CSG and SSG regions, accompanied by a substantial reduction in suitable niche areas for all subgroups. The analysis predicts significant habitat losses: NSG (−27.43 %), CSG (−85.64 %), and SSG (−73.59 %) (Table A5). This shift leads to the complete dissolution of the CSG-SSG niche overlap (Fig. 4.2b). Under the pessimistic scenario (SSP 5–8.5), suitable conditions remain mainly concentrated in CSG and SSG regions. While these areas remain suitable for CSG and SSG populations, the model predicts complete elimination of potential niches for NSG populations and associated niche overlap (Fig. 4.2c, Table A5).

For V. *paradoxa*, current distribution models indicate distinct suitable niches with no overlap between NSG and SSG populations. Future projections suggest significant climate change impacts under both scenarios, with more severe effects under SSP 5–8.5 by 2050 (Fig. 4.2h). The intermediate scenario (SSP 2–4.5) projects a southward shift in suitable conditions, resulting in a complete loss of the niche for NSG populations and an almost complete loss (−99.59 %) for CSG populations (Fig. 4.2d, Table A6, supplementary data). The SSP 5–8.5 scenario projects reduced suitability for SSG populations, while paradoxically indicating potential niche expansion for CSG and NSG populations. Specifically, the model predicts substantial losses for CSG (−97.70 %) and NSG (−96.58 %) populations, despite the previously predicted elimination of NSG suitable habitat.

### 3.4. Intraspecific niche overlap

The first two axes of the PCA, based on the current climate, better explain the interaction between the subgroups of each population of *P. biglobosa* and V. *paradoxa* (Fig. 5). Similarity tests between pairs of subgroups showed that there was no significant intraspecific niche overlap within the populations of each species ($I \cong 0$, $D \cong 0$, and $p > 0.5$). The same trends were observed for future climate scenarios (Fig. 6).

### 3.5. Interspecific niche overlap

The intersections in the current projection revealed suitable niches for the conservation of the subgroup pairs in terms of environmental conditions (Fig. 7). There will be suitable conditions for the conservation of two subgroup pairs (CSG and SSG) in both future climate scenarios. The values ($< 0.5$) of Hellinger's I distance and Schoener's D distance from the interspecific niche similarity test confirm the level of niche overlap level revealed by crosses (Fig. 8). These values show a clear regression for the NSG and CSG pairs, in contrast to the SSG pair. The level is higher for the SSG subgroup pair. These values show a clear regression under future climatic conditions.

## 4. Discussion

### 4.1. Model performance

Species distribution modelling is an essential tool to predict and guide conservation decisions (Fandohan et al., 2015; Toffa et al., 2022). This approach was used to assess the climate response of the *P. biglobosa* and V. *paradoxa* subgroups using the MaxEnt algorithm. Although MaxEnt is known for its excellent predictive power (Idohou et al., 2017; Kaky et al., 2020), it has some uncertainties related to input data, spatial errors and parameters of ecological interactions (Elith et al., 2011; Merow et al., 2016; Wisz et al., 2008; Yackulic et al., 2013).

Performance evaluation indices (AUC and SEDI) show a very good

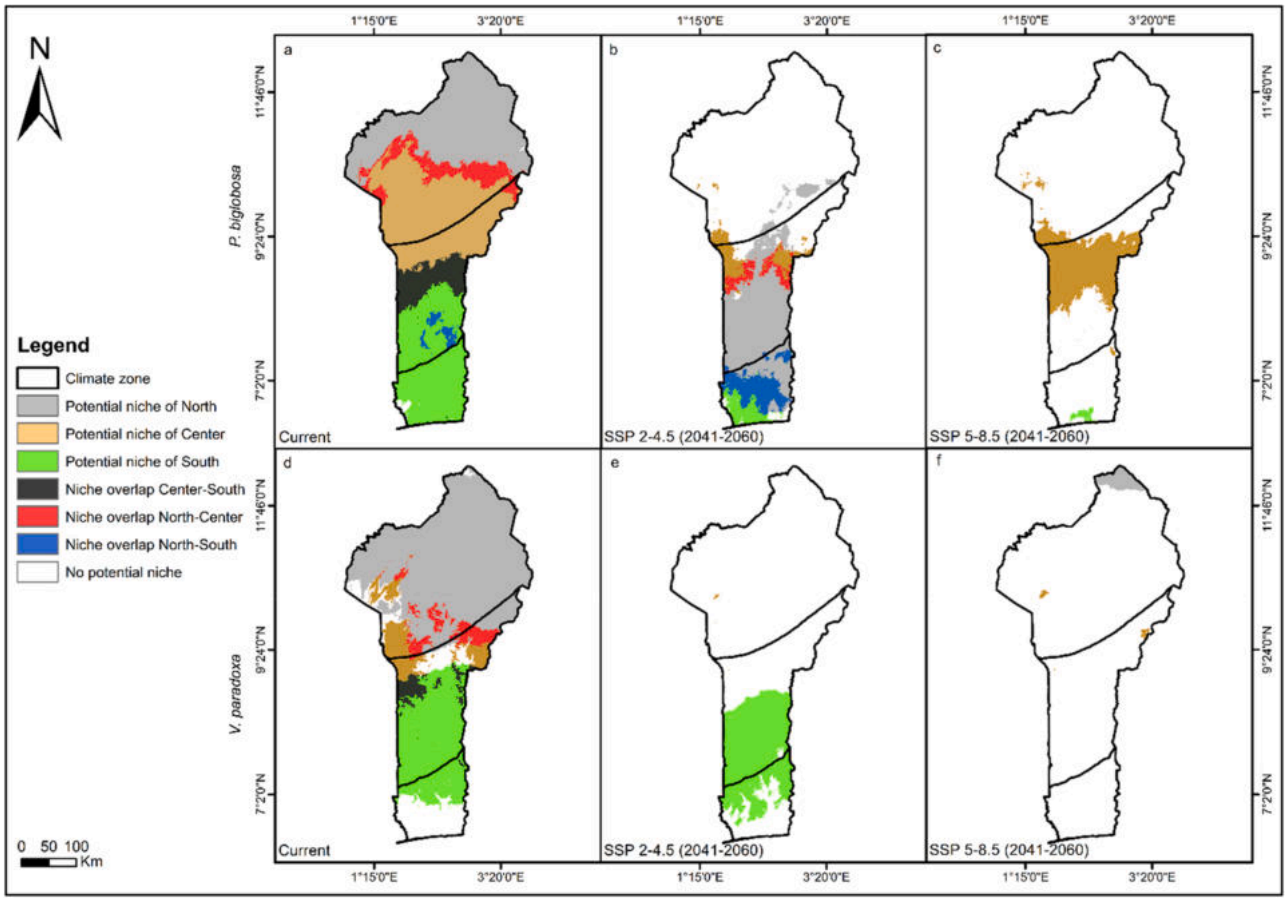



**Fig. 4.2.** Map of potential niches subgroups for *P. biglobosa* model (a, b and c) and V. *paradoxa* model (d, e and f).

performance of the models, except the NSG model of V. *paradoxa*, which raises questions about the robustness of the models mentioned above. The use of a large number of variables in a model can affect its performance due to possible redundancies. However, MaxEnt can regulate the contribution of correlated variables, which limits the effect of redundancy on model performance (Feng et al., 2019). Furthermore, small variations in data values can affect the reliability of climate projections (Beaumont et al., 2016). To minimize the risk of losing relevant information, all variables were included in our models without prior correlation tests between them.

The contributions and importance of the variables differ between the models for the two species, confirming the heterogeneity of the subgroups along the climatic gradient in Benin. Similar results have been observed in the country for widely distributed species such as *P. erinaceus* (Biaou et al., 2023), *D. senegalensis* (Sinadouwirou et al., 2022) and K. *africana* (Yamontche et al., 2024).

It should be noted that some uncertainties remain in climate projections, mainly due to the variability of climate scenarios, the limitations of the models used for downscaling and the lack of data on the biological response of species in these models. In this study, the weighted average of four models was used to reduce bias. As the models have different characteristics, it was not appropriate to use a single model. A more in-depth multi-model approach could be considered in future studies to refine our results. These uncertainties should be taken into account when interpreting the results.

### *4.2. Bioclimatic variable influence on subgroup differentiation of P. biglobosa and V. paradoxa along climatic gradient*

Our findings are consistent align with established research showing that species distribution patterns exhibit heterogeneity across climatic gradients, especially for species with large geographic ranges (Biaou et al., 2023; Chardon et al., 2020; Smith et al., 2019). The study revealed three bioclimatically distinct homogeneous subgroups for both *P. biglobosa* and V. *paradoxa* across their range in Benin. Notably, these bioclimatic subdivisions do not correspond perfectly to the three main climate zones of Benin probably because the traditional delineation of climate zones incorporates both climatic and phytogeographic factors (Adomou, 2005). This divergence underscores the complexity of species distribution patterns in response to bioclimatic factors and emphasizes the need for tailored sit-specific conservation strategies. In this paper, only two phytogeographic factors (soil characteristics and altitude) were used in addition to climate factors. In addition, the traditional delimitation of climate zones was established several years ago, while environmental conditions may have evolved under the influence of climate variability. As the bioclimatic and biogeographic variables used here are more recent, the subdivision approach based on the extraction of these variables was adopted to better identify recent changes induced by climate variability. This divergence highlights the complexity of species distribution patterns in response to bioclimatic factors and the need for conservation strategies adapted to each region.

The analysis revealed different bioclimatic drivers shaping the distribution of each subgroup within both species. Temperature-related variables predominantly influenced the northern subgroups of both *P. biglobosa* and V. *paradoxa*, while precipitation variables and altitude more strongly influenced their central subgroups. These patterns suggest that climate-driven adaptation mechanisms play a fundamental role in determining the distribution and survival strategies of these species across Benin's environmental gradients (Biaou et al., 2023). Understanding these factors can help target conservation and management

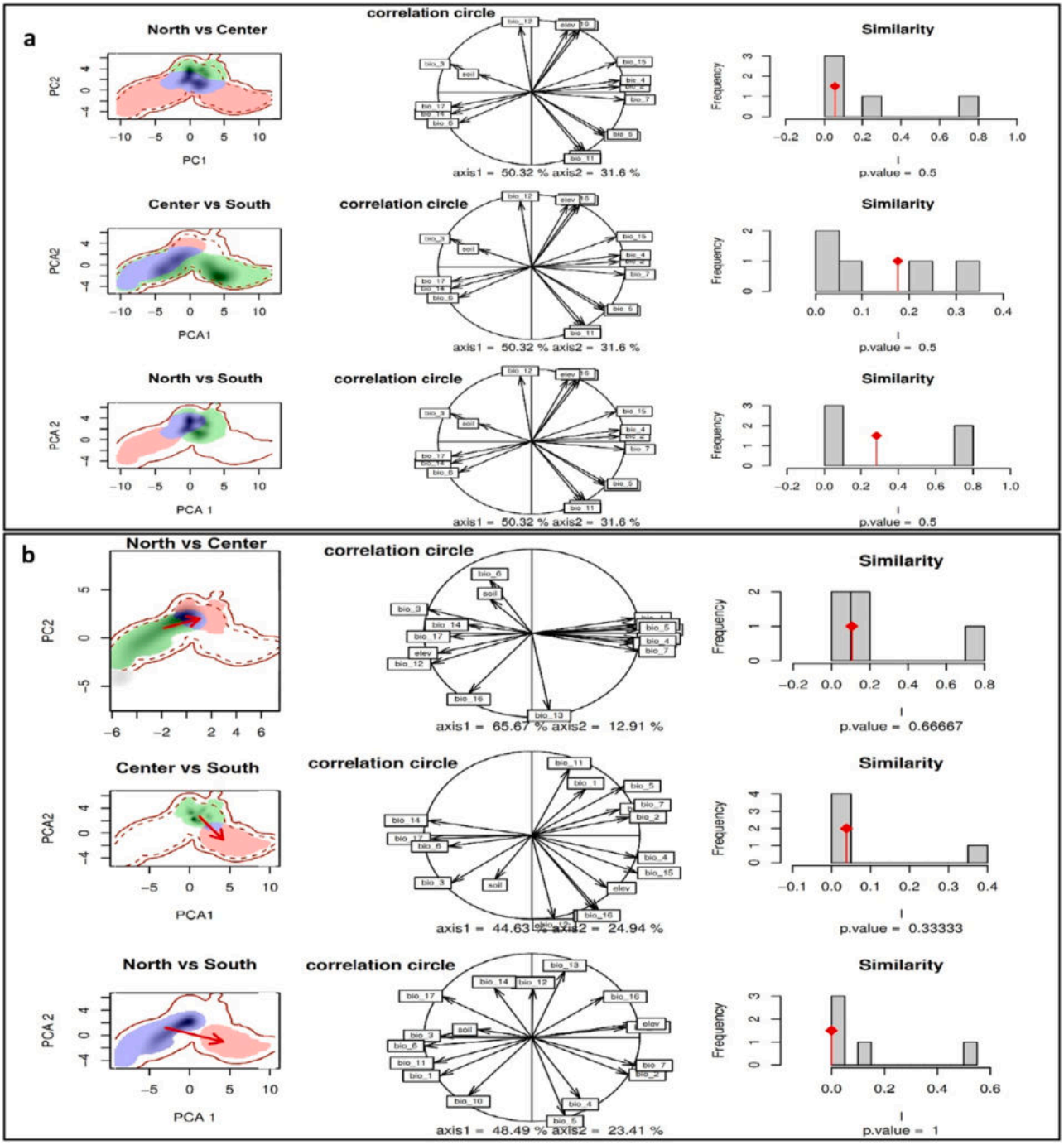



**Fig. 5.** The results of the ordination principal component analysis (PCA) of *P. biglobosa* (a) and *V. paradoxa* (b).

efforts for these species in different climatic zones. These results are consistent with Fandohan et al. (2015), who showed that environmental and climatic factors differentially characterize individuals within populations, leading to differential group formation. Our results support the initial hypothesis that *P. biglobosa* and V. *paradoxa* subgroups differentiate according to bioclimatic variables, reflecting ecological niche heterogeneity along the climatic gradient in Benin.

### *4.3. Impact of climate change on the niche distribution of each subgroup of P. biglobosa and V. paradoxa*

Ecological niche modeling of *P. biglobosa* and V. *paradoxa* using homogeneous subgroups showed high predictive performance. These findings support Biaou et al. (2023) and highlight the importance of incorporating intraspecific variation when modeling the niches of widely distributed species. Our methodological approach retained all variables without correlation testing, preserving potentially relevant information (Feng et al., 2019). The differential contribution and importance of variables across species models in predicting suitable niches further validate the subgroup heterogeneity along the climatic gradient. Similar patterns have been documented in Benin for other widely distributed species, including *Pterocarpus erinaceus* Poir (Biaou et al., 2023), *Detarium microcarpum* Guill & Perr. (Sinadouwirou et al., 2022), *Kigelia africana* (Lam.) Benth (Yamontche et al., 2024) and *Pseudocedrela kotschyi* (Schweinf.) Harms (Deguenonvo et al., 2024).

Projections for both species under different climate scenarios reveal

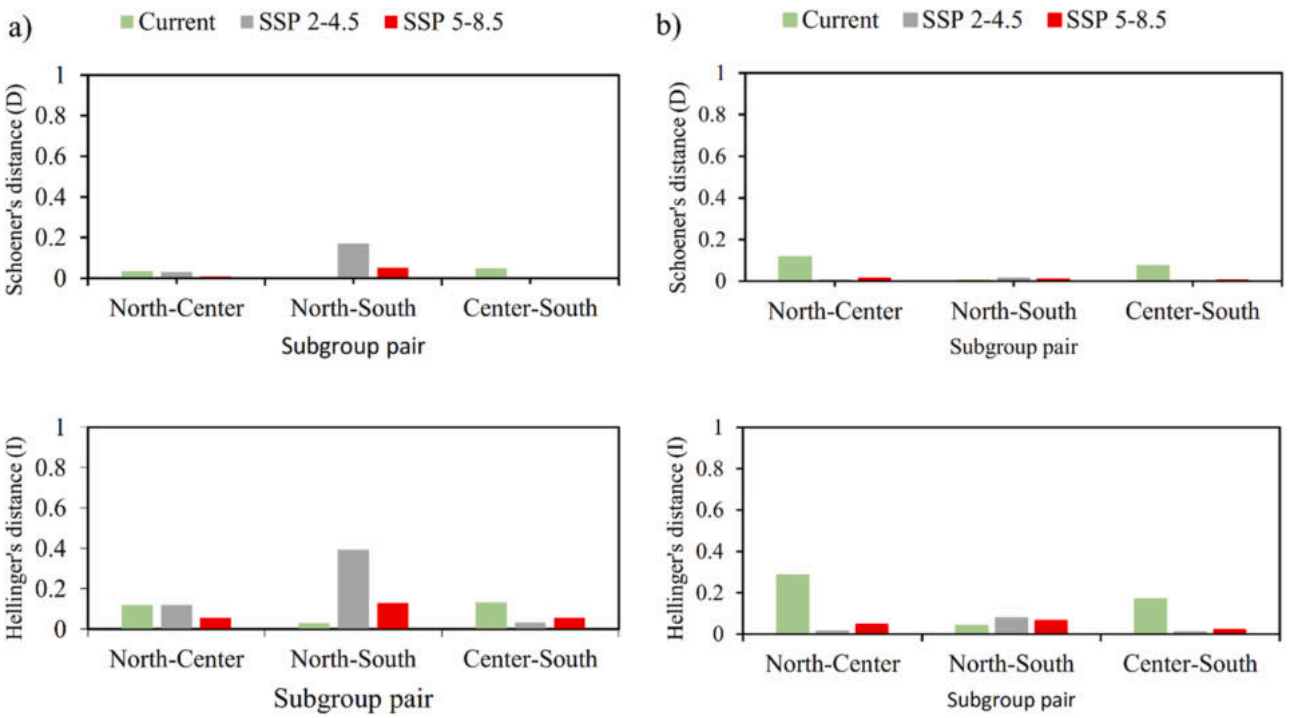



**Fig. 6.** Intraspecific niche overlap in current and future climate scenarios of *P. biglobosa* (a) and *V. paradoxa* (b).

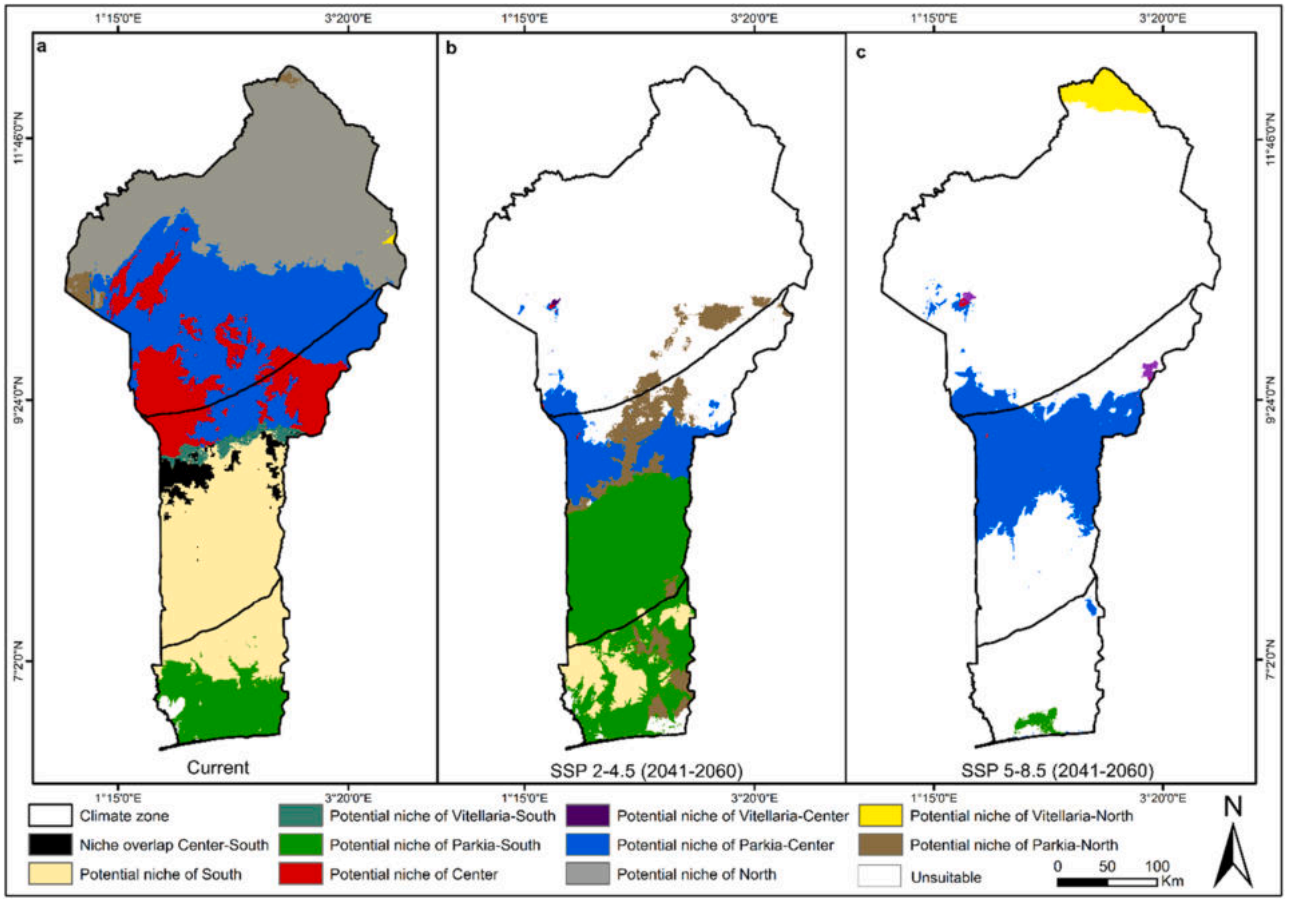



**Fig. 7.** Map of potential interspecific niches in Current (a), SSP 2–4.5 (b) and SSP 5–8.5 (c).

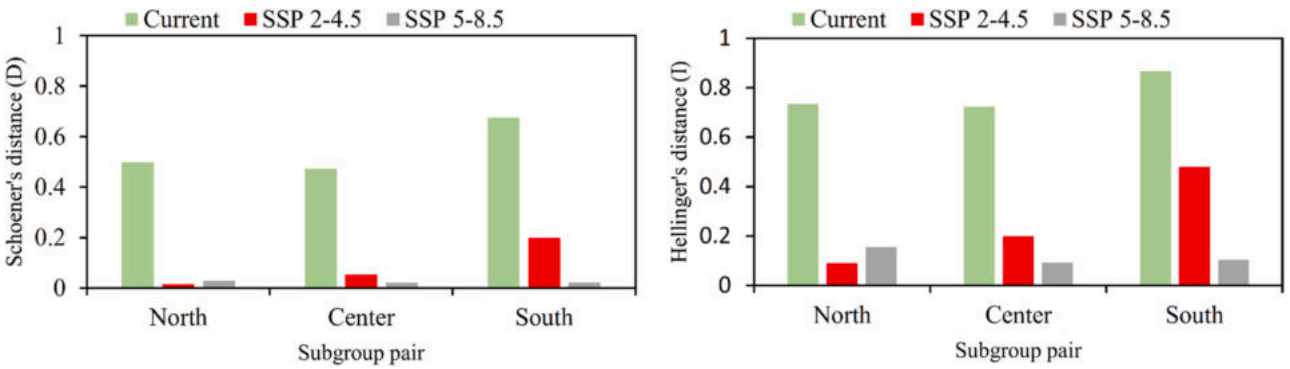



**Fig. 8.** Interspecific niche overlap between subgroup pairs in current and future climate scenarios.

substantial shifts in suitable niche distribution across Benin's climate zones, supporting our hypothesis of a climate change-induced reduction in suitable areas between intraspecific subgroups. For *P. biglobosa*, the current overlap between subgroups, particularly in the southern and central zones, demonstrates contemporary adaptability to different climatic conditions. However, future projections under both intermediate (SSP 2–4.5) and pessimistic (SSP 5–8.5) scenarios indicate severe habitat contraction, particularly for the central subgroup. This contraction could generate potential genetic isolation among subgroups, potentially affecting the long-term viability and resilience of the species. Future research could explore this dimension to improve our results. The fermented seeds of the species are used in the local diet, while the leaves and bark are used for traditional medicinal purposes (Dedehou et al., 2016; Odounharo et al., 2022). From an economic perspective, the sale of these products is an important source of income for rural households, especially for women involved in the processing and marketing of butter by-products (Houndonougbo et al., 2020; Vodouhe et al., 2011).

The northern subgroup exhibits a distinct dynamic, shifting from the Sudanian Zone toward the Sudano-Guinean and Guineo-Congolean Zones. This differential response pattern suggests greater resilience to current climatic changes in the Sudanean Zone compared to other subgroups. The projected southward shift indicates increasing climatic suitability for *P. biglobosa* establishment in these zones. These findings are in line with Biaou et al. (2023) and (Chardon et al., 2020), who emphasized the need for site-specific population management based on adaptive capacity. Similar distribution dynamics have been observed in the genus *Sclerocarya* across Africa (Jinga et al., 2021).

Current distribution patterns of V. *paradoxa* reveal a clear ecological separation between northern and southern subgroups, indicating the occupation of differentiated climatic niches. This marked niche differentiation potentially increases the species' vulnerability to climatic perturbations (Biaou et al., 2023; Chardon et al., 2020; Hällfors et al., 2016; Jinga et al., 2021). Projections under the SSP 2–4.5 scenario predict an almost complete loss of suitable niches for the northern and central subgroups, suggesting severe range contraction and possible local extinctions. The SSP 5–8.5 scenario, although indicating potential niche expansion in southern regions, projects more extensive overall habitat loss, further increasing the species' vulnerability to climate change.

The projected changes in suitable niches for both species have important implications for conservation and management strategies. The potential reduction of the northern subgroup's niche could lead to an expected loss of genetic diversity due to habitat fragmentation, thus requiring proactive conservation measures. These may include assisted migration programs and the establishment of conservation corridors to maintain connectivity between distinct populations (Biaou et al., 2023). Furthermore, these findings underscore the critical importance of incorporating climate change projections into conservation planning frameworks, particularly for ecologically and economically important species such as *P. biglobosa* and V. *paradoxa* in Benin.

The findings emphasize the urgency of implementing immediate actions to mitigate the impact of climate change on these species, to ensure their persistence and the continued provision of essential ecosystem services. Such actions are critical to maintaining both ecological integrity and economic stability in the region.

### 4.4. *Interspecific and intra-specific conservatism of climatic niches*

The difference in climatic tolerance observed between subgroups within each species reflect patterns of intraspecific niche conservatism. Analysis using approach of (Warren et al., 2008) revealed limited intraspecific niche conservatism for both species, despite the observed niche overlap. This finding is consistent with previous research (Cardoza-Martínez et al., 2019; Peterson, 2011; Qiao et al., 2017; Wiens and Graham, 2005), suggesting that higher levels of population conservatism correlate with more uniform responses to environmental gradients among different subgroups. Similar patterns have been documented for other species in the region, including *A. digitata* L., *P. erinaceus D. microcarpum*, K. *africana* and *P. kotschyi* (Atakpama et al., 2023; Biaou et al., 2023; Deguenonvo et al., 2024; Sinadouwirou et al., 2022; Yamontche et al., 2024). Current projections have identified suitable environmental conditions that support niche overlap between paired subgroups (Fig. 7). Future climate scenarios indicate continued suitability for central and southern subgroup pairs. Niche similarity tests yielded Hellinger's I distance and Schoener's D distance values greater the 0.5, confirming the projected niche overlap (Fig. 8). These metrics showed marked regression for the northern and central subgroup pairs, in contrast to the stability of the Southern subgroup pair. This differential regression in niche similarity may be attributed to the different family affiliations (Sapotaceae and Mimosaceae) of the study species (Ackerly, 2003; Ricklefs and Latham, 1992; Silvertown et al., 2001).

The persistence of favorable climatic conditions for certain subgroup pairs may reflect shared climatic zone occupancy, as species within similar climatic zones often exhibit comparable environmental adaptations (Jenkins and Joppa, 2009; Svenning and Skov, 2004; Wiens and Graham, 2005). These findings support our third hypothesis that population-level niche conservatism correlates with climatic tolerance across environmental gradients. This relationship mirrors documented patterns of rapid ecological niche evolution (Almpanidou et al., 2017; Ascanio et al., 2024; Ashraf et al., 2023; Berriozabal-Islas et al., 2020).

### 4.5. *Implication for the conservation or sustainable management of both species in Benin*

Local adaptation is a very important aspect of species conservation (Lascoux et al., 2016). The significant reduction in suitable niches, particularly in the SZ for *P. biglobosa* and in some subgroups of V. *paradoxa*, highlights the urgent need to reassess conservation strategies. Adaptive management of habitats is essential to improve their resilience to climate change. This could include measures such as restoring

degraded habitats to maintain their functionality and ability to support target species. In this context, translocation of species to more suitable habitats could also be considered, although this approach requires careful planning to avoid negative impacts on new populations and to ensure that target habitats are ecologically compatible, particularly given the low similarity and lack of an observed conservation niche. Ecological risks associated with the translocation of *P. biglobosa* and V. *paradoxa* include the disruption of local ecosystems (competition with native species, alteration of soil dynamics), potential introduction of diseases or pests, and possible climatic incompatibility with the new areas. To ensure that new habitats are suitable, it is essential to select sites with similar ecological conditions, use climate projections to assess long-term viability, and ensure post-relocation monitoring to adjust management strategies.

The results of this study could inform agroforestry and reforestation strategies in Benin, with a focus on the most vulnerable areas. Integrating local knowledge and community conservation efforts would strengthen the relevance of the proposed strategies, in line with the Sustainable Development Goals (SDGs 13 and 15) and the climate mitigation commitments of Benin under the Paris Agreement. The two most suitable climatic zones are not only providing a reservoir of local biodiversity, but also ensure regional ecological stability. Indeed, their biodiversity richness and their capacity to maintain functional ecosystems make them strategic areas for the development of sustainable conservation strategies. These results can be applied to other tropical and subtropical species under similar climatic pressures, guiding conservation strategies adapted to different ecosystems.

## 5. Conclusion

Our investigation revealed distinct bioclimatic variables influencing potential niche distribution across subgroups for both species. For *P. biglobosa*, climate change projections under SSP 2–4.5 indicate a north-south niche shift, while SSP 5–8.5 scenarios predict a severe reduction in suitable habitat. Among the subgroups studied, the northern subgroup of P. *biglobosa*, shows the highest vulnerability to climate change, while the central subgroup shows an increased potential to adapt to projected warming. Conversely, for V. *paradoxa*, northern and central subgroups show increased vulnerability, with the southern subgroup showing better adaptation to future climate conditions. Climate vulnerability of the northern subgroups is regulated by temperature extremes and climate seasonality for *P. biglobosa*, whereas water availability, especially in the dry season, is the main factor for V. *paradoxa*. The Sudano-Guinean and Guineo-Congolean Zones emerge as critical conservation areas for both species to mitigate the effects of climate change. In fact, according to future climate projections, potential niches converge in these two zones, providing natural climatic refuges. They offer suitable environmental conditions that could ensure the viability and resilience of the species in the face of climate stress. Therefore, these areas could serve as a reference for reforestation policies and long-term conservation strategies for both species. Subgroup-specific responses to climatic conditions revealed minimal niche similarity and pronounced niche differentiation within species populations. Interspecific analysis suggests a higher potential for niche sharing between southern subgroup pairs under current conditions, although the probability of future coexistence remains low. These findings provide important insights for the development of sustainable conservation strategies. Strengthening the role of both species in Benin's agroforestry parks is essential to maintain ecosystem services, ensure food security, and support the livelihoods of rural communities through improved management practices. Policies should aim to promote diversity within agroforestry systems, particularly through mixed parks. This approach could help strengthen the diversity of rural livelihoods. For effective implementation, it is essential to adopt policies that provide economic and regulatory incentives to encourage the integration of agroforestry species, and to develop selection and multiplication programs for adapted varieties. It is also essential to involve local communities through training and participatory management. Integrating agroforestry diversification into national climate change adaptation strategies and strengthening value chains for products from these systems will help ensure the economic and environmental viability of agroforestry parks. Next steps in research include further validation of models by incorporating genetic data, long-term monitoring of habitats and species populations, and exploration of new methods for modeling mitigation and adaptation strategies to refine projections.

## Statements

NA.

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## CRediT authorship contribution statement

**Chaffra Charles Yabi:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jacques Idohou Kadjogbé Ayena:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Séverin Biaou:** Writing – review & editing, Visualization, Validation, Formal analysis. **Serge Adomou:** Investigation, Data curation. **Thierry Dèhouégnon Houehanou:** Writing – review & editing, Project administration, Data curation, Conceptualization. **Gérard Nounagnon Gouwakinnou:** Writing – review & editing, Supervision, Project administration, Data curation, Conceptualization.

## 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.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2025.100830.

## Data availability

The authors undertake to provide all necessary information or details on the data and methodology upon reasonable request in order to facilitate reproducibility and further scientific research. Interested parties may contact the corresponding author for further clarification or specific requests regarding the data used in this study.

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