

Spatial distribution, hypervolumes, niche overlaps, and dynamics of the forest plant-community of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria* in the context of climate change across Africa

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Research Article

Keywords: Plant-community, *Triplochiton scleroxylon*, *Terminalia superba*, *Antiaris toxicaria*, spatial distribution, ecological niche, niche overlaps, niche shift, niche occupancy, hypervolume, climate change, Benin, Africa

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Abstract

Climate change is the main driver of biodiversity loss across continents and its effects need to be investigated seriously to inform decisions on possible mitigation measures to assure conservation and sustainable use of natural resources. We therefore examined the effect of climate change on the spatial distribution, ecological niches, niche overlaps, and niche shifts of the plant-communities of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria*. We used SDM packages that offered the possibility to compare the performances of several modelling methods. Based on the results on algorithms' performances in our previous studies, we used three machine learning algorithms: MaxEnt, Boosted Regression Trees (BRT), and Random Forests (RF).

From the main results, RF and Maxent outperformed BRT algorithm with respect to the key statistic values, AUC and TSS. However, Maxent outperformed the other algorithms with respect to its realistic predictions at present.

Confidence intervals of Sorensen and Jaccard overlap statistics approved the hypervolumes' overlaps of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria* at 95% degree of confidence and therefore confirmed their degree of community. The degree of community between the three species is also confirmed in the future scenarios, SSP 245 and SSP 585, horizon 2040 with the General Circulation Model (GCM), Model for Interdisciplinary Research on Climate version 6 (MIROC6).

Under climate change, there will be niche shifts as a response of the plant community and species to track more favorable environmental conditions for survival. Also under climate change, the plant-community will extend its spatial distribution mainly in West and Central Africa but will retract its distribution in East and Southern Africa where it will however survive with only one or two of the dominant species, namely *Terminalia superba* and / or *Antiaris toxicaria*.

Management interventions are suggested to enhance in time and space, sustainable wood and biomass production of the plant-community.

Keywords: Plant-community, *Triplochiton scleroxylon*, *Terminalia superba*, *Antiaris toxicaria*, spatial distribution, ecological niche, niche overlaps, niche shift, niche occupancy, hypervolume, climate change, Benin, Africa

1-Introduction

Forest ecosystems are important components of biodiversity which is of utmost importance to the survival of people through many ecosystem services such as provisioning ecosystem services of woods, meats, roots and tubers, foods, genetic resources etc. (MA, 2005, IPBES, 2024; FAO, 2025); regulating ecosystem services that assure regulation of winds, cyclones, mitigation of the effect of climate change through carbon storage etc. (FAO, 2025); cultural ecosystem services through spiritual enrichment, recreation, and aesthetic features, tourism (MA, 2005; IPBES, 2024; FAO, 2025); supporting ecosystem services for examples primary production, nutrient dispersal and cycling, soil protection, seed dispersal, and water cycling etc. which are necessary for the production of all other ecosystem services (MA, 2005; IPBES, 2024; FAO, 2025).

Many studies proved that forest ecosystems or vegetation in general are not just a set of plant species but, they are structured in plant communities as a response of the ecological affinities of species to the combined effects of environmental factors such as soils, rainfall, temperature, topography, slopes, geomorphology etc. (Ganglo, 2024; Ganglo and De Foucault, 2006; Ganglo, 2005; Awokou et al., 2009). Most of those authors highlighted the relationships between plant-communities and environmental factors and forest productivity or soil fertility as an asset for forest management and the sustainable use of forest resources. Furthermore, plant-communities, especially undergrowth non-pioneer plant-communities, are basic forest units where homogeneity of ecological and biological factors are met so as to serve as reliable indicators of forest sites, levels of forest productivity, types of silvicultural treatments, and sustainable forest managements (Ganglo, 2024; Aoudji et al., 2011; Awokou et al., 2009; Noumon et al., 2006; Ganglo and De Foucault, 2006; Sokpon et al., 2006; Ganglo, 2005; Noumon and Ganglo, 2005; Kelly and Iremonger, 1997).

Ganglo (2024) in his study on the structural characteristics of the understory vegetation in Toffo forest plantations (South Benin), identified and characterize nine plant-communities clearly determined by ecological factors mainly types of soils and topography. The plant-communities so identified are indicative of forest sites and the levels of forest productivity. They are quite useful in sustainable forest management and biodiversity conservation purposes.

Undergrowth plant-communities in Pahou Forest reserve in South Benin were also identified and described (Aoudji et al., 2011). The authors highlighted the relationships between the plant-communities identified, the ecological factors, and the forest sites' productivities. They also pointed out the usefulness of plant-communities in sustainable forest management and biodiversity conservation.

Sokpon et al. (2006) identified in the open woodland forest in northern Benin, four plant-communities which structural characteristics, mostly determined by site conditions served as basis for sustainable forest exploitation and management.

Kelly and Iremonger (1997) in their floristic and environmental studies in Ireland, distinguished seven (7) vegetation groups that served to recommend active conservation measures

Research works focusing on plant-communities rather than individual species are therefore quite useful and commendable for sustainable forest management.

Climate change is known as an exacerbating factor of the threats to biodiversity, through warming trends in temperature and climate related extremes such as heat waves, droughts, floods, cyclones, and wildfires observed at global scale and across regions (IPCC, 2023).

Research works therefore need to tackle seriously and closely the current and future effects of climate change on the diverse types of ecosystems across the world.

Studies of the impacts of climate and global changes on the spatial distribution of individual species are quite abundant in literature and contribute to support decisions on the management and sustainable use of the resources of diverse ecosystems across the world (Xu et al. 2024; Ganglo, 2023; Wang et al., 2023; Amiri et al., 2021; Harrison et al., 2020 ; Li et al., 2019; Santana et al., 2019; Ganglo et al., 2017; Leng and Huang, 2017).

Xu et al. (2024) investigated on *Aconitum leucostomum*, a poisonous grass of grassland populations and livestock development in China. They used MaxEnt to predict the distribution of the species across the country. They found out that while Human activities inhibit the spread of *A. leucostomum*, climate change promotes its growth, with areas of high suitability mainly in northern Xinjiang and northern Yunnan.

Ganglo (2023), in his study on the ecological niche model transferability of the white star apple (*Chrysophyllum albidum* G. Don) across tropics, predicted an extension of the suitable areas of the species mostly in West, East, Central, and Southern Africa as well as in East Madagascar. He also predicted a successful introduction of *C. albidum* in Latin America and tropical Asia, both at present and in the future.

Wang et al. (2023) investigated the spatial distribution of five *Pyrus* species in China, and evaluated the consistency between the actual production area and the modeled climatically suitable area under the current climate conditions. The authors proved that the consistency analysis between suitable planting area and actual production regions can help evaluate the potential planting risk of the species

The studies addressing the spatial distribution of plant-communities in the context of climate change are also quite common (Feeley et al. 2020; Niu et al., 2019; Franklin et al., 2016; Manish et al. 2016; Maclean et al., 2015; Cannone and Pignatti, 2014; Yang et al., 2011; Trivedi et al. 2008; Kupfer et al., 2005).

Feeley et al. 2020 analyzed millions of records of thousands of species and found that the plant communities in most ecoregions in North, Central and South America have experienced thermophilization over the past four decades (1970–2011). Thermophilization was fastest in ecoregions with intermediate temperatures and was positively correlated with warming rates within many biomes. They concluded that climate-driven changes in plant community composition will affect the function and stability of the New World ecoregions.

Niu et al. (2019) surveyed the plant community in term of species composition, diversity and biomass across 189 sites on a hill of the Tibetan Plateau and analyzed the individual and integrated effects of soil temperature and moisture on the plant community. They found out that the integrated effects of increasing soil temperature and decreasing moisture are expected to

lead to a rapid decrease in species richness. They emphasized that integrated effects of soil temperature increasing and moisture decreasing caused a shift from sedge-controlled to gramineae-controlled communities in alpine meadow.

Studying the impacts of climate and global changes on plant-communities is not possible without objectifying the degree of community or niche overlaps of the characteristic species that determine in nature the physiognomy or visual traits of the plant-communities under investigation. Hutchinson (1957) introduced the concept of ecological niche as a region of an n-dimensional hyper-space of environmental factors acting on the species. The concept of n-dimensional hyper-space is appraised through the concepts of hypervolume, hypervolume occupancy, and related statistics (Blonder, 2018; Blonder et al., 2022, Chen et al., 2024; Jin et al., 2024). An n-dimensional hypervolume is a shape defined with multiple continuously valued dimensions for which distance metrics can be calculated (Blonder, 2018; Chen et al., 2024). It allows geometric interpretations of high-dimensional datasets and can be used to produce statistics for dataset shapes, volumes and overlaps.

Jin et al. (2024) estimated the global geographical distribution patterns and ecological niche overlaps of three *Diabrotica* beetles and derived useful recommendations on the management of invasive crop pests on maize production of North America and Europe.

Niche overlaps between species in experimental grassland communities was investigated by Mason et al. (2011) in South Bohemia, Czech Republic in Central Europe; the authors found out that the importance of niche overlap in grassland communities, decreases with increasing biomass and increase with disturbance in the grassland communities.

The forest plant-community of *Triplochiton scleroxylon* K. Schum, *Terminalia superba* Engl. & Diels, and *Antiaris toxicaria* (Pers.) Lesch, is quite characteristic of the physiognomy of the secondary forests of the subequatorial climate area in Benin (Akoegninou et al., 2006; Hall and Bada, 1979). Its dominant species *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria* are light-demanding species of young and old secondary forests in the subequatorial zone of West and central Africa, stretching from Guinea to DRC across Atlantic Ocean coastal countries (PROTA4U, 2025a, b; Akinagbe et al., 2019; Adedeji et al., 2018; Siaw et al., 2014; Hall and Bada, 1979). *Terminalia superba* extends further to Cabinda in Angola (PROTA4U, 2025b).

Antiaris toxicaria, compared to the other two species, is extremely widespread; in Africa, it occurs from East Senegal to southern Ethiopia, and South to Zambia and Angola; it is also found in Madagascar; it occurs in tropical Asia, islands of the Pacific Ocean (East to Fiji and Tonga) and northern Australia (PROTA4U, 2025c).

In their natural ranges, the target species are useful in many respects.

Indeed according to PROTA4U (2025a), the wood of *Triplochiton scleroxylon* is widely used for interior joinery, panelling, moulding, furniture, boxes and crates, sculptures, matches, pencils etc. The leaves of the species are prepared as a cooked vegetable or sauce in traditional cuisine in Côte d'Ivoire and Benin. The bark is applied in traditional medicine to treat oedemas and as an anodyne.

The wood of *Terminalia superba* is used for construction, furniture, flooring and other high-quality wood products (PROTA4U, 2025b; Houghton et al., 2004). According to Rolland et al. (2024), the ethanolic extract of *Terminalia superba* can be used to manage the cerebral malaria due to its antioxidant and anti-inflammatory properties on neurons. Bark decoctions and macerations are used in traditional medicine to treat wounds, sores, haemorrhoids, diarrhoea, dysentery, malaria (PROTA4U, 2025b).

According to PROTA4U (2025c), the wood of *Antiaris toxicaria* is used for interior joinery, panelling, moulding, shuttering, furniture, strip flooring etc. Its latex is used in dart and arrow poisons. It's applied to cuts, wounds and skin complaints and is taken internally as a purgative. It is also reported to be used as a fish poison and birdlime. Its seeds, leaves and bark are used as a febrifuge. The fruit is edible and the leaves are used as fodder etc.

Because of the usefulness of the dominant species of the plant-community of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria*, we decided to investigate on the possible impacts of climate change on its ecological niche and the related implications on its spatial distribution. More precisely, our research questions were as follows: 1) Do niche overlaps exist between the dominant species of the plant-community? 2) How does climate change impact the dynamics of the hypervolumes of the dominant species of the community? 3) How does climate change impact the spatial distribution the plant-community? Answering those key questions can help design and implement, in the context of climate change, appropriate management strategy for the sustainable use of the resources of the plant-community of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria* across Africa.

2-Material and methods

Species data

The species data were downloaded from the Global Biodiversity Information Facility (GBIF, www.gbif.org) site. They are available at the following links: <https://doi.org/10.15468/dl.88j43j> for Samba (*Triplochiton scleroxylon*) downloaded on 4th December 2023; <https://doi.org/10.15468/dl.me822x> for Limba / Fraké (*Terminalia superba*) downloaded on 4th December 2023; and <https://doi.org/10.15468/dl.e8b5vp> for Antiaris / false Iroko (*Antiaris toxicaria*) downloaded on 4th December 2023. We then cleaned the data by removing duplicates, data without coordinates, and data from introduced species or forest plantations. In order to thin the data at the adequate mean spacing of 5 km apart so as to comply with the spatial resolution of 2.5 arc minutes of the environmental data used in the models, we ran the spThin R package version 0.2.0 (Aiello-Lammens et al., 2015). The datasets used in the model calibration are displayed in **Figure 1**.

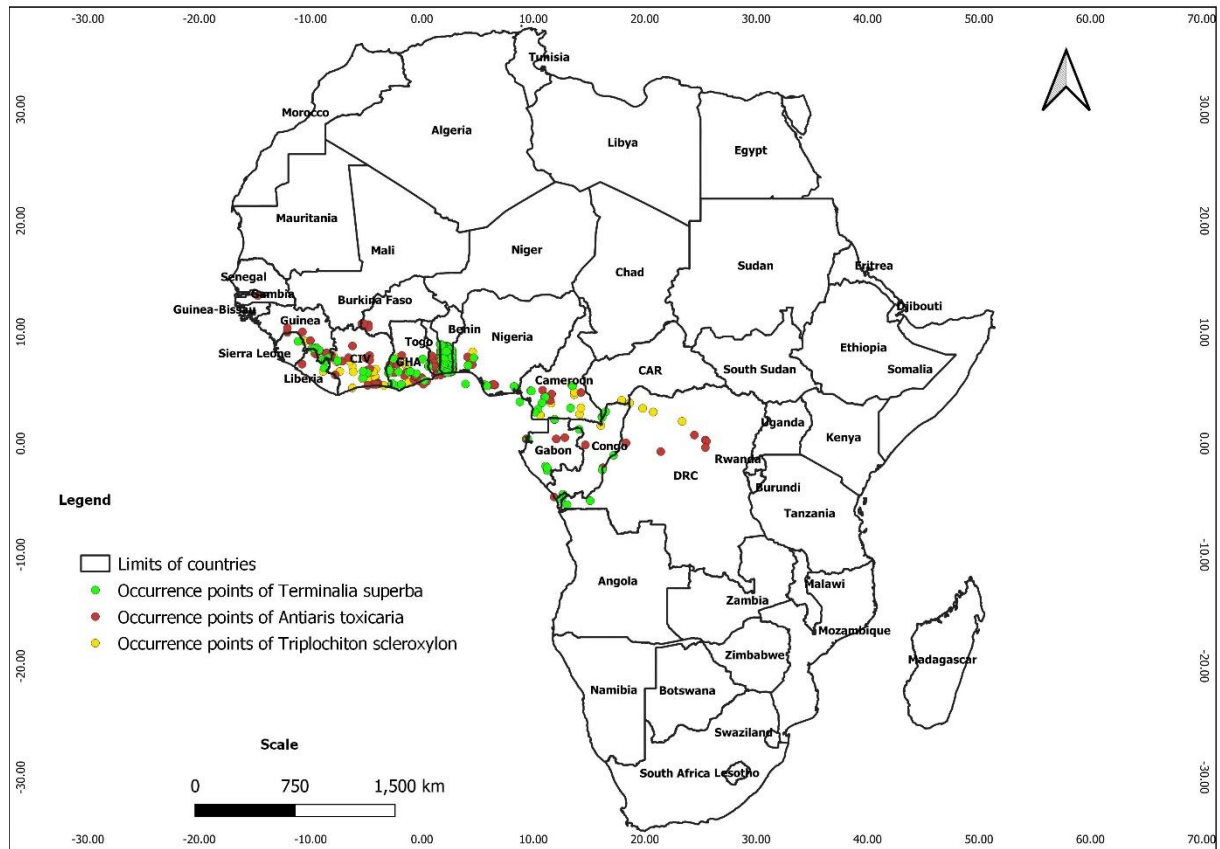


Figure 1. Occurrence data used in the models. The map was generated via QGIS 3.18.1 (<http://qgis.osgeo.org>) and WGS84 as the coordinate reference system.

Predictor data

In order to match the spatial density of occurrence data of *T. scleroxylon*, *A. toxicaria* and, *T. superba*, we used predictor data at a resolution of 2.5 arc minutes. They were 19 bioclimatic variables of the present, downloaded on WorldClim site (Fick and Hijmans, 2017; <https://www.worldclim.org/data/worldclim21.html>), and human population density used as a proxy for human pressure on vegetation, downloaded at the same resolution from the Socio-Economic Data and Application Center (SEDAC) (<https://sedac.ciesin.columbia.edu/theme/population>).

Future bioclimatic data for projections were also downloaded on Worlclim site (Fick and Hijmans, 2017; <https://www.worldclim.org/data/worldclim21.html>). We therefore used the Model for Interdisciplinary Research on Climate version 6 (MIROC6) (Tatebe et al. 2019). The tropical climate systems and the mid-latitude atmospheric circulation are significantly improved in MIROC6 in comparison with MIROC5 (Tatebe et al. 2019).

Collinearity between environmental variables can induce bias in parameter estimation by inflating variance of regression parameters and therefore mislead in the choice of the relevant predictors of models (Dormann et al., 2013; Naimi and Araudjo, 2016). To account for this, we extracted per species, the values of the predictors at occurrence points and ran the variance inflation factor (VIF) function in the SDM package (Naimi and Araudjo, 2016). We therefore

retained the less correlated variables in the models per species (threshold value of $VIF = 0.9$). Following this, the less correlated variables of the three species were put together and the duplicated ones were removed. A vector mask was generated around the occurrence points using QGIS 3.18.3 (QGIS Development Team, 2021). The mask was used to calibrate the predictor variables to the extents of occurrence data before running the models. From many species model approach, we thereafter achieve preliminary running of the models to retain, among the less correlated variables, the most contributing ones to the models of the three species considered together.

SDM package, model fitting, and evaluation

We used sdm package (Naimi and Araudjo, 2016) for data modelling purposes in R (R Core Team, 2025) in order to have the required facilities to compare the predictive performances of several algorithms / modeling methods and to achieve the desired ensemble models.

Based on the results on algorithms' performances in our previous studies (Ganglo, 2023), we used three machine learning algorithms: MaxEnt (Phillips et al., 2006), Boosted Regression Trees (BRT, Friedman 2001), and Random Forests (RF, Breiman 2001).

In model calibration, the default settings (Naimi and Araudjo, 2016) were used. However, when creating the sdm object data, we generated 10,000 random background points. The cross validation method with 2 replications, making a total of 10 replications per species and per algorithm was applied to run the models. We therefore obtained 90 (10 replications x 3 species x 3 algorithms) models for the three species.

As reported in Ganglo (2023), the predictive performances of the models generated were measured through their discrimination capacities and reliabilities using different statistics, namely the area under the curve (AUC) of the receiver-operating characteristics plot (Liu et al., 2011, Hao et al., 2020), the True Skill Statistics (TSS) (Allouche et al., 2006), the point biserial correlation (COR), and the proportion of explained deviance (Deviance) (Liu et al., 2011). All those statistics were implemented in the default setting of the sdm package (Naimi and Araudjo, 2016). Ensemble models were generated using the threshold that maximized the TSS. This threshold was shown to produce the most accurate predictions (Barbet-Massin et al., 2012; Shabani et al., 2018). That threshold was also used to achieve binary transformation of the outputs of the models in QGIS 3.18.3 (QGIS Development Team, 2021).

When generating ensemble models, we combined the 30 models generated for the three species per algorithm (10 replications per species). This approach is better to take into account the impact of the interactions between species living in communities on their spatial distributions and ecological niches than the approach of considering individual models generated per species (Stohlgren et al. 2010; Jin et al. 2024).

Niche overlap analysis

The three species we considered in this study are living in community and therefore, their degree of community or overlap of their ecological niches must be appraised. We therefore used

the package of Hypervolume (Blonder et al., 2022) and its associated multiple functions to generate with respect to the three species, hypervolumes, hypervolume occupancy, hypervolume intersections, hypervolume overlaps and related statistics etc. We then performed some associated tests in order to objectivize niche overlaps between the three species. The four most contributing environmental variables to the models of the three species were considered in generating the n-dimensional hypervolumes of the species. The four most contributing variables to the models were then z- transformed (centered relative to mean and scaled relative to standard deviation) prior to hypervolume construction (Blonder et al., 2022). In order to evaluate the ecological niche overlap between the three forest species, we mapped the hypervolumes onto an orthogonal axis composed of paired environmental variables. The hypervolume distance between centroids (Euclidean distance) and the similarity between hypervolumes (Jaccard and Sorensen indices) were then calculated to characterize the degree of overlap in the ecological niches of the three species (Blonder et al., 2022; Jin et al. 2024). Niche evolution over time and space was appraised. Indeed, niche estimation can vary over time according to intrinsic population, environmental, sampling, or temporal scale factors (Vilas et al., 2022). In our case, we appraised niche evolution with regards to the two scenarios of climatic change, SSP 245 and SSP 585. We therefore computed statistics like volume, distance between centroids and similarity between hypervolumes at present and in the future.

In order to appraise the effect of climate change on the most contributing variables to the models as well as temperature and precipitation evolution, we used the tool “Random points inside polygons” of the function “Vector creation” of QGIS 3.18.1 to add 10,000 to 100,000 random points across countries in Africa and thereafter, we used the “extract” function of the Raster package in R to extract the values of the variables considered at the random points set across Africa. Their mean values and standard deviation (sd) were then calculated to appreciate the effect of climate change on their evolution and their contribution to the suitability of the habitat of the target species with respect to the climatic model and scenarios used.

3-Results

We first present the variable selection process and model performance then, niche overlap and its dynamics overtime. We finally present the predictions of the ecological niches at present and in the future.

3.1-Selected variables and model validation

After preliminary running the models and taking into account the contribution of each variable to the performance of the models, we retained eight (8) variables: population density (pop); Isothermality (bio3); Temperature Seasonality (bio4); Min Temperature of Coldest Month (bio6); Precipitation of Wettest Month (bio13); Precipitation of Driest Month (bio14); Precipitation Seasonality (bio15); and Precipitation of Coldest Quarter (bio19). The relative variables' importance is presented per species on **Figure 2** and variable importance for individual models per species are presented in **Appendices 1 to 9** in supplementary material at https://docs.google.com/document/d/18mO63_mvLBa3jPWFTWZAkq323ZhtGGQc1eC3zarZSM8/edit?usp=sharing. The mean performance of the models per species is presented on **tables 1 to 3**.

Table 1: Mean values of the statistics of models' performance evaluation with respect to samba

Methods	AUC	COR	TSS	Deviance
Maxent	0.97 (0.007)	0.60 (0.029)	0.83 (0.010)	0.15 (0.009)
BRT	0.88 (0.028)	0.65 (0.045)	0.73 (0.009)	0.13 (0.008)
RF	0.97 (0.008)	0.69 (0.042)	0.82 (0.036)	0.09 (0.010)

Table 2: Mean values of the statistics of models' performance evaluation with respect to Fraké

Methods	AUC	COR	TSS	Deviance
Maxent	0.95 (0.017)	0.54 (0.039)	0.78 (0.013)	0.18 (0.019)
BRT	0.90 (0.046)	0.56 (0.054)	0.74 (0.070)	0.13 (0.010)
RF	0.96 (0.022)	0.68 (0.062)	0.81 (0.070)	0.09 (0.015)

Table 3: Mean values of the statistics of models' performance evaluation with respect to Antiaris

Methods	AUC	COR	TSS	Deviance
Maxent	0.94 (0.017)	0.56 (0.039)	0.79 (0.014)	0.20 (0.013)
BRT	0.88 (0.033)	0.61 (0.087)	0.69 (0.043)	0.14 (0.014)
RF	0.95 (0.016)	0.66 (0.059)	0.79 (0.043)	0.11 (0.013)

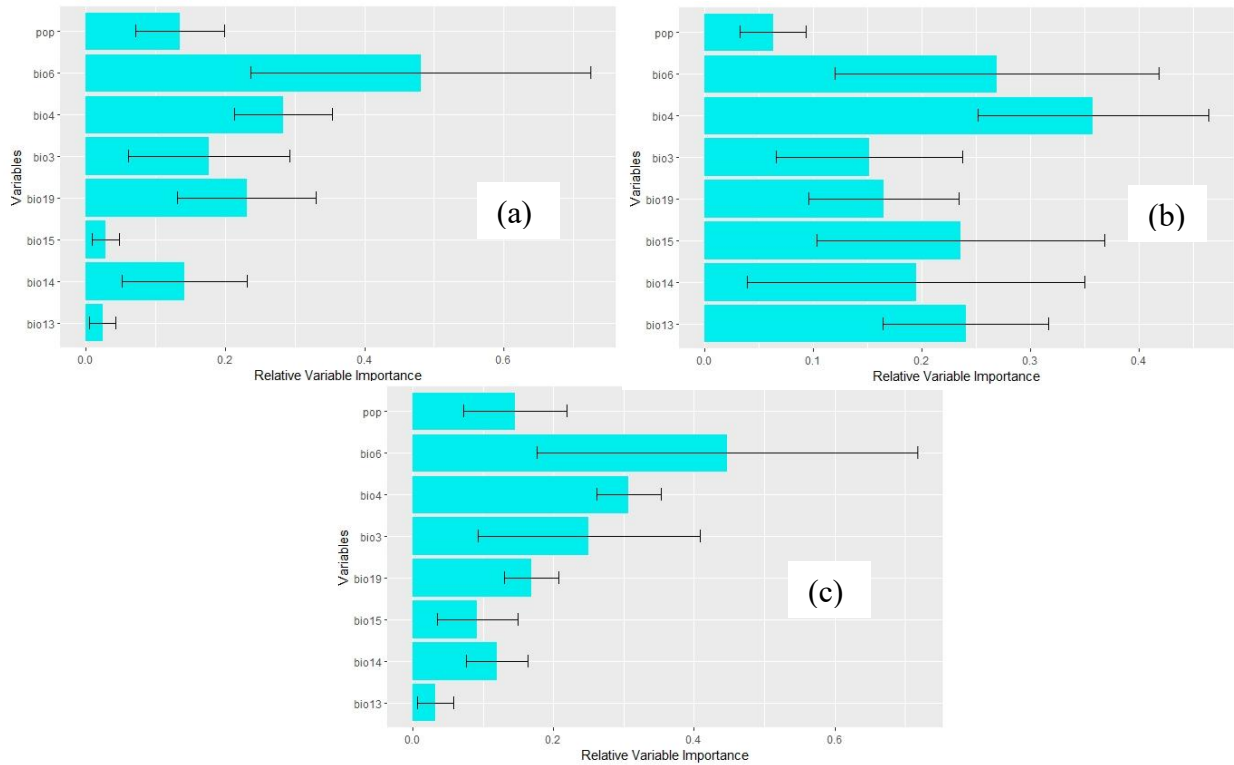


Figure 2: Relative environmental variable importance in the combined models (Maxent, BRT, and RF) with respect to species: a) case of Samba (*Triplochiton scleroxylon*); b) case of Fraké (*Terminalia superba*); c) case of Antiaris (*Antiaris toxicaria*); the bar plots were generated using R version 4.1.3 ([https:// www.R- project. org/](https://www.R-project.org/)).

From **Figure 2**, the Min Temperature of Coldest Month (bio6) and Temperature Seasonality (bio4) are the most contributing variables whatever species considered. When we consider Samba and Antiaris, the least contributing variables to the models are Precipitation of Wettest Month (bio13) and Precipitation Seasonality (bio15) whereas population density (pop) and Isothermality (bio3) are the least contributors to the models of Fraké. The other environmental variables had intermediate contributions to the models.

From **tables 1 to 3**, the mean values of the Area Under the Curve (AUC) ranged from 0.88 to 0.97 and the mean values of True Skill Statistic (TSS) ranged between 0.69 to 0.83. We therefore deduced that the models performed better than random models.

From **Tables 1 to 3**, when we consider Maxent, the AUC values ranged from 0.94 to 0.97 whereas TSS values ranged from 0.78 to 0.83 for either species; with respect to BRT, the AUC values ranged from 0.88 to 0.90 whereas TSS values ranged from 0.69 to 0.74 for either species; on the other hand, when we consider RF, the AUC values ranged from 0.95 to 0.97 whereas the TSS values ranged from 0.79 to 0.83 for either species. From those values, BRT with the lowest values of both statistics is the least efficient model compared to Maxent and RF. Maxent and RF are roughly equivalent with respect to AUC and TSS statistics.

Globally, with respect to the values of AUC and TSS, Maxent and RF outperformed BRT, however, in terms of reliable predictions, Maxent outperformed RF. Indeed from **Figure 3b**, we can note that RF predicted at present, as favorable areas to the plant-community studied, the desert regions of Egypt, Lybia, Algeria etc. which is opposed to the known ecology of the species.

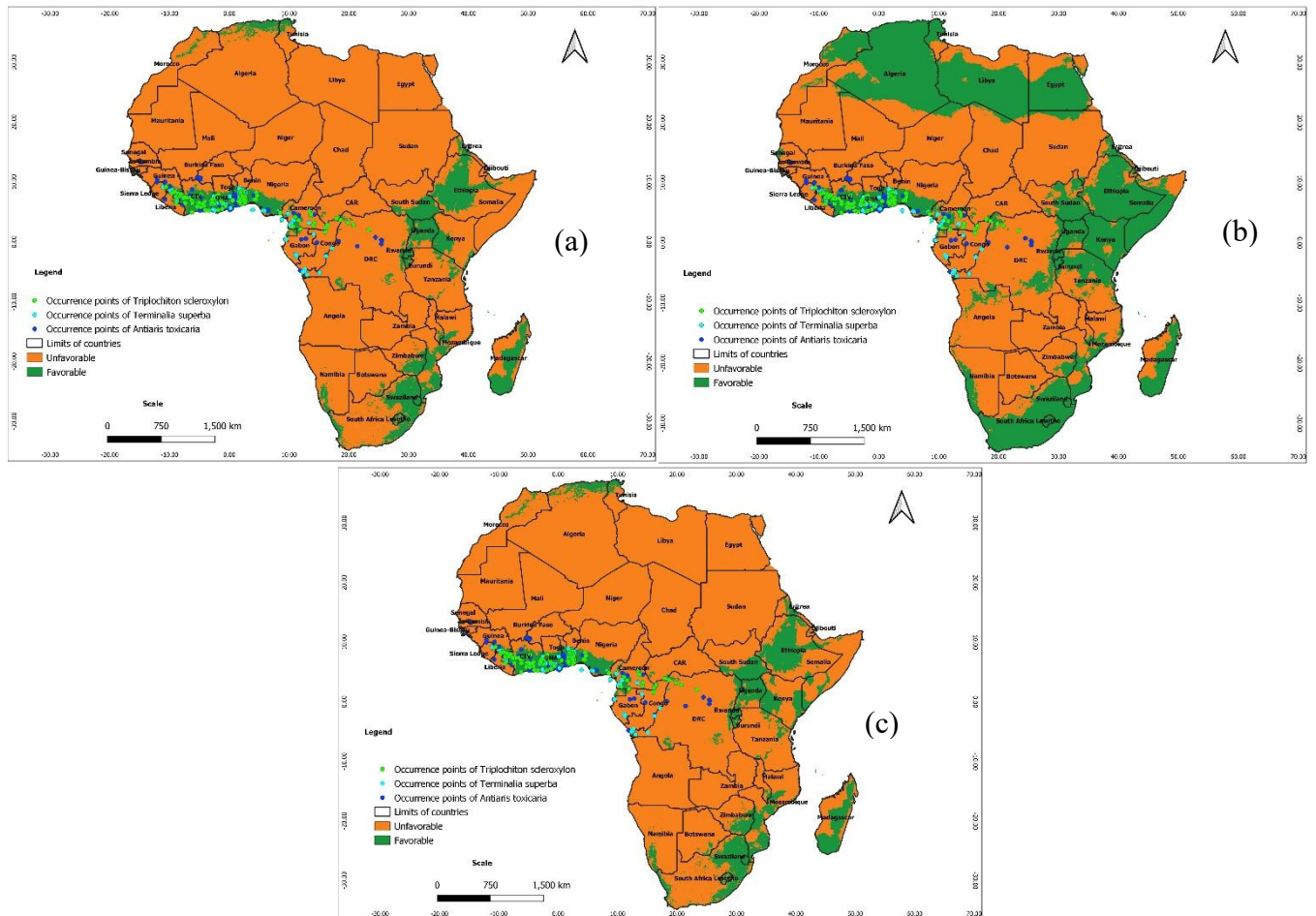


Figure 3: Predictions at present of the spatial distributions of the forest plant-community of *Triplochiton scleroxylon*, *Antiaris Toxicaria*, and *Terminalia superba* across Africa: a) according to Maxent; b) according to RF; c) according to BRT.

3.2-Hypervolumes and niche overlaps of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria* at present

3.2.1-Hypervolumes and hypervolume occupancy

In order to achieve the hypervolumes (shape defined within more than three dimensions) and hypervolume occupancies (number of hypervolumes including each random / given point) of

the three species, we considered the four variables that mostly impacted Maxent distribution model of the species. Indeed, according to our results (§ 3.1), among the algorithms used, only Maxent made reliable predictions at present with favorable and unfavorable areas of the spatial distribution of the plant community studied. The four variables considered are Isothermality (bio3), Temperature Seasonality (bio4), Min Temperature of Coldest Month (bio6), and Precipitation of Coldest Quarter (bio19). The volume of *Antiaris* hypervolume is 0.219; that of *Fraké* is 0.255, whereas the volume of the hypervolume of *Samba* is 0.133. **Figure 4** presents the evolution at 5% of probability level of the confidence intervals around the hypervolumes of the target species with different sample sizes. We can globally deduce that, the higher the sample sizes, the more confident the estimation of the hypervolumes of the species and the more the estimated volumes converged towards the true volumes.

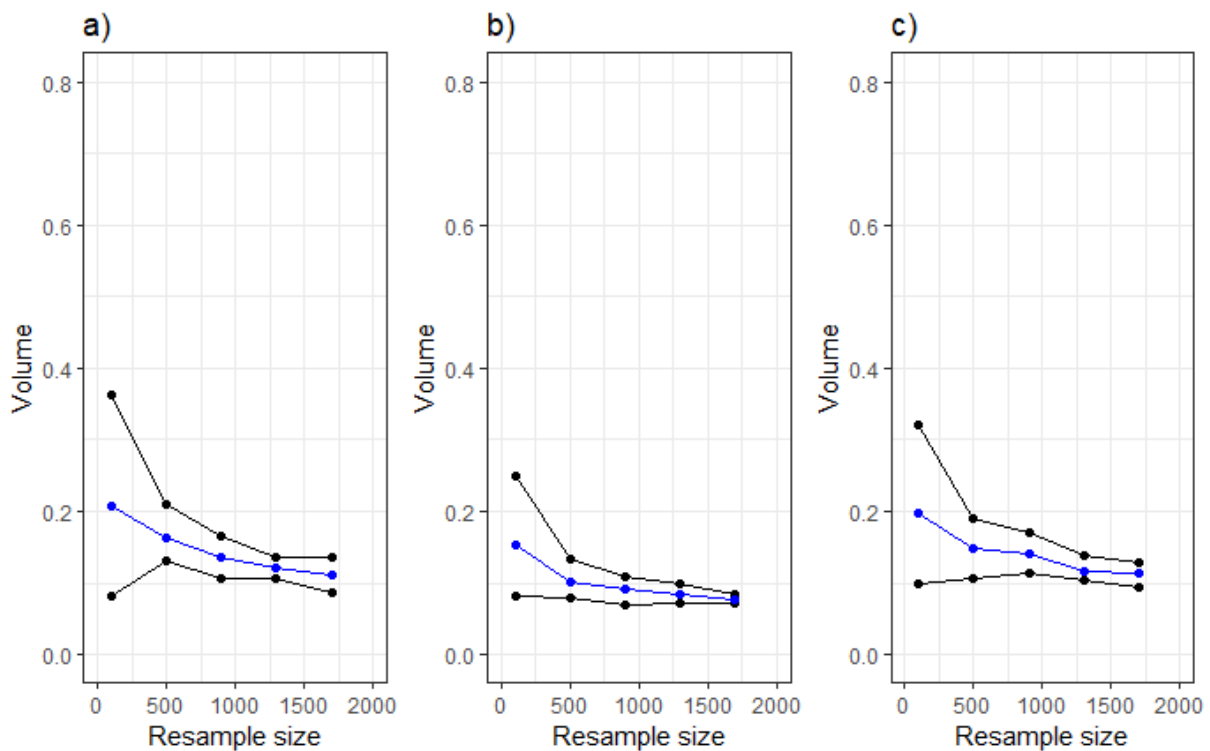


Figure 4: Evolution of confidence intervals at 5% of probability level around hypervolumes at different sample sizes: a) case of *Antiaris toxicaria*; b) case of *Triplochiton scleroxylon*, and c) case of *Terminalia superba*

Figures 5 and **6** respectively present the hypervolumes and hypervolume occupancies of the species. Those figures clearly denoted the niche overlaps between the three species expressing then, their degree of community. The figures also highlighted the large tolerance of *Antiaris toxicaria* (in red) with respect to the environmental factors, widely spreading along the values of the environmental variables considered. This confirmed the large amplitude of the spatial distribution of *Antiaris toxicaria* (in red) and its abundant regeneration already noted in many forests of Benin.

3.2.2-Degree of niche overlaps of the species

Confidence intervals of Sorensen and Jaccard overlap statistics confirmed the hypervolumes' overlaps of the species at 95% degree of confidence and therefore their degree of community (**table 4**). Indeed, the confidence intervals of Sorensen statistics included the threshold values ≥ 0.5 of community and confirmed overlaps of the hypervolumes of the species; the confidence intervals of Jaccard statistics exclude zero and also confirmed overlaps between the hypervolumes of the species.

The calculated distance between the centroids of the hypervolumes showed the degree of ecological affinity between the three species. Indeed, *Triplochiton scleroxylon* and *Terminalia superba* proved closer in environmental space with only 0.129 as distance between the centroids of their respective hypervolumes, than *Triplochiton scleroxylon* - *Antiaris Toxicaria* and *Terminalia superba* - *Antiaris toxicaria* with respectively 0.218 and 0.326 as distance between the centroids of their respective hypervolumes. Furthermore, the degree of ecological affinity between the three species is shown by the significance of the difference between their occupancy values at 5% of probability level (**Figure 7**). Indeed, on that figure, the red and green colors that respectively represent the difference of occupancy between *Antiaris toxicaria* and *Triplochiton scleroxylon* (Samba) and *Antiaris toxicaria* and *Terminalia superba* (Fraké) are dominant, compared to the cyan color that represents the difference of occupancy between *Triplochiton scleroxylon* (Samba) and *Terminalia superba* (Fraké). One note that cyan color is less represented as *Triplochiton scleroxylon* (Samba) and *Terminalia superba* (Fraké) are ecologically closer.

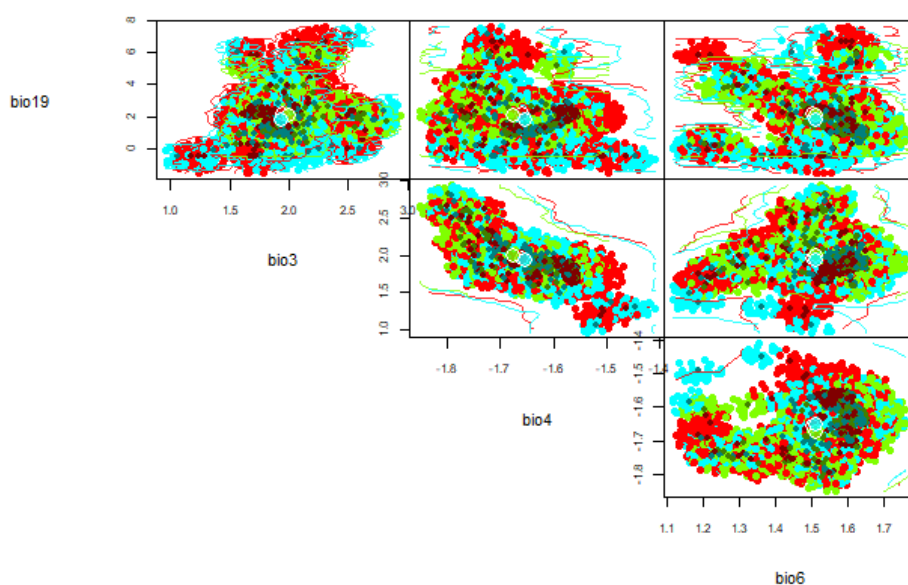


Figure 5: Hypervolumes of *Antiaris toxicaria* (Upas tree in red), *Terminalia superba* (Fraké in green), and *Triplochiton scleroxylon* (Samba in cyan)

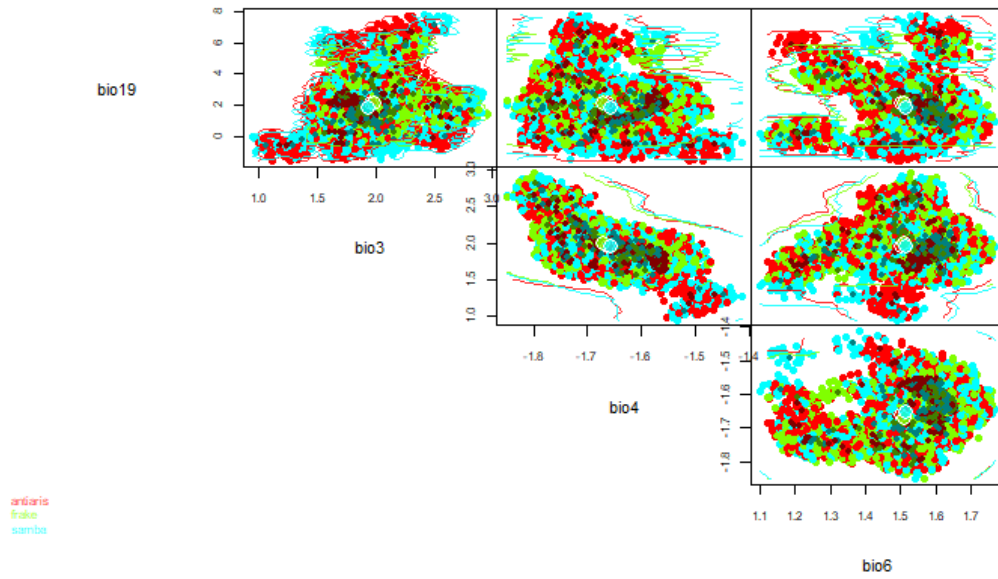


Figure 6: Hypervolume occupancy of *Antiaris toxicaria* (Upas tree in red), *Terminalia superba* (Fraké in green), and *Triplochiton scleroxylon* (Samba in cyan)

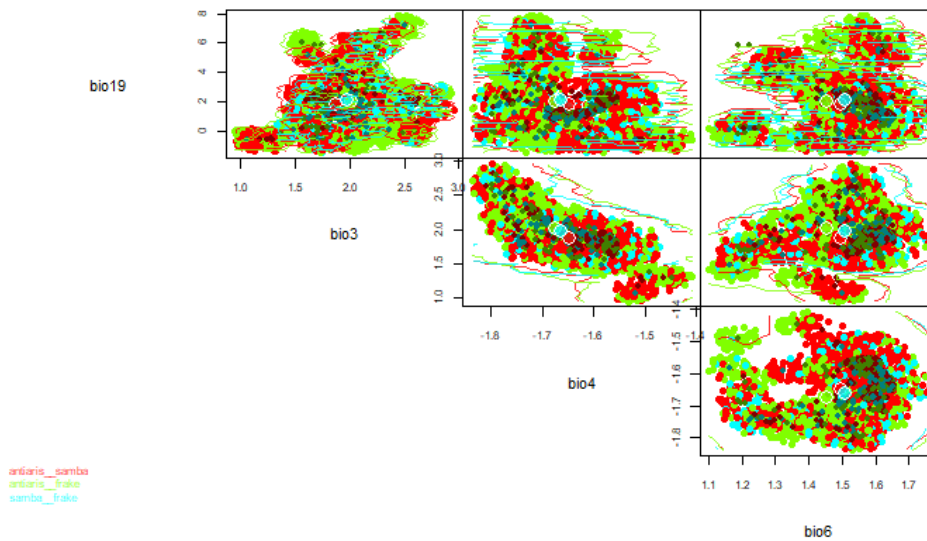


Figure 7: Significance of the difference between occupancy values of the three species at 5% of probability level, at present: *Antiaris toxicaria* vs. *Triplochiton scleroxylon* (samba) in red; *Antiaris toxicaria* vs. *Terminalia superba* (Fraké) in green; and *Triplochiton scleroxylon* (samba) vs. *Terminalia superba* (Fraké) in cyan

Table 4a: Confidence intervals of overlap Sorensen statistics at 95% degree of confidence between hypervolumes (Hv) of the three plant-community species at present and at future, scenario SSP 245, horizon 2040

Hypervolumes according to species	Confidence intervals of niche overlaps between species				
	Hv_Fraké_present	Hv_Samba_present	Hv_Antiaris_245	Hv_Fraké_245	Hv_Samba_245
Hv_Antiaris_present	0.5064876 - 0.7179732	0.4279714 - 0.7240648	0.5341000 - 0.7008906	-	-
Hv_Fraké_present	-	0.4283219 - 0.6716643	-	0.5075015 - 0.7453040	-
Hv_Samba_present	0.4283219 - 0.6716643	-	-	-	0.5082237 - 0.7182479
Hv_Antiaris_245	-	-	-	0.3841345 - 0.7667422	0.4816547 - 0.7494609
Hv_Fraké_245	-	-	-	-	0.4468862 - 0.7674980

Table 4b: Confidence intervals of overlap Jaccard statistics at 95% degree of confidence between hypervolumes (Hv) of the three plant-community species at present and at future, scenario SSP 245 at horizon 2040

Hypervolumes according to species	Confidence intervals of niche overlaps between species				
	Hv_Fraké_present	Hv_Samba_present	Hv_Antiaris_245	Hv_Fraké_245	Hv_Samba_245
Hv_Antiaris_present	0.3391251 - 0.5600298	0.2722424 - 0.5674777	0.3643496 - 0.5395163	-	-
Hv_Fraké_present	-	0.2725252 - 0.5056435	-	0.3400349 - 0.5940116	-
Hv_Samba_present	-	-	-	-	0.3406839 - 0.5603644
Hv_Antiaris_245	-	-	-	0.237727 - 0.621721	0.3172236 - 0.5993103
Hv_Fraké_245	-	-	-	-	0.2877388 - 0.6227155

3.3-Dynamics of the hypervolumes and niche overlaps of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria*, in the context of climate change

3.3.1-Case of the scenario SSP 245 at horizon 2040

Confidence intervals of Sorensen and Jaccard overlap statistics under the scenario SSP 245 at horizon 2040, clearly showed that climate change will not affect the degree of community of *Antiaris toxicaria*, *Triplochiton scleroxylon* (samba) and *Terminalia superba* (Fraké). Indeed, the hypervolumes' overlaps of the species at 95% degree of confidence is also confirmed at

future (**table 4**); according to that table, the confidence intervals of Sorensen statistics included the threshold values ≥ 0.5 of community and confirmed overlaps of the hypervolumes of the species in the future; the confidence intervals of Jaccard statistics exclude zero and also confirmed overlaps between the hypervolumes of the species at future.

Under the scenario SSP 245, horizon 2040, the volume of the hypervolume of *Antiaris* will be 0.270, hence a slight increment compared to the volume at present (0.219); this underlines better environmental conditions that will favor the expansion of the species at future.

The volume of the hypervolume of Fraké at future SSP 240, horizon 2040 is 0.153 and denotes a sensible retraction compared to the volume at present (0.255); less favorable environmental conditions compared to the present will then hinder the expansion of the species at future.

The volume of the hypervolume of Samba at future SSP 245, horizon 2040 is 0.240 and denotes a sensible increment compared to the volume at present (0.133); this also underlines better environmental conditions that will favor the expansion of the species at future.

Under the scenario SSP 245 at horizon 2040, the distance between the centroids of the hypervolumes are 0.450 between *Antiaris* and Samba, compared to the value at present (0.218); we can therefore deduce that the degree of affinity between the two species will decrease at future. The distance between the centroids of the hypervolumes of *Antiaris* and Fraké is 0.19 at future compared to 0.326 at present; this underlines that the degree of affinity between the two species will increase at future. The distance between the centroids of the hypervolumes of Fraké and Samba is 0.28 at future against 0.129 at present and highlights that their degree of affinity will decrease.

Under the scenario SSP 245, horizon 2040, we also noted slight distances between the centroids of the hypervolumes of each of the target species compared to the present. Indeed, the distance between the centroids of the hypervolumes of Fraké at present and at future is 0.12; that of Samba at present and at future is 0.16; and that of *Antiaris* at present and at future 0.23. *Antiaris toxicaria* will then be more affected in terms of spatial shift of its hypervolumes than the two other species.

Furthermore, under the scenario SSP 245, horizon 2040, the degree of ecological affinity between the three species is shown by the significance of the difference between their occupancy values at 5% of probability level (**Figure 8**). Indeed, on that figure, the red and green colors that respectively represent the difference between *Antiaris toxicaria* and *Triplochiton scleroxylon* (Samba) and *Antiaris toxicaria* and *Terminalia superba* (Fraké) are dominant, compared to the cyan color, less represented as *Triplochiton scleroxylon* (Samba) and *Terminalia superba* (Fraké) are ecologically closer. We noted that the degree of affinity highlighted on **Figure 8** is not necessarily affected by the distances between the centroids of the hypervolumes at future.

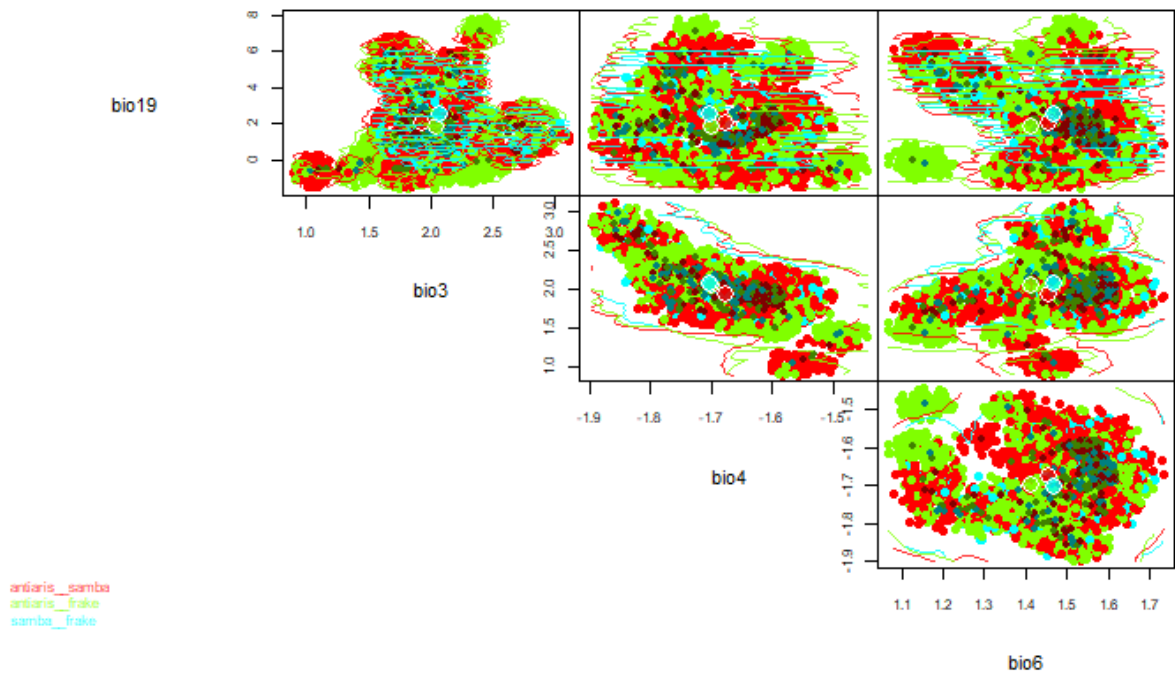


Figure 8: Significance of the difference between occupancy values of the three species at 5% of probability level under scenario SSP 245, horizon 2040: *Antiaris toxicaria* vs. *Triplochiton scleroxylon* (samba) in red; *Antiaris toxicaria* vs. *Terminalia superba* (Fraké) in green; and *Triplochiton scleroxylon* (samba) vs. *Terminalia superba* (Fraké) in cyan

3.3.2-Case of the scenario SSP 585 at horizon 2040

Confidence intervals of Sorensen and Jaccard overlap statistics under the scenario SSP 585 at horizon 2040, also clearly showed that climate change will not affect the degree of community of *Antiaris toxicaria*, *Triplochiton scleroxylon* (samba) and *Terminalia superba* (Fraké). Indeed, the hypervolumes' overlaps of the species at 95% degree of confidence is also confirmed at future (**table 5**); according to that table, the confidence intervals of Sorensen statistics included the threshold values ≥ 0.5 of community and confirmed overlaps of the hypervolumes of the species in the future; the confidence intervals of Jaccard statistics exclude zero and also confirmed overlaps between the hypervolumes of the species at future.

Under the scenario SSP 585, horizon 2040, the volume of the hypervolume of Antiaris will be 0.219, which is the same as in the present. The volume of the hypervolume of Fraké at future SSP 585, horizon 2040 is 0.142 and represent a further retraction compared to the volume at present (0.255). The volume of the hypervolume of Samba at future SSP 585, horizon 2040 is 0.207 and denotes a sensible increment compared to the volume at present (0.133).

Climate change will also cause further distance (0.467) between the centroids of Antiaris and Samba under scenario SSP 585, horizon 2040, compared to the value at present (0.218).

Under the scenario SSP 585, horizon 2040 a distance of 0.218 between the centroids of Antiaris and Fraké is noted compared to the distance of 0.326 at present; this underlines that the degree of affinity between the two species will also increase compared to the present.

The distance between the centroids of the hypervolumes of Fraké and Samba is 0.26 at future under scenario SSP 585, horizon 2040 against 0.129 at present and highlights that their degree of affinity will decrease in the future under the scenario considered.

Under the scenario SSP 585, horizon 2040, more sensible spatial shifts of hypervolumes will be noted with a distance of 0.185 between the hypervolumes of Fraké at present and in the future; a distance of 0.240 between the hypervolumes of Samba at present and in the future; and a distance of 0.410 between the hypervolumes of Antiaris at present and in the future. We can deduce that Antiaris will still be the more affected in terms of spatial shift of its hypervolumes than the two other species.

Table 5a: Confidence intervals of overlap Sorensen statistics at 95% degree of confidence between hypervolumes of the three plant-community species at present and at future, scenario SSP 585, horizon 2040

Hypervolumes according to species	Confidence intervals of niche overlaps between species		
	Hv_Antiaris_585	Hv_Fraké_585	Hv_Samba_585
Hv_Antiaris_present	0.4668808-0.6123838	-	-
Hv_Antiaris_585	-	0.3861550-0.7684299	0.5516129-0.7610886
Hv_Fraké_present	-	0.3864544-0.5489562	-
Hv_Samba_present	-	-	0.4342598-0.6376038
Hv_Samba_585	-	0.4367951-0.7894641	-

Table 5b: Confidence intervals of overlap Jaccard statistics at 95% degree of confidence between hypervolumes of the three plant-community species at present and at future, scenario SSP 245 at horizon 2040

Hypervolumes according to species	Confidence intervals of niche overlaps between species		
	Hv_Antiaris_585	Hv_Fraké_585	Hv_Samba_585
Hv_Antiaris_present	0.3045306-0.4413207	-	-
Hv_Antiaris_585	-	0.2392766-0.6239433	0.3808469-0.6143220
Hv_Fraké_present	-	0.2395066-0.3783182	-
Hv_Fraké_585	-	-	0.2794231-0.6521608
Hv_Samba_present	-	-	0.2773522-0.4680018

Furthermore, under the scenario SSP 585, horizon 2040, the degree of ecological affinity between the three species is shown by the significance of the difference between their

occupancy values at 5% of probability level (**Figure 9**). Indeed, on that figure, the red and green colors that respectively represent the difference between *Antiaris toxicaria* and *Triplochiton scleroxylon* (Samba) and *Antiaris toxicaria* and *Terminalia superba* (Fraké) are dominant, compared to the cyan color, less represented as *Triplochiton scleroxylon* (Samba) and *Terminalia superba* (Fraké) are ecologically closer. We noted that the degree of affinity highlighted on **Figure 9** is not necessarily affected by the distances between the centroids of the hypervolumes at future.

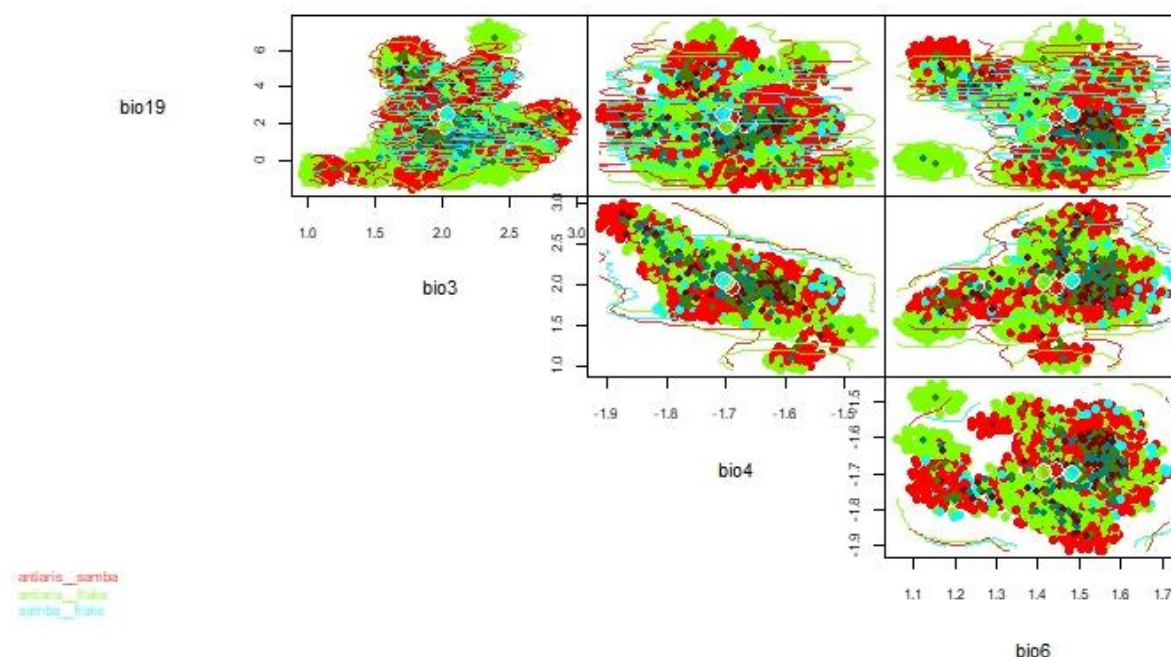


Figure 9: Significance of the difference between occupancy values of the three species at 5% of probability level under scenario SSP 585, horizon 2040: *Antiaris toxicaria* vs. *Triplochiton scleroxylon* (samba) in red; *Antiaris toxicaria* vs. *Terminalia superba* (Fraké) in green; and *Triplochiton scleroxylon* (samba) vs. *Terminalia superba* (Fraké) in cyan

3.4-Predictions of the spatial distribution of the forest plant community of *Triplochiton scleroxylon*, *Antiaris toxicaria*, and *Terminalia superba* at Africa level

3.4.1-Predictions at present

According to our results, only Maxent made reliable predictions with favorable and unfavorable areas of the spatial distribution of the plant community of *Triplochiton scleroxylon*, *Antiaris toxicaria*, and *Terminalia superba* (**Figure 10**). **Figure 10a** shows, in geographic space, the spatial distribution at present of the plant-community. This plant-community portrays the physiognomy of the secondary forest in south Benin. Its favorable area in West Africa is a large

band along the Atlantic Ocean coast from Côte-d'Ivoire to Nigeria, extending northwards up to 08° of North latitude in Benin. Its favorable area also exists in East Africa (Ethiopia, Somalia, South Sudan, Uganda, and Kenya). In Southern Africa, the plant-community can extend to East Mozambique, Zimbabwe, Swaziland, and South Africa. In Madagascar, the favorable area of the plant community covers the South of the country and extends northwards in an almost eastern band (**Figure 10a**). The predictions of the other two algorithms (BRT and RF) failed in showing reliable extensions of the plant-community (please see **Figure 3**).

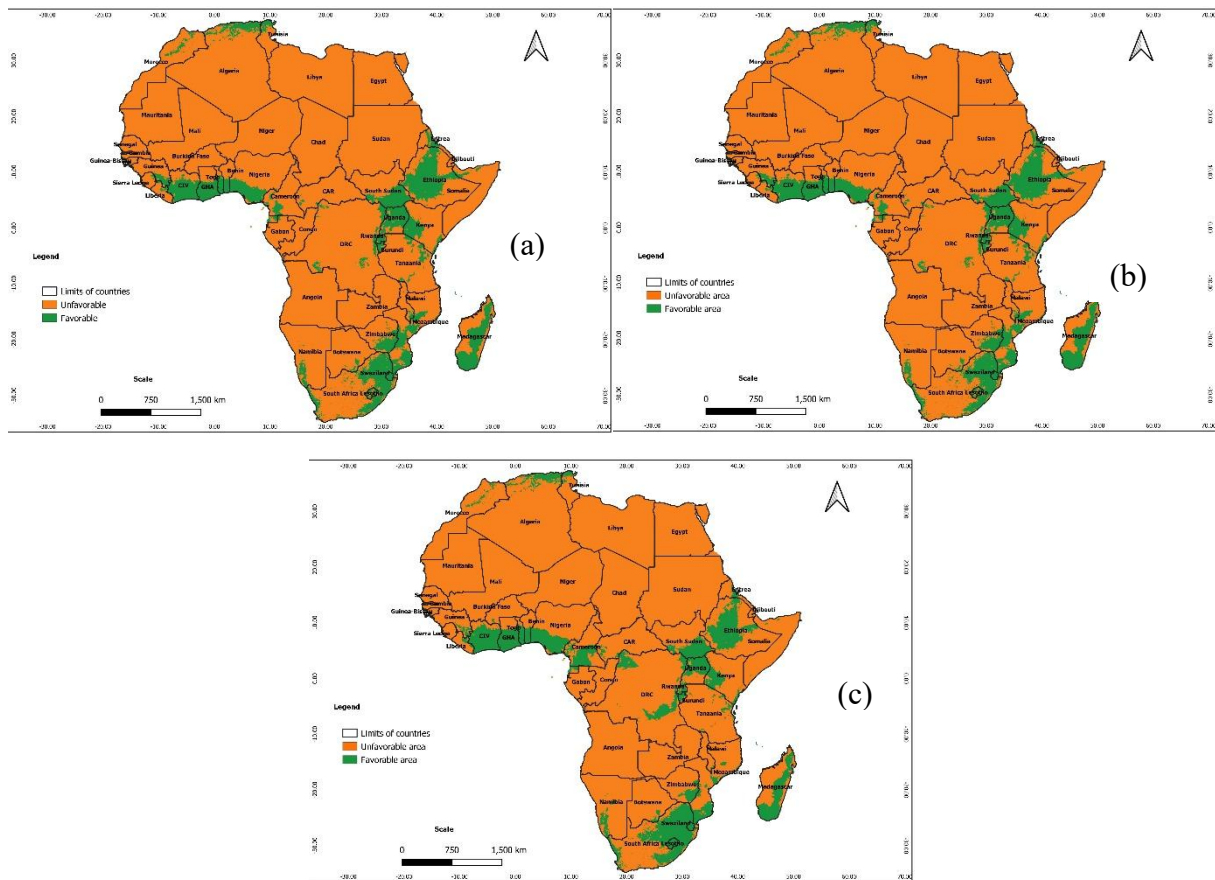


Figure 10: Predictions, according to Maxent, of the spatial distribution of the forest plant-community of *Triplochiton scleroxylon*, *Antiaris Toxicaria*, and *Terminalia superba* across Africa; a) at present; b) at horizon 2040, SSP245; c) at horizon 2040, SSP585

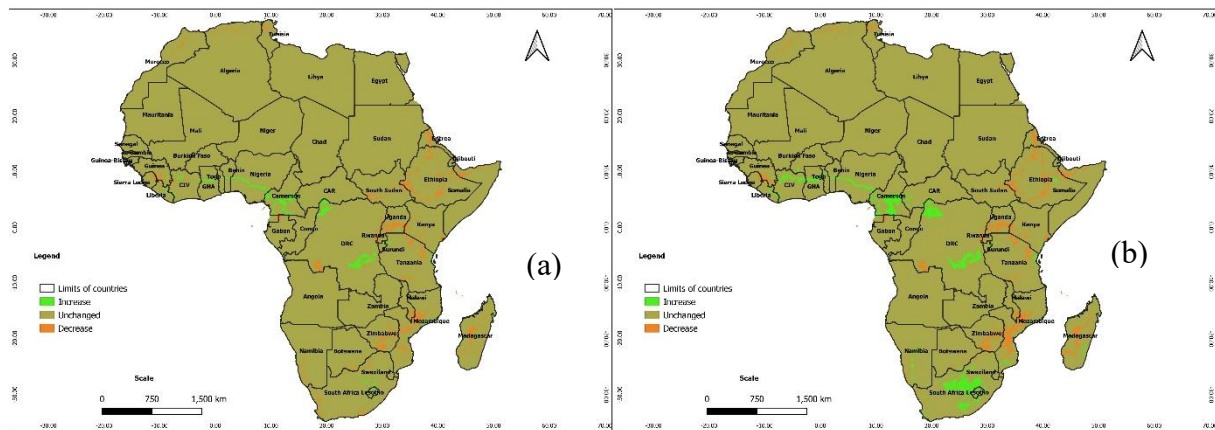


Figure 11: Predictions, according to Maxent, of the impact of climate change on the spatial distribution of the forest plant-community: a) at horizon 2040, SSP245; b) at horizon 2040, SSP585

3.4.2-Predictions at future and impacts of climate change on the spatial distribution of the plant community

Only Maxent made reliable predictions at present and is therefore considered for future projections (**Figure 3**). According to **Figures 10b, 10c, and 11**), the forest plant-community of *Triplochiton scleroxylon*, *Antiaris Toxicaria*, and *Terminalia superba* will undergo dynamics in its expansion throughout Africa compared to its spatial distribution at present (**Figure 10a**), with noticeable increases mostly in West and central Africa in DRC, and South Africa (**Figure 11**). Some reductions will however be noted across Africa, particularly in North, East, and Southern Africa as well as in Madagascar (**Figure 11**).

4-Discussion

4.1-Performance of the modeling methods and ecology of the species versus environmental factors governing their spatial distribution

4.1.1- Performance of the modeling methods

Performance of the models are measured by values of key statistics, AUC, TSS, COR, and deviance. AUC and TSS are correlated (Barbet-Massin, 2012). They are measurements of the ability of the models to discriminate real presence from absence (Elith et al., 2006). From **Tables 1-3**, when we consider Maxent, the AUC values ranged from 0.94 to 0.97 whereas TSS values ranged from 0.78 to 0.83 for either species; with respect to BRT, the AUC values ranged

from 0.88 to 0.90 whereas TSS values ranged from 0.69 to 0.74 for either species; finally, when we consider RF, the AUC values ranged from 0.95 to 0.97 whereas the TSS values ranged from 0.79 to 0.83 for either species. From those values, BRT with the lowest values of both statistics is the least performant model compared to Maxent and RF. Maxent and RF are roughly equivalent with respect to AUC and TSS statistics.

The point biserial correlation COR is the measurement of the models' reliability (Liu et al., 2011). The reliability measures the aptitude of the models in predicting real presence (Liu et al., 2011). In this study, Maxent has the lowest values (0.54-0.60) against the highest values, (0.66-0.69) for RF and the intermediate values (0.56-0.65) for BRT. With respect to COR statistic, Maxent is therefore among the least performant models.

Deviance is the measurement of the deviation of the overall mean prediction values with respect to the overall presence and absence of the species (Liu et al., 2011); it is a measurement of the goodness of fit of the models. The higher its value, the least efficient is the model. In this study Maxent has the highest values (0.15-0.20) against the lowest values, (0.09-0.11) for RF and the intermediate values (0.13-0.14) for BRT. With respect to Deviance statistic, Maxent is also the least efficient model.

Globally, with respect to the values of the statistics AUC and TSS, Maxent and RF outperformed BRT, however, in terms of reliable predictions, Maxent outperformed RF; indeed on **Figure 3b**, we can note that RF predicted as favorable areas of the plant community studied, the desert regions of Egypt, Lybia, Algeria etc. while Maxent predicted reliable areas with respect to the known ecology of the species (Akinagbe et al., 2019; Adedeji et al., 2018; Siaw et al., 2014; Hall and Bada, 1979). Another limitation of the algorithm RF in predictions is its propensity to over fit models (Ganglo, 2023; Maphanga et al., 2025).

Many research works compared the performance of the most common algorithms used in ecological niche modelling with various and even contrasting results. Indeed, from their findings, model performances depend on the target species, the quality of the training data, and, temporal predictions. For examples, Maxent outperformance over BRT and RF in this study, is in line with the previous results we obtained when comparing the same models with respect to their predictions on the spatial distribution of *Chrysophyllum albidum* across Africa (Ganglo, 2023). Our results is also supported by those of Kaky et al. (2020) who found that Maxent outperformed several algorithms of which BRT and RF, in their study on medicinal plants in Egypt. Furthermore, our results are in line with those of Shabani et al. (2016) who tested at global scale the performance of several algorithms including Maxent, BRT, and RF on eight plant species; they found that Maxent outperformed BRT and RF although efficiency of models vary with species. To account for variability of the efficiency of models, they suggested the use of ensemble models including many algorithms instead of using only one algorithm in predicting species ranges. Valavi et al. (2022) explored patterns in predictive performance across several methods, by reanalyzing a data set of 225 species from six different regions; they found that Maxent and BRT were among the top performing models among others including RF. Acharya et al. (2019) in mapping Environmental suitability of Scrub Typhus in Nepal, concluded that Maxent performed better than other algorithms among which RF and BRT.

However, on the other hand, Zhao et al. (2022), while predicting the potential distribution of the endangered amphibian *Quasipaa boulengeri* in China, found that RF outperformed Maxent in terms of prediction of habitat suitability with higher discrimination and greater heterogeneity. Models performance also depends on data quality, and temporal predictions (Moreno-Arzate

and Martínez-Meyer, 2024); indeed, in evaluating the performance of seven popular modeling algorithms in transferring ecological niche models (ENM) across time using Mexican endemic rodents, those authors concluded that not all species or algorithms are suited for temporal projections; their results highlighted that input data quality and algorithm choice significantly impact model accuracy and that algorithm performance varied between forecasting and hindcasting; finally they concluded that RF generally showed better performance for forecasting, while Maxent performed better in hindcasting. Tong et al. (2023), in their study on the key factors impacting species distribution modeling in benthic marine environments worldwide, found that globally, BRT and RF outperformed Maxent; their findings were further supported by the analysis of smoothed residuals and the uncertainty associated with the predicted habitat suitability of a zigzag coral, *Madrepora oculata*. Maphanga et al. (2025) in studying bush encroachment under climate change savanna rangelands in southern Africa using several algorithms in ecological modelling, concluded that RF outperformed Maxent; they also underlined that RF is susceptible to overfitting training data. Schatz et al. (2017), in studying worldwide the impacts of climate change on the distribution of the pathogen spread *Batrachochytrium dendrobatidis*, a devastating infectious fungus of amphibians, concluded that RF and BRT outperformed Maxent etc.

4.1.2-Ecology of the species versus environmental key factors governing their spatial distribution

Triplochiton scleroxylon, *Terminalia superba*, and *Antiaris toxicaria* are light-demanding species of young and old secondary forests in the subequatorial zone of West and central Africa, stretching from Guinea to DRC across Atlantic Ocean coastal countries (PROTA4U, 2025a, b; Akinnagbe et al., 2019; Adedeji et al., 2018; Siaw et al., 2014; Hall and Bada, 1979). *Terminalia superba* extends further to Cabinda in Angola (PROTA4U, 2025b). *Antiaris toxicaria* compared to the other two species, is extremely widespread; in Africa, it occurs from East Senegal to southern Ethiopia, and South to Zambia and Angola; it is also found in Madagascar; it occurs in tropical Asia, islands of the Pacific Ocean (East to Fiji and Tonga) and northern Australia (PROTA4U, 2025c).

The ecology of the dominant species of the plant-community studied is therefore dominated by temperature and precipitation, and their interactions in various forms. This is in line with our results where Isothermality (bio3), Temperature Seasonality (bio4), Min Temperature of Coldest Month (bio6), Precipitation of Driest Month (bio14), Precipitation Seasonality (bio15), and Precipitation of Coldest Quarter (bio19) contributed to the models' performance whatever species considered.

The large ecological amplitude of *Antiaris toxicaria* across Africa and beyond is demonstrated by the high values of isothermality (large diurnal temperature amplitude, bio3 (60 to 90%), **Appendix 16a**); high values (100 to 250%) of temperature variability (temperature seasonality, bio4, **Appendix 16b**) as well as high values of precipitation seasonality (bio15, 50 to 100%, **Appendix 16f**).

Furthermore, low temperature values of the coldest month ($\text{bio6} \leq 12^{\circ}\text{C}$, **Appendix 16c**) favor the presence of the species as well as low precipitation of the wettest month ($\text{bio13} \leq 100\text{mm}$, **Appendix 16d**); low precipitation of the driest month (bio14, 0 to 12mm, **Appendix 16e**) and low precipitation of Coldest Quarter ($\text{bio19} \leq 300\text{ mm}$, **Appendix 16g**). As for human pressure,

population density up to 30,000 habitants per Km² does not affect the probability of presence of the species (**Appendix 16h**).

We therefore deduce that the main ecological traits of *Antiaris toxicaria* are characterized by its large ecological amplitude coupled with the droughtiness of its environments and its resilience to moderate anthropogenic disturbance.

When we consider *Terminalia superba*, its ecological traits are also globally characterized by relative droughtiness, large ecological amplitude as well as resilience to moderate anthropogenic disturbance.

Indeed, when we consider temperature seasonality, we note that, high temperature variability (bio4 $\geq$ 200%, **Appendix 17b**) is an asset for the distribution of the species as well as high diurnal temperature amplitude (Isothermality, bio3 $\geq$ 65%, **Appendix 17a**). Precipitation seasonality (bio15, **Appendix 17f**) exhibited however a Gaussian bell-shaped form indicating that extreme values of precipitation variability don't favor the presence of the species.

Low values of the temperature of the coldest month (bio6, 0 to 10°C, **Appendix 17c**) coupled to nearly absence of precipitation in the coldest quarter (bio19, **Appendix 17g**) indicate the affinity of the species to cold and drought environments. Furthermore, the species thrive in drought environments with low values (0-100 mm) of precipitation of the wettest month (bio13, **Appendix 17d**) although high values of precipitation of the driest month (bio14 $\geq$ 100 mm, **Appendix 17e**) can favor its presence. The species is not sensitive to moderate human pressure (population density $\leq$ 30,000 inhabitants / km², **Appendix 17h**)

When we consider Samba (*Triplochiton scleroxylon*), high weights of diurnal temperature amplitude with respect to annual temperature amplitude (Isothermality, bio3 $\geq$ 70%, **Appendix 18a**) favor the presence of the species; likewise, high values of temperature variability (seasonality, $\geq$ 100%, **Appendix 18b**) are also favorable to the presence of the species as well as high values of precipitation seasonality (bio15 $\geq$ 70 mm, **Appendix 18f**).

Low values of temperature of the coldest month (bio6 $\leq$ 12°C, **Appendix 18c**) are an asset for the presence of the species; high values of precipitation of the wettest month (bio13 $\geq$ 100 mm, **Appendix 18d**) and nearly absence of precipitation in driest month (bio14, **Appendix 18e**) favor the presence of the species as well as low values of precipitation of Coldest quarter (bio 19 (0 to 75 mm), **Appendix 18g**). Furthermore the species is not sensitive to moderate human pressure (population density $\leq$ 30,000 inhabitants / km², **Appendix 18h**).

I therefore deduce that the species is also characterized by large ecological amplitude, relative droughtiness of its environment and resilience to moderate human pressure.

From the analysis above, the three target species are quite close with respect to their ecological traits mainly, their large ecological amplitude that favor their spatial expansion. However, *Antiaris toxicaria* is closer to *Terminalia superba* with respect to the low values of the precipitation of the wettest month (bio 13 < 100 mm (figures in Appendices 16d, 17d) as opposed to *Triplochiton scleroxylon* which grows in more humid environment with high values of precipitation of the wettest month (bio13 $\geq$ 100 mm, **Appendix 18d**).

4.2-Niche overlaps, spatial distributions of the characteristic species of the forest community studied, and dynamics in the context of climate and global changes

4.2.1-Niche overlaps and dynamics in the context of climate and global changes

According to Ganglo (2023), general and regional circulation climatic models are consistent in predicting an increase in the mean annual temperature of at least 02 °C, at horizon 2060 across the continents. This will induce the phenomenon of thermophilization in the sense of Feeley et al. (2020). Thermophilization is actually the increase of the relative abundance of heat-loving or heat-tolerant species. As a consequence of this phenomenon, the species composition of plant communities will be impacted (Feeley et al., 2020). Temperature increase, will alter rainfall and the combined effects will induce dynamics of the niches in terms of shifts of the natural ranges of species as well as changes in species composition of plant-communities (Feeley et al., 2020; Niu et al., 2019; Manish et al., 2016; Maclean et al., 2015).

Niche overlaps between the target species are confirmed by Sorensen and Jaccard overlap statistics at 95% degree of confidence (**table 4**). This confirmed their degree of community and therefore their coexistence in similar environmental conditions using the same resources. Niche overlaps are also confirmed at 95% degree of confidence under both scenarios SSP245 and SSP585 horizon 2040 despite niche dynamics.

The distance between the centroids of the hypervolumes showed the degree of ecological affinity or similarity between the three species. From our results, *Triplochiton scleroxylon* and *Terminalia superba* proved closer in environmental space (only 0.129 as distance between their centroids at present) sharing then similar environmental conditions at present, in comparison with *Triplochiton scleroxylon* and *Antiaris Toxicaria* or *Terminalia superba* and *Antiaris toxicaria* with respectively 0.218 and 0.326 as distance between the centroids of their respective hypervolumes showing more dissimilarities between *Antiaris Toxicaria* and the two other species at present. At future under both scenarios, the niche dynamics will however cause further distance and therefore further dissimilarities in optimal environmental conditions sharing between *Triplochiton scleroxylon* and *Antiaris* as opposed to more closeness between *Terminalia superba* and *Antiaris toxicaria* at future. Our results at present on the ecological affinity between the species are confirmed by the hypervolume occupancy test between the three species (**Figures 7 to 9**), clearly showing the closer ecological affinity and then similarity in optimal environmental conditions sharing between *Triplochiton scleraxylon* and *Terminalia superba* as opposed to more dissimilarities or more difference in the optimal environmental conditions sharing between *Antiaris toxicaria* and the two other species. Our results at present are consistent with the difference observed between the natural ranges of the three species. Indeed, their common natural ranges stretch from Guinea to DRC across Atlantic Ocean coastal countries in West and Central Africa (PROTA4U, 2025a, b; Akinagbe et al., 2019; Adedjei et al., 2018; Siaw et al., 2014; Hall and Bada, 1979). However, *Antiaris toxicaria* is extremely widespread in Africa and occurs also in Madagascar and in tropical Asia and northern Australia (PROTA4U, 2025c).

Niche shifts as a response of the species to changing environmental conditions will be noted for each of the species. Globally, under the scenario SSP245 horizon 2040, niche shifts of the species will be less perceptible compared to that of the scenario SSP585 at the same horizon. Indeed, under scenario SSP 585, horizon 2040, more sensible spatial shifts of hypervolumes will be noted with a distance of 0.185 between the hypervolumes of Fraké at present and in the future; a distance of 0.240 between the hypervolumes of Samba at present and in the future; and a distance of 0.410 between the hypervolumes of Antiaris at present and in the future. That scenario will therefore induce more severe environmental conditions and force species to track better optimal environmental conditions for their survival, hence niche shifts. As noted, Antiaris will be the more affected in terms of spatial shift of its hypervolumes than the two other species.

As for volume dynamics, from our results, the hypervolume of *Antiaris toxicaria* will increase under scenario SSP 245, horizon 2040 (0.270 vs. 0.219 at present), as a result of better environmental conditions induced by climate change. However, stability of the hypervolume of the species will be noted under the scenario SSP 585, at the same horizon compared to present. This implies stability in environmental conditions of the species despite its dynamics due to climate change.

The hypervolume of *Terminalia superba* at future will undergo retraction under both scenarios with its hypervolume of 0.153 and 0.142 respectively under SSP245 and SSP585, horizon 2040 against 0.255 at present. Climate change will therefore induce less favorable environmental conditions for the two species.

The hypervolume of *Triplochiton scleroxylon* will increase under scenario SSP 245, horizon 2040 (0.240 vs. 0.133 at present), as a result of better environmental conditions induced by climate change. Under scenario SSP 585, horizon 2040, the hypervolume of the species will also increase (0.207) although at less extent. Globally, climate change will then induce more favorable environmental conditions for the species.

We therefore deduce that, although the degree of community is confirmed for the three species under the climate change scenarios considered, niche dynamics is noted through niche shifts. This must be taken into account when designing strategies of the conservation of the target plant community under climate and global changes. The concept of niche shifts is quite controversial in literature although useful in biodiversity conservation and sustainable use of biodiversity resources. Indeed, according to Pearman et al. (2008) there has been no basis for predicting niche dynamics over relevant timescales, from tens to a few hundreds of years. According to them, niche shifts and conservatism have both occurred within the last 100 years, with recent speciation events, and deep within clades of species. As stated by Pearman et al. (2008), our findings can improve confidence in SDM-based predictions of the impacts of climate change and species invasions on species distributions and biodiversity.

According to Atwater et al. (2018) studies on about 50 species in Europe and North America yielded contradictory results with respect to niche shifts although proved evident in the present study. The authors found evidence of climatic niche shifts in 65–100% of 815 terrestrial plant species introduced across five continents. Although species responses were distinctive, they generally saw that niche shifts reflected changes in climate at the continent scale and were largest in long-lived and cultivated species. They also added that smaller intercontinental niche shifts occurred within species' native ranges. Our findings on niche shifts of *Triplochiton*

scleroxylon, *Antiaris Toxicaria*, and *Terminalia superba* which are long-lived and native species are therefore in line with the results of Atwater et al. (2018).

We do agree with Guisan et al. (2014) that studies of niche shifts through consensual / unified methods will provide new insights into the nature of climate niche shifts and our ability to anticipate invasions, and may help in guiding the design of experiments for assessing causes of niche changes.

4.2.2-Impacts of climate and global changes on the spatial distribution of the plant-community and implications for the management of the forests of *Triplochiton scleroxylon*, *Antiaris Toxicaria*, and *Terminalia superba*

From figures **10a** (projection at present), **11a** (impact at future, scenario SSP 245, horizon 2040), and **11b** (impact at future, scenario SSP 585, horizon 2040) we deduce that the favorable areas of the plant community will extend northwards in West Africa (from Liberia to Nigeria), throughout Cameroon, northern and Southern DRC, central South Africa, and Southeastern Madagascar. The increment of the favorable areas of the plant-community will be more notable under scenario SSP 585, horizon 2040 than under scenario SSP 245, horizon 2040. Decrease of the favorable areas of the plant-community will be notably experienced in Eastern Africa including Eritrea, Ethiopia, Uganda, and Tanzania; Southern Africa including Mozambique and Zimbabwe and Central Madagascar.

When we examine tables in **appendix 19**, we realize that the most contributing variables of the model, notably Isothermality (bio3), Temperature Seasonality (bio4), and Precipitation of Coldest Quarter (bio19) as well as Annual Precipitation (bio12) are those leading the impacts of climate change on the spatial distribution of the plant-community. Annual Temperature (bio1) matters less. The global trend is that, sensible increase of the values of those variables, will induce, an extension of the spatial distribution of the plant-community under both scenarios whereas, decrease or limited increase of the values of the variables will cause retraction of the spatial extension of the plant community.

For example, over West Africa and part of Central Africa, including Ghana, Togo, Benin, Nigeria, and Cameroon, where the extension of the spatial distribution of the plant-community will be noted, the Annual precipitation (bio12) will increase from 52 to 125 mm with mean values ranging from 103 mm (SSP 585) to 120 mm (SSP 245).

According to the same table, in the same countries considered, Isothermality (bio3) will increase for both scenarios from 0.10% to 1.76% with mean values of 0.67% (SSP 245) and 0.82% (SSP 585) over the countries. When we consider Temperature Seasonality (bio4), we can note that in West and part of Central African countries we referred to above, the values of the variable will globally increase from 6% to 23% with mean values of 10% (SSP 245) and 21% (SSP 585).

According to the same table, the increment of Precipitation of the Coldest Quarter (bio19) will also play an important role in the extension of the plant-community in West and part of the Central Africa. Indeed, bio19 will increase by 31 mm to 167 mm across the countries with mean values of 83 mm (SSP 245) and 86 mm (SSP 585).

As opposed to the countries above, the spatial distribution of the plant community will decrease in East African countries, notably, Somalia, Uganda, Ethiopia, Eritrea, and South Sudan as well as in Southern Africa (Zimbabwe, Mozambique) and Madagascar. In those countries, the Annual precipitation will either decrease by 37 mm to 109 mm (Mozambique and Madagascar respectively), or will achieve limited increase from 2 mm to 85 mm (Somalia, Uganda, Ethiopia, Eritrea, and South Sudan). A global limited mean increase from 12 mm (SSP 245) to 15 mm (SSP 585) of precipitation will be noted over those countries.

According to the same table, in the countries considered, Isothermality (bio3) will decrease for both scenarios by 0.13 % to 1.88 % with mean values of 0.23% (SSP 245) and 0.56% (SSP 585) over the countries.

When we consider Temperature Seasonality (bio4), from the table in **Appendix 19**, we can also note that in East and Southern African countries we referred to as well as in Madagascar, the values of the variable will globally decrease from 5% to 35% with a mean value of 1.0% (SSP 245) and a limited mean increase value of 1.37% (SSP 585). In the countries considered, we can point out that slight increase in bio4 of 11% (SSP 245) to 15% (SSP 585) is noted in Mozambique and Madagascar.

According to the same table, decrease of Precipitation of the Coldest Quarter (bio19) will also play an important role in the retraction of the spatial distribution of the plant-community in East and Southern Africa, and Madagascar. Indeed, over those countries, bio19 will globally decrease by a mean value of 14 mm (SSP 245) and limited increase mean value of 0.73 mm across the countries. We however noted appreciable increase of the Precipitation of the Coldest Quarter (bio19) (43.56 mm, SSP 245; 84.49 mm, SSP 585) in Eritrea.

To our knowledge, this work is the first one addressing the impact of climate change on the plant-community of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria*. It is noteworthy that in East and Southern Africa areas where decrease will be noted in its spatial distribution, the plant-community will however survive with some changes in its physiognomy and therefore floristic composition. Indeed, in those areas, as shown on figures in **appendices 10 to 14**, the plant community will be reduced to either one or two species, namely *Terminalia superba* and / or *Antiaris toxicaria* with additional vicarious species that can be discovered and identified through vegetation inventories in the areas. Our results are supported by Niu et al. (2019) who surveyed plant communities in terms of species composition, diversity and biomass across 189 sites on a hill of the Tibetan Plateau; they analyzed the individual and integrated effects of soil temperature and moisture on the plant communities and found out that the integrated effects of increasing soil temperature and decreasing moisture induced a rapid decrease in species richness. Indeed, decrease in the values of the key variables such as Isothermality (bio3), Temperature Seasonality (bio4), Precipitation of Coldest Quarter (bio19), and Annual Precipitation (bio12) will induce soil moisture decrease and increase temperature and then ultimately induce reduction in species richness of the plant community.

As for the management of the plant-community in its natural range or in areas of its future extensions (**Figures 10 and 11**), we suggest appropriate silvicultural interventions in terms of weeding, liana cuttings, and thinning to favor well shaped and vigorous individual throughout their occurrence areas. This will increase, their wood and biomass productivity. Furthermore,

for a sustainable production, management plan should be elaborated to cover the whole areas and clearly design in time and space, where interventions in terms of cultural operations (weeding, liana cuttings, thinning) will take place. Wood exploitation in matured stands will be well planned in time and space on the basis of well-informed rotation to assure sustainability. In East Africa, where only one or two species (*Antiaris toxicaria* and *Terminalia superba*) will survive I recommended the identification of various species through forest inventories to supplement the absence of lacking species so as to achieve adequate level of wood and biomass productivity

5-Conclusion

This study examined the effect of climate change on spatial distribution, ecological niches, niche overlaps, and niche shifts of the plant-communities of *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria*. From the main findings, climate change will impact the spatial distribution and ecological niches of the main component species and the plant communities as a whole. Niche overlaps between *Triplochiton scleroxylon*, *Terminalia superba*, and *Antiaris toxicaria* is well demonstrated assuring an obvious degree of community between the species. Niche shifts will occur as response to the needs of tracking suitable environmental conditions by the species under climate change. The plant community will extend its niche globally in West and central Africa but also reduce it in response to climate change mostly in East Africa. In the latter case, it will survive with one or two of the dominant species namely *Terminalia superba* or *Antiaris toxicaria*. In that extreme cases, vicarious species will be considered to fill species gaps and assure sustainability of wood and biomass production of the plant community in time and space under the constraints of climate change.

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