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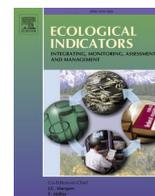
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Original Articles

Tree species diversity analysis using species distribution models: A *Faidherbia albida* parkland case study in Senegal

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ABSTRACT

Around the world, SDMs have been widely used to support forest management planning and biodiversity conservation. Beyond the prediction of species distribution provided by the SDMs, this study aimed to analyze the spatial distribution of tree species diversity using SDMs. The study area is a *Faidherbia albida* parkland in Central Senegal. It is characterized by a tree-based farming system dominated by *Faidherbia albida*.

Using a robust and representative dataset of 9258 tree species occurrence, we first determined by an SDM the current potential spatial distribution of the 16 main tree species forming the parkland. Specifically, using 6 SDM algorithms and applying several modeling techniques with different categories of predictor variables (e.g., climate, topography, soil properties and human impact) we benchmarked 576 SDMs to achieve best model predictions for tree species. Then, tree species diversity maps were created on the basis of the resulting SDM predictions. Finally, the spatial dynamics of tree species diversity were discussed in relation to landscape characteristics, including heterogeneity, composition and human impact.

The results showed that there is no single 'best' SDM algorithm (among the 6 algorithms tested) or modeling approach for all species. Benchmarking several modeling techniques allowed strengthening SDM performance, achieving AUC values that ranged from 0.64 (intermediate accuracy) to 0.87 (very good accuracy). The spatial dynamics of tree species diversity is related to the landscape heterogeneity and composition. In the Sahelian agroforestry systems (AFS), tree diversity is sustained by anthropization. A significant negative correlation with the distance to the village was found, i.e. the closer you get to the village, the greater the diversity of trees.

This study could be crucial for analyzing tree species diversity when abundance information is not available.

1. Introduction

Trees are an integral part of African smallholder family farming systems with a close relationship between tree species and smallholder livelihoods and resilience to future changes (e.g. Bayu, 2019; Rosenstock et al., 2019). In Sahelian agroforestry systems (AFS), the configuration of the parkland, both in its composition and structure, is shaped by the socioeconomic practices of farmers and local populations. Tree species are selected for their usefulness, either in terms of agroforestry properties or in terms of food, phytomedicine or revenue sources, among others

(Sambou et al., 2017; Bayala et al., 2014; Michon and De Foresta, 1999). The rich biodiversity of agroforestry parklands makes them ecologically resilient with increasingly better ecological and socioeconomic functions (Achiso & Masebo, 2019; Bucheli & Bokermann, 2017).

Understanding the spatial distribution of tree species is crucial for achieving successful conservation of parkland biodiversity and predicting responses to environmental and climatic changes (Cabello et al., 2012). Thus, an up-to-date and accurate spatial description of parkland tree diversity is critical for designing and implementing management strategies to improve agroforestry system productivity for food security

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and sustainable development (Chen et al., 2018). The exhaustive inventory of trees remains the most robust method for monitoring tree diversity, but it is difficult to implement at a large landscape scale. Because of their spatial completeness and long time series, remote sensing and derived proxies of landscape ecology represent useful data sources for mapping tree species (Fassnacht et al., 2016) and biodiversity characterization (e.g., Geller et al., 2017) at the landscape scale. In particular, multispectral and hyperspectral images with very high spatial resolution (<2 m) have been used for mapping trees (e.g., Brandt et al., 2020) and tree species (e.g., Hycza et al., 2018; Karlson et al., 2016; Lelong et al., 2020; Pu and Landry, 2012). However, due to spectral similarity between tree species, the existing very high spatial resolution images do not yet allow for complete identification and mapping of tree species in complex landscapes, such as the Sahelian agroforestry parklands (Lelong et al., 2020).

In this context, species distribution models (SDMs) therefore remain valuable tools enabling tree species mapping and monitoring (Falk and Mellert, 2011; Vila-Viçosa et al., 2020). Around the world, SDMs have been widely used to support forest management planning (Pecchi et al., 2019) and biodiversity conservation, e.g., in protected areas (Rahman et al., 2019; Swan et al., 2021). SDMs combine information collected on species locations and environmental conditions to infer habitat suitability to predict species distributions (Elith & Leathwick, 2009; Franklin, 2010). However, SDM performance can vary significantly because of several factors related to modeling components or approaches (Angelov, 2018; Bucklin et al., 2015; Khatchikian et al., 2011; Senay and Worner, 2019).

First, the predictors or environmental variables used in SDMs may be derived from different sources (Araújo et al., 2019). Early studies of species distributions used only climatic variables as predictors (Huntley et al., 1995; Sykes et al., 1996). Subsequently, several studies have shown that combining different types of variables, e.g., including satellite-derived climatic variables with nonclimatic variables (land cover, topography, phenology, etc.) can improve SDM performance (e.g., Austin and Van Niel, 2011; Burns et al., 2020; Fournier et al., 2017; Suárez-Seoane et al., 2004; Vila-Viçosa et al., 2020). Currently, environmental variables used in SDMs are related to climate, topography, substrate, land cover and vegetation, phenology, measures of landscape patterns, and information about other species (biotic interactions), among others (Amiri et al., 2020; Austin and Van Niel, 2011; Burns et al., 2020; Fournier et al., 2017; Gardner et al., 2019; Nguyen et al., 2015; Vila-Viçosa et al., 2020).

Second, there are various methods for selecting relevant environmental variables used as predictors in ecological modeling (Lin and Chiu, 2020). Pradhan (2016) showed the importance of taking into account the correlation between variables to minimize collinearity, with a risk of missing out on very important variables. Some authors first performed ecological niche factor analysis (ENFA) to identify the best variables that define species ecological niches and then used these variables to predict species distributions (Ciss et al., 2019).

Third, in the last two decades, many SDM approaches have been developed (Elith et al., 2006; Guisan et al., 2007; Norberg et al., 2019). The increasing number and complexity of modeling techniques (Hegel et al., 2010) challenge the choice of the best approach to make predictions for a given occurrence (Merow et al., 2014). Based on studies that have compared different SDM methods and performance (Elith and Graham, 2009; Elith et al., 2006; Norberg et al., 2019; Segurado and Araújo, 2004), it appears that there is no “best” SDM algorithm or approach that is relevant in all circumstances. It has therefore been suggested to test a suite of algorithms and modeling techniques for benchmarking their predictive ability under the particular circumstances of a study (Norberg et al., 2019; Qiao et al., 2015).

Species distribution models (SDMs) are generally used to explain and predict species ranges and environmental niches. However, computing species diversity indices to assess tree species diversity from SDM predictions is still challenging. Some studies have reported the use of SDMs

to appreciate the spatial distribution of species richness (Kwon et al., 2018; Luo et al., 2020; Vila-Viçosa et al., 2020). But for diversity indices such as Shannon's and Simpson's, which are commonly used to assess species diversity, it is important to infer species abundances from the SDM predictions for their computation. Some studies investigated the suitability of deriving species abundance estimates from SDM predictions, i.e., the relationship between species abundance and habitat suitability. The reported results are not clear-cut and would depend on the study species or the used variables to define habitat suitability (Dallas & Hastings, 2018; Gutiérrez et al., 2013; Martin & Canham, 2020; Van Couwenberghe et al., 2013; VanDerWal et al., 2009; Young & Carr, 2015). Using only climate variables, authors found the relationship to be weak and not significant (Dallas & Hastings, 2018; Martin & Canham, 2020). In contrast, a significant relationship was found in studies with more assorting environmental variables integrating climatic and non-climatic variables (Gutiérrez et al., 2013; Van Couwenberghe et al., 2013; VanDerWal et al., 2009; Young & Carr, 2015).

Conducted in a *Faidherbia albida* parkland in Central Senegal, the main objective of this paper was to analyze the spatial distribution of tree species diversity using SDMs. Specifically, the purpose was to derive tree diversity indices from SDM predictions and then to analyse their spatial dynamics. This is original considering that applications of SDM methods are generally limited to explain and predict species ranges and environmental niches. In other words, this study proposes an approach that goes beyond simple predictions of species distribution to calculate diversity indices to analyze tree species diversity. This is especially innovative in agroforestry parklands in Senegal for which we are not even aware of work conducted using SDMs.

To achieve our goal, we proceed in 3 steps. (i) First, the probabilities of occurrence of the main tree species forming the *Faidherbia albida* parkland were predicted using SDMs. Several SDM techniques are benchmarked to improve the SDM predictions. (ii) Then, tree diversity indices were derived from the predicted probabilities of occurrence of tree species. This allowed tree diversity mapping (iii) Finally, the spatial dynamics of tree species diversity were discussed in relation to landscape characteristics, including heterogeneity, composition and human impact.

2. Materials and methods

2.1. Study area

The study area is located in the Senegalese Peanut Basin, covering 20 × 20 km around Ngayokheme village (Fatick region – Fig. 1). It is a Sahelian agroforestry parkland dominated by *Faidherbia albida*, which is a nitrogen-fixing species with an inverted phenology. *Faidherbia albida* is known to increase soil fertility and crop yields in farm fields. The region is characterized by rainfed agriculture, with millet and groundnut being the main staple and cash crops, respectively. The climate is semiarid. The average annual rainfall is around 500 mm during the recent period 1985–2015, with a strong interannual variability (Lalou et al., 2019). The rainy season lasts from July to October. Soils can generally be classified into two main types: sandy ‘dior’ soils mainly located in flat and dune areas and more clayish ‘deck’ soils mainly located in lowland and interdune areas, with intermediate categories (deck-dior - Lericollais, 1999). With almost 60 % of the country's rural population, the Senegalese Peanut Basin is facing strong demographic pressure (Bignebat & Sakh-Jimbira, 2013).

2.2. Data

2.2.1. Tree species occurrence data

A field campaign for tree species data collection was carried out in May 2018. To prevent the sampling bias frequently found in species occurrence records, we used an optimized sampling strategy based on landscape heterogeneity classification (see Ndao et al., 2021 for more

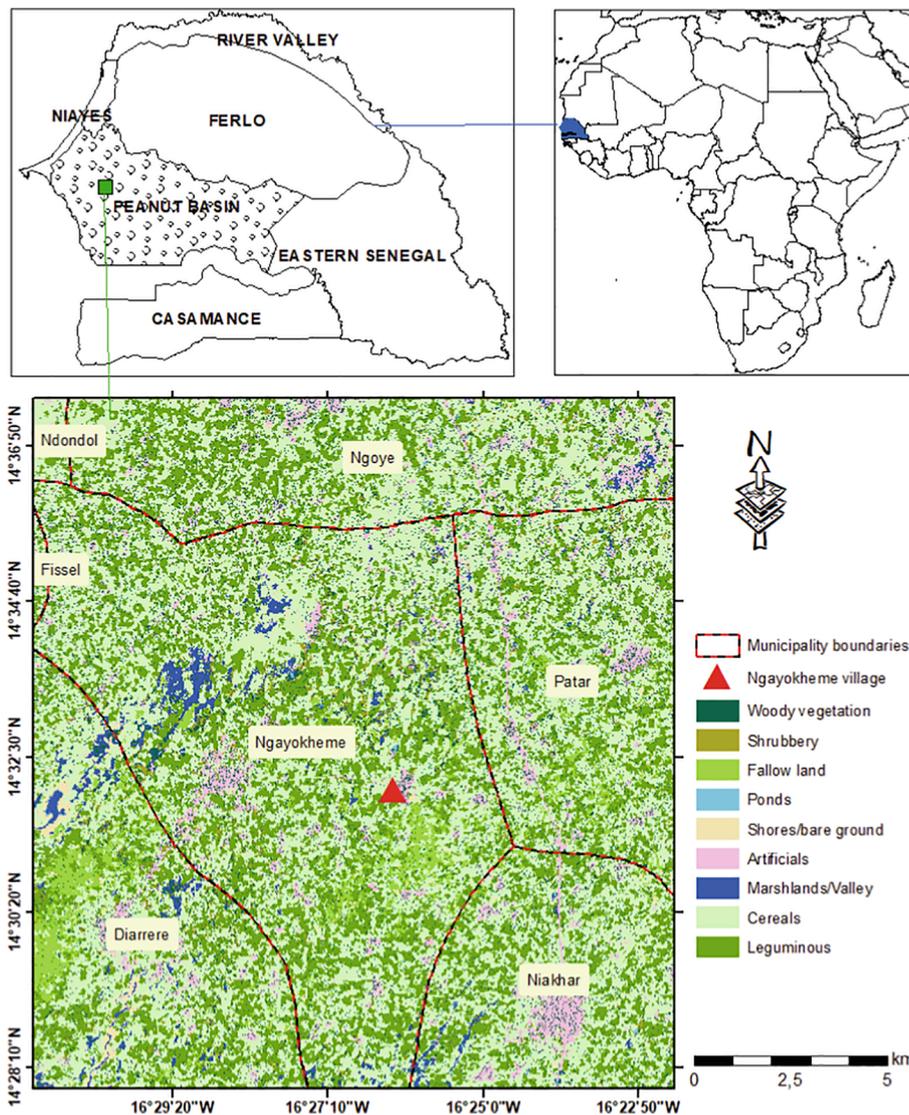


Fig. 1. Location (green square) and land use/land cover map (from Ndao et al., 2021) of the study area in the Senegalese Peanut Basin. The names on the map are the municipality names. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

details). It is a weighted stratified sampling of 213 observation sites distributed according to a landscape heterogeneity gradient. At each site, an exhaustive inventory of the trees in a 1 ha plot was carried out. In addition, extra species (not present in the plot) observed within a radius of 400 m were included to increase the odds of recording all species in the area. Individual tree location and species were recorded with a Garmin GSMAP 64 GPS device. Due to a GPS-reported accuracy of 3 m, the location of each individual tree was then adjusted by photointerpretation using Pleiades images (0.5 m spatial resolution). In all, a dataset of 9258 georeferenced trees encompassing 63 different species was collected. Abundance analysis of the species in the dataset showed the existence of many relatively rare species, each representing <1 % of the population (Ndao et al., 2021).

The entire database of 9258 georeferenced trees was used. But, as most SDM methods are sensitive to the sample size (Stockwell and Peterson, 2002; Wisz et al., 2008), we only modeled species with >100 individuals recorded. These are the 16 majority species whose numbers constitute 94 % of the surveyed population (the database). For each species, the presences correspond to the occurrences, i.e. the locations where the species was recorded. The absences are the other locations where the species has not been recorded, i.e. all locations of the tree species that are different from the considered one (Table 1).

2.2.2. Predictor variables

Different types of environmental variables derived from various sources of geospatial data and remote sensing methods were used as predictor variables. These are a suite of 36 variables related to (i) climate, (ii) soil properties, (iii) human impact, (iv) vegetation phenology and productivity, and (v) watershed topography. We pre-processed the environmental variables by setting them on the same projection system (WGS 84, UTM, Zone 28 N), cropping them to the same extent and resampling them at the same spatial resolution (250 m) using the nearest neighbor resampling approach.

2.2.2.1. Climatic data. Bioclim variables are widely used as predictors in plant species distribution modeling studies (Gardner et al., 2019). The climatic variables used in this study correspond to the standard list of 19 “Bioclim” variables extracted from the WorldClim database version 2 (<http://www.worldclim.com/>). The 19 “Bioclim” variables represent the average conditions of temperature and rainfall for the years 1970–2000. As more biologically meaningful variables, they represent annual trends (e.g., mean annual temperature and annual precipitation), seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting climatic factors (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters – 1/4 of

Table 1

List of the main tree species forming the *F. albida* parkland (each species has >100 individuals recorded; >1% of the surveyed population). For example, the presence of *Acacia seyal* was recorded 107 times in the database of 9258 georeferenced trees. The remaining 9151 records (i.e. 9258–107) consisting of species different from *Acacia seyal* represent its absences.

Species	Presence (Number of trees)	% Presence in the database	Absence (Number of trees)
<i>Acacia seyal</i>	107	1 %	9151
<i>Prosopis juliflora</i>	107	1 %	9151
<i>Celtis integrifolia</i>	148	2 %	9110
<i>Tamarindus indica</i>	152	2 %	9106
<i>Sclerocarya birrea</i>	153	2 %	9105
<i>Bauhinia rufescens</i>	215	2 %	9043
<i>Ziziphus mauritiana</i>	215	2 %	9043
<i>Piliostigma reticulatum</i>	225	2 %	9033
<i>Borassus aethiopicum</i>	248	3 %	9010
<i>Azadirachta indica</i>	272	3 %	8986
<i>Diospiros mespiliformis</i>	272	3 %	8986
<i>Acacia nilotica</i>	357	4 %	8901
<i>Adansonia digitata</i>	573	6 %	8685
<i>Anogeissus leiocarpus</i>	810	9 %	8448
<i>Balanites aegyptiaca</i>	1017	11 %	8241
<i>Faidherbia albida</i>	3872	42 %	5386
Others (<1%)	515	6 %	8743

the year) (Fick and Hijmans, 2017).

2.2.2.2. Soil property data. Soil properties are one of the most important factors controlling the growth, distribution and abundance of tree species (Ben-Shahar, 1991; Freycon et al., 2003; Nguyen et al., 2015). Soil property data were obtained from the recently released AfSoilGrids database (Hengl et al., 2015, Hengl et al., 2017). AfSoilGrids products are generated using machine learning algorithms with soil samples from >500,000 sites covering the period 1950–2012 and a set of soil covariables used as proxies for soil-forming processes (landform, vegetation, lithology and climate). Seven soil properties in the topsoil (0–30 cm) were considered in this study, namely, soil texture fraction clay, organic carbon, soil texture fraction silt, soil pH in H₂O, total nitrogen, soil texture fraction sand and total phosphorus.

2.2.2.3. Topographic data. Closed relationships between topographic characteristics and the presence and abundance of tree species have been well demonstrated (Nguyen et al., 2015). In this study, topographic variables were derived from the 30 m NASA Shuttle Radar Topography Mission (SRTM) digital elevation model (<https://dwtkns.com/srtm30m/>) using the Soil and Water Assessment Tool (SWAT, <https://swat.tamu.edu/>). SWAT was used to delineate the sub-watersheds within the study area (Winchell et al., 2010). A total of 69 subbasins were extracted in a vector file format, with their attribute table composed of 7 topographic variables: subbasin slope, subbasin tributary reach slope, field slope length, longest path within the subbasin, elevation of the subbasin centroid, subbasin tributary reach width and subbasin tributary reach depth. See (Table 2).

2.2.2.4. Phenological data. The phenology of vegetation is affected by environmental factors such as precipitation, temperature or latitude (Han et al., 2020). Sometimes, as an adaptive trait, phenology may be a proxy for species distribution (Chuine, 2010). Two phenological metrics were used in this study, namely, the start of the growing season (SOS) and the small integral (SINT), i.e., the normalized difference vegetation index (NDVI) integral between the start and the end of the growing

Table 2

List of the variables tested to model the species distribution. The codes used in the modeling process, the units and the spatial resolution (SR) are provided.

Category of variables	Variables	Codes	Units	SR
Climatic	Annual Mean Temperature	Bio1	°C	1 km
	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Bio2	°C	1 km
	Isothermality (Bio2/Bio7) (×100)	Bio3		1 km
	Temperature Seasonality (Stand. Dev. × 100)	Bio4	°C	1 km
	Max Temperature of Warmest Month	Bio5	°C	1 km
	Min Temperature of Coldest Month	Bio6	°C	1 km
	Temperature Annual Range (Bio5-Bio6)	Bio7	°C	1 km
	Mean Temperature of Wettest Quarter	Bio8	°C	1 km
	Mean Temperature of Driest Quarter	Bio9	°C	1 km
	Mean Temperature of Warmest Quarter	Bio10	°C	1 km
	Mean Temperature of Coldest Quarter	Bio11	°C	1 km
	Annual Precipitation	Bio12	mm	1 km
	Precipitation of Wettest Month	Bio13	mm	1 km
	Precipitation of Driest Month	Bio14	mm	1 km
	Precipitation Seasonality (Coefficient of Variation)	Bio15		1 km
	Precipitation of Wettest Quarter	Bio16	mm	1 km
	Precipitation of Driest Quarter	Bio17	mm	1 km
	Precipitation of Warmest Quarter	Bio18	mm	1 km
	Precipitation of Coldest Quarter	Bio19	mm	1 km
Soil properties	Soil texture fraction clay	CLYPPT	g/250 m	
	Organic carbon	ORCDRC	g/kg	250 m
	Soil texture fraction silt	SLTPPT	g/100 g	250 m
	Soil pH in H ₂ O	PHIHOX		250 m
	Total nitrogen	NTO	g/kg	250 m
	Soil texture fraction sand	SNDPPT	g/100 m	250 m
	Total phosphorus	P	mg/kg	250 m
Topographic	Subbasin slope	slo	[%]	30 m
	Subbasin tributary reach slope	Csl	[%]	30 m
	Field slope length	sll	m	30 m
	Longest path within the subbasin	Len1	m	30 m
	Elevation of the subbasin centroid	Elev	m	30 m
	Subbasin tributary reach width	wid1	m	30 m
	Subbasin tributary reach depth	dep1	m	30 m
Phenological metrics	Start of the Season	SOS		250 m
	Small Integral (NDVI integral between the start and the end of the season)	SINT		250 m
Human impact	Distance to the village	DTV	km	250 m

season. The mean SOS and SINT over the 2000–2018 period were derived from the 16-day MODIS NDVI time series (MOD13Q1 product) using Timesat software (Eklundh and Jönsson, 2011).

2.2.2.5. Human impact data. In addition to biophysical drivers, farmers play a key role in the selection and preservation of trees in parklands, depending on the socioecosystem services they provide (Sambou et al., 2017). To account for the potential human impact on the distribution of

tree species, a distance-to-village variable was derived from the village location provided by Open Street Map (<https://www.openstreetmap.org/>). To do so, the Euclidean distance between each element of a grid with 250 m cells and the nearest village was computed.

2.3. Method

2.3.1. Selection of determining variables of the species spatial distribution

Making a subjective choice or inappropriate selection may reduce prediction accuracy (Lecours et al., 2016). The environmental variables relevant for each species were thus selected by performing ecological niche factor analysis (ENFA; Basille et al., 2008; Hirzel et al., 2002). To this end, we used the R CENFA package (Rinnan, 2020), which allows ENFA to be performed and the results to be visualized via a biplot. The environmental variables are represented by arrows in the biplot. The length of the arrow is proportionate to the contribution of a given environmental variable to the definition of the axes of the ENFA (Basille et al., 2008). The longest arrows represent the critical variables in terms of habitat selection (Basille et al., 2008; Costa et al., 2016). As reported by Basille et al. (2008), “The ENFA is a factorial analysis that extracts one axis of marginality and several axes of specialization. The marginality identifies the preference of the individual, population or species for specific conditions of the environment, among the whole set of possibilities. The specialization appears as a consequence of the narrowness of the niche on some environmental variables”. An illustration of the ENFA biplot for *F. albida* is provided in Fig. 2.

2.3.2. SDM benchmarking for best prediction performance

SDM benchmarking consisted of selecting the best combination of models, cross-validation approaches, and variable data sets to predict the probability of the presence of a given species. After selecting the most relevant variables for each species using ENFA, different types of models were tested to identify the best model: profile models (Domain and Bioclim), regression models (GLMs), and machine learning models (random forest, SVM and MaxEnt).

Two approaches of cross-validation (cv) were applied: a *random k-fold cv* and a *k-fold blocked cv*, both with 5 folds (i.e., 80 % of the data were used for model fitting, and 20 % were used for model testing). Cross-validation consists of partitioning the data into *k* parts (*fold*s) and then iteratively using one part for testing and the remaining part (*k* -1-fold) for model fitting until all folds have been used for testing. If the data partitioning is done randomly, it is called *random k-fold cv*. When the data are first stratified into blocks taking into account environmental, temporal or spatial factors and then the folds are constructed based on these blocks, this is called *k-fold blocked cv*. The blocking technique is used to account for spatial autocorrelation (Roberts et al., 2017; Valavi et al., 2019). Spatial blocking was computed using the R BlockCV package (Valavi et al., 2019), which splits the data into units of geographic area (blocks) grouped with similar characteristics while accounting for spatial autocorrelation. Within a given unit, all species data are treated together and allocated to the same fold of cv as training or testing data. Several blocks could be allocated to one cv fold. For instance, in Fig. 3, the spatial blocking of the occurrence data of *F. albida* generated 29 blocks for model fitting and 7 blocks for testing.

Both approaches of cross-validation were performed first using only climatic variables and then integrating climatic and nonclimatic variables, including and not including variables of human impact. To summarize, for each of the 16 main species, we calculated 36 SDMs combining six models (Domain, Bioclim, GLM, random forest, SVM and MaxEnt), two cross-validation approaches (*random k-fold* and *k-fold blocked*), and three different variable sets (only climatic variables, climatic and nonclimatic variables without human impact variables, and climatic and nonclimatic variables including human impact variables), leading to a total number of 576 SDMs for benchmarking.

The area under the ROC curve (AUC; Yang and Berdine, 2017) was used to assess prediction errors and to compare the models' performance. The AUC is commonly used as a measure of model performance in SDMs (Fielding and Bell, 1997; van Proosdij et al., 2016).

As a result of the benchmark analysis, the best model and modeling approach (regarding the AUC values) obtained for each studied species

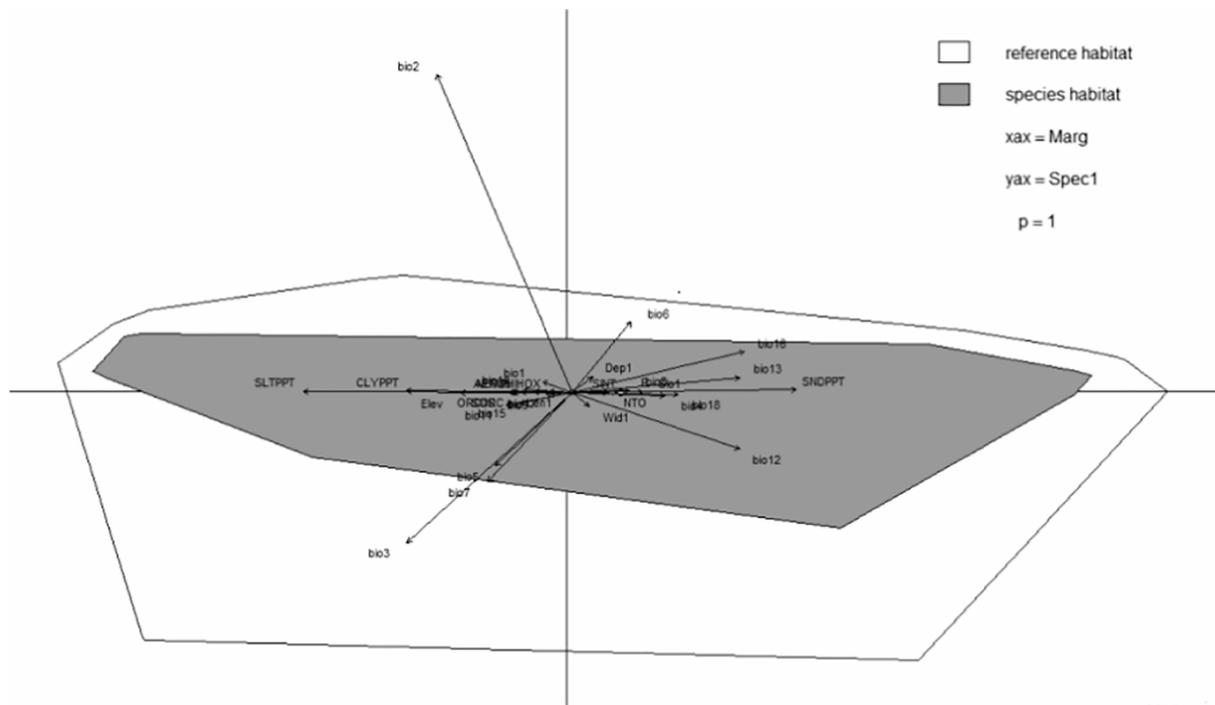


Fig. 2. Illustration of ENFA for *F. albida*, the most abundant species in the studied parkland. Marginality is represented on the X-axis, and the first specialization axis is represented on the Y-axis. The white area represents the multivariate environmental space available in the study area. The darker gray area represents the species niche.

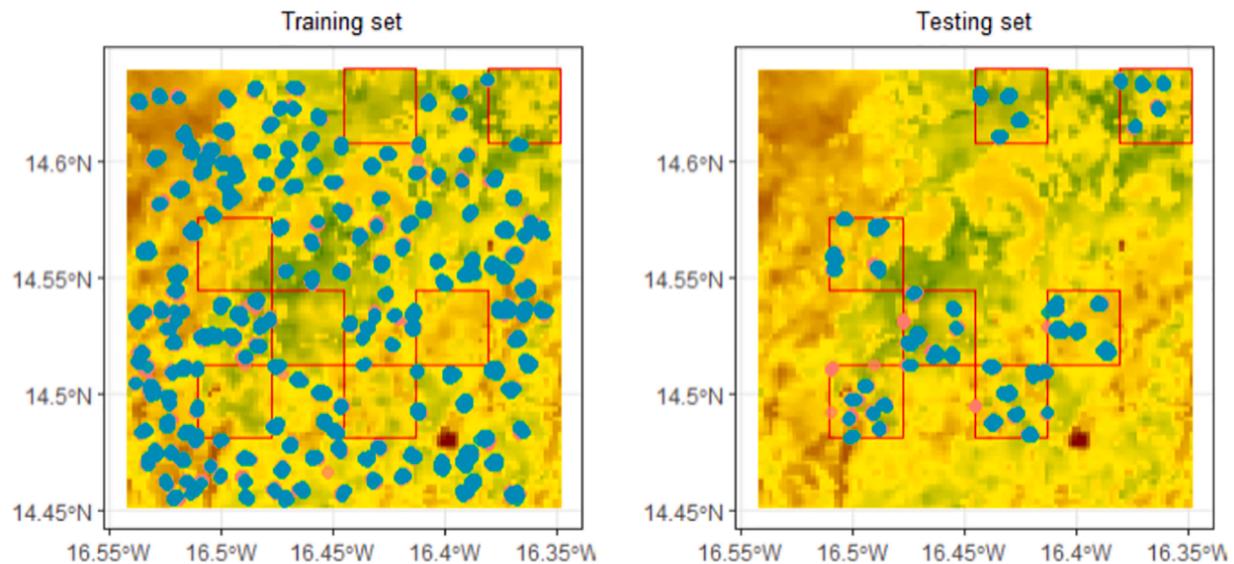


Fig. 3. Spatial blocking of the occurrence data of *F. albida*. Blue dots represent records of *F. albida* (i.e., presence of *F. albida*) selected for the training set and testing set. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was used to predict and map the species probability of presence.

2.3.3. Tree species diversity mapping

The compilation of all predicted species distribution maps allowed us to derive the species richness index from the sum of presence of all species at pixel scale (250 m × 250 m) then carry out the species richness map. Indeed, the maps of the species probability of presence constitute a prediction of the presence of species and can therefore be expressed as a binary map with pixels where the species is present and pixels where the species is absent. Thus, the superposition of all the presence/absence maps of the different species allowed us to have at each pixel the number of species present by summing up the presences: this is the species richness index.

Then, we hypothesized that by considering assorting environmental variables of different categories we have, as reported by Van Couwenberghe et al. (2013), a significant relationship between the relative abundance of tree species and their environmental conditions. Indeed, it is well known that the presence and development of a given species are closely related to environmental conditions. The more favorable the environmental conditions are for a given species, the better its development will be. On this basis, since SDM predictions are driven by environmental variables, we hypothesized that between two species, if the probability of presence from the SDM is higher for one species, the environmental conditions are more favorable for it. Subsequently, assuming a significant correlation between tree species abundance and their environmental conditions (Van Couwenberghe et al., 2013), will allow to hypothesize that “the higher the probability of presence of a species, the greater its abundance relative to other species”. Based on this hypothesis, the probabilities of species presence predicted by the SDMs were translated into relative abundances of species. The latter were used to calculate the Shannon’s diversity index (SHDI; Shannon, 1948), Simpson’s diversity index (SIDI; Simpson, 1949) and Pielou’s evenness index (Pielou, 1966).

2.3.4. Tree species diversity analysis

After the diversity indices mapping, the potential human impact on tree diversity was investigated using a nonparametric Kruskal-Wallis one-way analysis of variance to compare tree diversity indices among different distance-to-village (DTV) classes. Using a k-means clustering method, five DTV classes were defined. Focused principal component analysis (FPCA) was also used to complete the explanatory analysis. In addition, landscape heterogeneity analysis in the same study area of

Ndao et al. (2021) was used to further discuss and appreciate the spatial dynamics of species diversity.

3. Results

3.1. Analysis of the determining variables of the species spatial distribution

The most relevant predictors of each of the main species are identified through ecological niche factor analysis (ENFA). Fig. 4 shows the number and types of variables selected as predictors for each species. The detailed list with the names of the variables selected per species is presented in the appendix as supplementary data (Table S1).

The climatic variables related to temperature variability are relevant for all species. The climatic variables related to rainfall and its temporal distribution are also relevant for several species (13 species out of 16), as well as the variables related to the physical properties of the soil (14 species) and to topography (11 species). The phenological metrics are less relevant (3 species).

Depending on the species considered, the type of variables and number of relevant variables may be very different. For example, all types of variables are relevant for *A. digitata*, whereas only 3 types of variables are retained for *A. nilotica* or *F. albida*. Similarly, for *B. rufescens*, a total of 19 variables are relevant, while only 8 are retained for *F. albida*. It is also interesting to note that for 8 species, namely, *B. aegyptiaca*, *A. digitata*, *A. indica*, *D. mespiliformis*, *B. aethiopicum*, *S. birrea*, *T. indica*, and *C. integrifolia*, the distance to the village contributes significantly to the definition of their ecological niches, indicating that these species are sensitive to the anthropization of their environment.

3.2. Modeling the spatial distribution of tree species

3.2.1. Benchmarking of modeling approaches

Figs. 5 and 6 present the comparison of the predictive model performances according to the type of variables (climatic variables, non-climatic variables, human impact variable) and the cross-validation modeling approaches (random k-fold cv vs k-fold blocked cv), respectively.

Generally, the MaxEnt model provided the best performance (Fig. 5 and Fig. 6). In addition, Bioclim and Domain models could provide good prediction performances depending on the species of interest (Fig. 5 and Fig. 6). However, it should be noted that these three models predicted

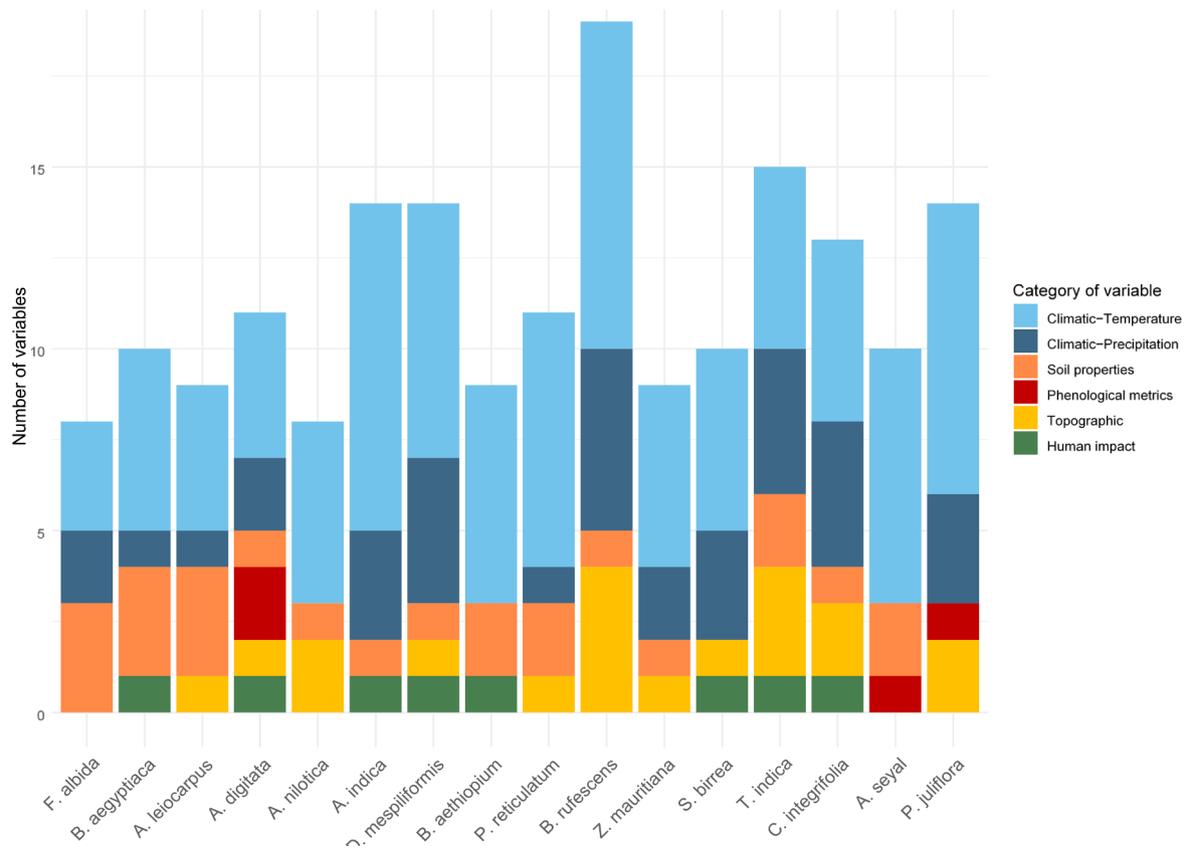


Fig. 4. Number and types of variables selected as relevant predictors for each of the main species according to ENFA.

the different species in very different ways (high variability of AUC). Depending on the model, for some species, they provided very good performance ($AUC > 0.7$), while for others, the performance was low to poor ($AUC < 0.6$). On the other hand, the GLM, random forest and SVM models yielded very poor to mediocre performance, although they were more consistent in prediction (all species predicted in almost the same way – low variability of AUC).

Overall, Fig. 5 shows that integrating nonclimatic variables in addition to climatic variables does not systematically and significantly improve the performance of the SDMs. Additionally, taking into account the anthropization of the environment does not always improve the performance of the models. Fig. 6 shows that dealing with spatial autocorrelation by choosing folds with spatial blocking in cross-validation tends to decrease model performance.

3.2.2. Using the best SDM for predicting a given species

Table 3 presents for each species the best modeling approach (model, cross-validation approach and sets of variables) selected from the SDM benchmarking on AUC criteria. It was used to predict the spatial distribution of species.

Two species were predicted with intermediate performance ($AUC > 0.60$), eleven with good performance ($AUC > 0.70$), and three with very good performance ($AUC > 0.80$). For most species, integrating nonclimatic variables allowed us to achieve the best performance of the model. The best performances were achieved with the three model types previously identified as high performers, namely, MaxEnt, Bioclim and Domain models. For most species, the MaxEnt model performed the best prediction with the k-fold blocked cv approach.

We used the 16 best SDMs obtained to predict the probability of presence for each of the main species. From these predictions, we derived the four tree species diversity indices: Species richness, Shannon's diversity index (SHDI), Simpson's diversity index (SIDI) and Pielou's evenness index.

3.3. Tree species diversity index mapping

Fig. 7 presents the maps of the tree species diversity indices, namely, Species richness, Shannon's diversity index (SHDI), Simpson's diversity index (SIDI) and Pielou's evenness index. The richness, SHDI and SIDI showed progressive spatial dynamics of tree diversity from northeast to southwest. The northeastern part is the least diversified, while the southwestern part presents a greater diversity of tree species. However, the high values of Pielou's evenness index ($J > 0.8$) suggest that the species abundances are fairly similar at the local scale (pixel scale 250 m), although there may be disparities from one locality to another.

3.4. Effect of human impact and landscape characteristics on tree species diversity

To explore the effect of human impact on tree species diversity, Fig. 8 and Fig. 9 present the results of the Kruskal-Wallis one-way analysis of variance and the FPCA of the tree diversity indices relative to distance to the village (DTV), respectively. The analysis of the relationship between tree diversity and DTV as a proxy of human impact showed very significant differences in tree species diversity values according to DTV classes (Fig. 8) and a significant correlation between the DTV and the tree species diversity indices (Fig. 9). The species richness as well as the SHDI and SIDI decrease as the DTV increases (negative correlation), i.e., tree species around villages are more diverse close to villages than in remote areas. On the other hand, Pielou's evenness index increases as the DTV increases (positive correlation), i.e., near villages, some species tend to dominate the stand (Fig. 9).

Fig. 10 provides a comparative view of the tree species diversity index (Richness – Fig. 10a), the stratification of landscape heterogeneity (Fig. 10b) and the land use/land cover (Fig. 10c) maps. The stratification of the landscape heterogeneity shows that in the southwestern part, where the species diversity indices are higher, the four identified

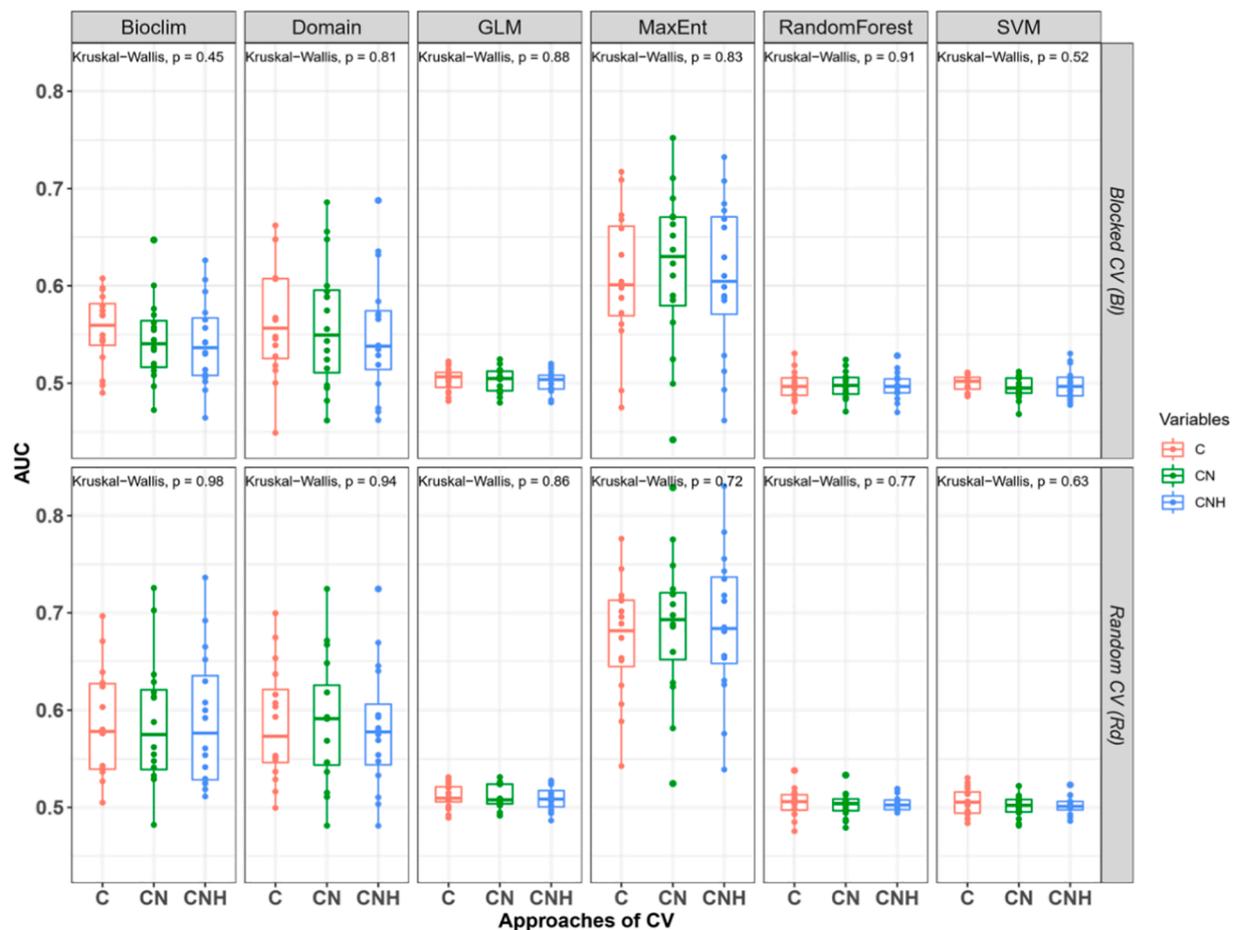


Fig. 5. Comparison of the 6 predictive models according to the different sets of variables (only climatic variables (C), climatic and nonclimatic without human impact variables (CN), and climatic and nonclimatic including human impact variables (CNH)), for both cross-validation approaches (k-fold blocked (BI) and random k-fold (RD)). The box plots represent the performances (AUCs) of the 6 predictive models computed for the 16 main species.

landscape classes are intermingled and the area is more heterogeneous than that in the northeastern part (Fig. 10b). The southwestern part is also characterized by the relative importance of small wetlands (numerous ponds, swamps, marshlands and ephemeral rivers – Fig. 10c – Ndao et al., 2021).

4. Discussion

4.1. Optimizing the prediction accuracy of the SDM for mapping tree species distribution

Different factors impacting the quality of the accuracy were benchmarked to achieve the best prediction of the distribution of each of the studied species. We first identified the best environmental variables, then the best variable set and finally the best calibration approach to use for each of the studied species.

4.1.1. ENFA allows us to select the relevant predictors of a given species

An important aspect that has a pivotal role in the accuracy of the prediction for a given species is the selection of relevant environmental variables used as predictors during the modeling flow. Making a subjective choice or inappropriate selection may reduce prediction accuracy (Lecours et al., 2016). The right method of variable selection is closely related to the aims and questions of the study. Since high probabilities of presence are often linked to high habitat suitability, ecological niche factor analysis (ENFA) was used in this study to identify the environmental variables of importance for the suitability of a species' habitat. Good to very good accuracy was reached by combining ENFA for

environmental variable selection with MaxEnt for the prediction of the probability of species presence (Ciss et al., 2019). In fact, important variables for habitat suitability in ecological niche modeling will be important for the probability of presence in the SDM. The ENFA results showed that the relevant types and number of predictors differ according to the species (Fig. 4), strengthening the importance of having a selection strategy of predictors specific to each species to be able to define its ecological niche. Thus, the application of ENFA to the different species allowed us to customize for each species the specific predictors used subsequently during the modeling phase.

4.1.2. Climate and soil property variables are relevant for modeling plant species distribution

The ENFA results also showed that climatic variables and soil property variables are very common to the different species (Fig. 4). In fact, the climatic variables from WorldClim (Hijmans et al., 2005) used in this study are often noted as relevant in plant SDMs. Out of 150 SDM studies analyzed by Gardner et al., (2019) identifying 289 unique climatic variables, the top 10 variables used as predictors were “Bioclim” variables from WorldClim. Distal variables such as “Bioclim” variables are assumed to correlate proximal variables that are directly related to plant physiology and development (Gardner et al., 2019; Kearney and Porter, 2009). They provide a good description of average environmental conditions in a given climate (Bennie et al., 2014). Proximal variables such as physiological variables (e.g., soil water content) are nevertheless suggested to be more robust in plant SDMs (Austin, 2002; Gardner et al., 2019). However, many of the proximal variables directly affecting plants are difficult to obtain or unavailable for many regions (Kearney

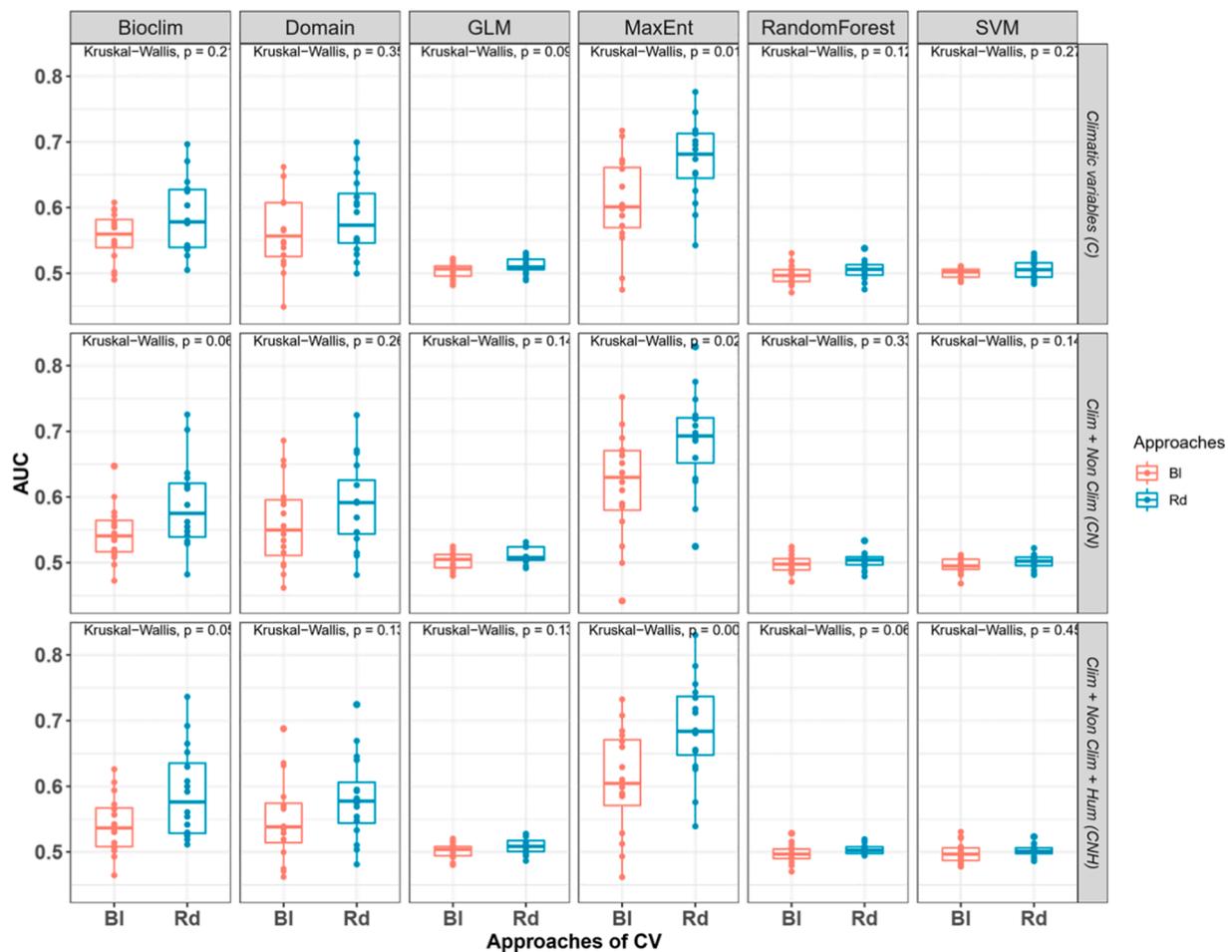


Fig. 6. Comparison of the 6 predictive models according to the 2 cross-validation approaches (k-fold blocked cv (BI) and random k-fold cv (Rd)) for the 3 scenarios of variable sets (only climatic variables (C), climatic and nonclimatic without human impact variables (CN), and climatic and nonclimatic including human impact (CNH)). The box plots represent the performances (AUCs) of the 6 predictive models computed for the 16 main species.

Table 3

The best SDM obtained for each of the main species: model performance (area under the ROC curve) and modeling approaches (model type, cross-validation approach and variable set). For the variable set, C represents only climatic variables, CN represents climatic and nonclimatic variables without the human impact variable, and CNH represents climatic and nonclimatic variables including the human impact variable.

Species	AUC	Model type	Cross-validation approach	Variable set
<i>P. juliflora</i>	0.87	MaxEnt	k-fold blocked	CN
<i>A. seyal</i>	0.86	MaxEnt	Random k-fold	CN
<i>D. mespiliformis</i>	0.83	MaxEnt	k-fold blocked	C
<i>B. aegyptiaca</i>	0.80	MaxEnt	k-fold blocked	CNH
<i>A. indica</i>	0.80	MaxEnt	k-fold blocked	CNH
<i>C. integrifolia</i>	0.78	Domain	k-fold blocked	CNH
<i>Z. mauritiana</i>	0.77	Bioclim	k-fold blocked	C
<i>A. digitata</i>	0.76	MaxEnt	k-fold blocked	CNH
<i>B. rufescens</i>	0.76	MaxEnt	Random k-fold	CN
<i>S. birrea</i>	0.72	Domain	k-fold blocked	C
<i>A. leiocarpus</i>	0.72	Domain	k-fold blocked	CN
<i>A. nilotica</i>	0.72	Domain	k-fold blocked	CN
<i>B. aethiopicum</i>	0.72	MaxEnt	k-fold blocked	CN
<i>P. reticulatum</i>	0.71	MaxEnt	Random k-fold	CN
<i>T. indica</i>	0.66	Bioclim	k-fold blocked	CN
<i>F. albida</i>	0.64	MaxEnt	k-fold blocked	CN

and Porter, 2009). That is why Bioclim variables and several others derived from remote sensing and GIS technology remain useful and resourceful as a good compromise for SDMs (Amiri et al., 2020; Austin,

2002; Kearney and Porter, 2009). Regarding soil property variables, studies have reported that they are also generally good and relevant predictors for plant SDMs (Buri et al., 2017; Hageer et al., 2017). Whether at the global or local scale, edaphic data add useful information for plant SDMs (Velazco et al., 2017).

4.1.3. Integrating nonclimatic variables in the SDMs is inconclusive

The possibility of using only climatic variables for the SDMs is known (Amiri et al., 2020; Gardner et al., 2019; Huntley et al., 1995; Sykes et al., 1996). However, integrating different types of variables, including climatic variables with nonclimatic variables (land cover, topography, phenology, etc.), is suggested to improve SDM performances, i.e., to increase the reliability of predictions (Austin and Van Niel, 2011; Burns et al., 2020; Fournier et al., 2017; Suárez-Seoane et al., 2004; Vila-Viçosa et al., 2020). Gardner et al. (2019) showed that generally building models with both climatic and soil variables provides better performances than dealing with only climatic variables. However, in this study, we found that, although suggested in several studies, the integration of climatic and nonclimatic variables does not systematically improve SDM performances (Fig. 5). Even if in this study the best performance for most species was obtained by integrating nonclimatic variables, the results varied depending on the species or model considered. Bucklin et al. (2015) found that the addition of nonclimatic variables has a relatively minor effect on the performance of climate-based SDMs and predictions, and they suggested that using only climatic predictors may already provide satisfactory accuracy. In their study, the addition of human influence predictors was the only one that provided

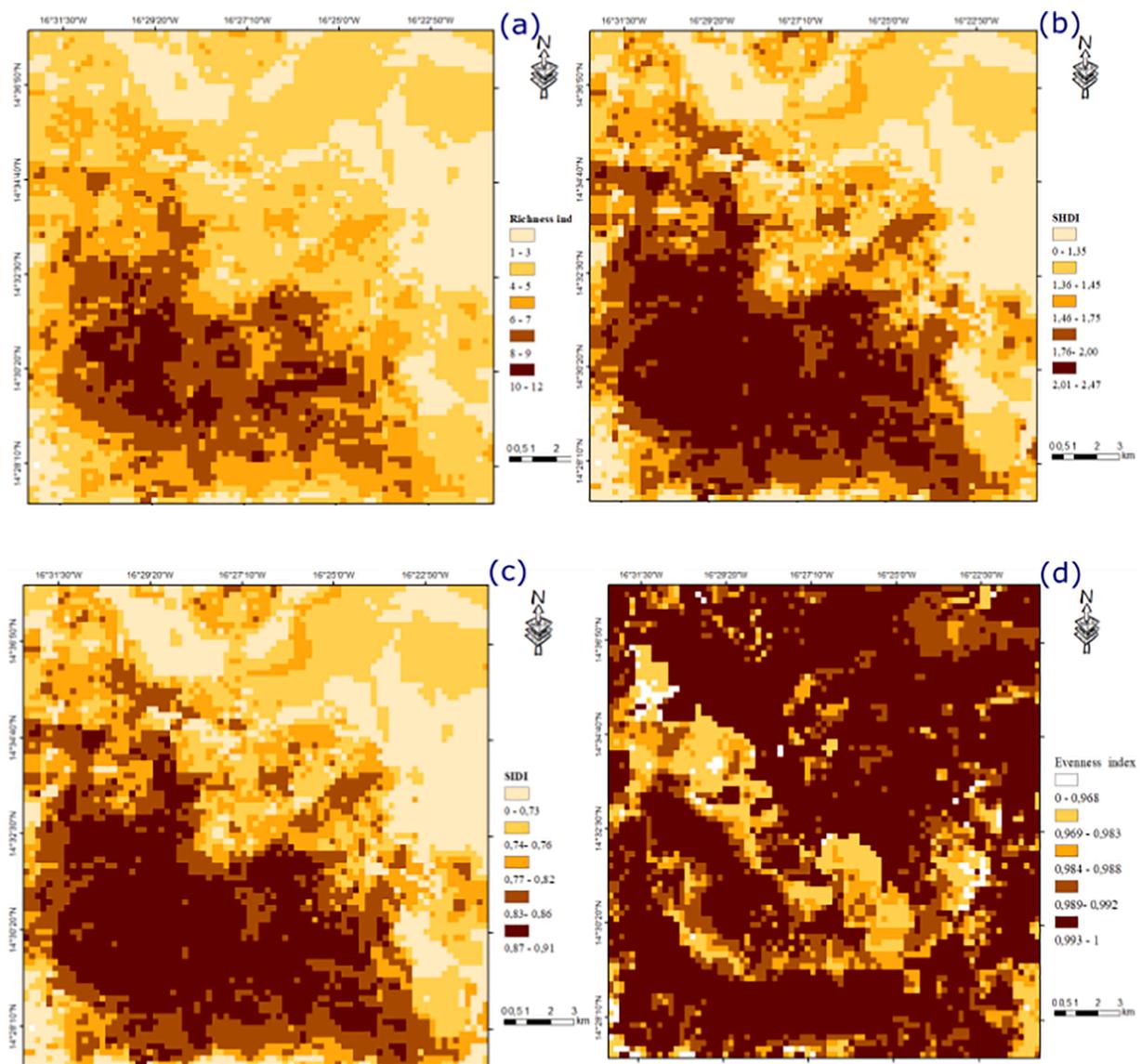


Fig. 7. Maps of the tree species diversity indices derived from the probabilities of presence maps: a) richness index, b) Shannon's diversity index - SHDI, c) Simpson's diversity index - SIDI and d) Pielou's evenness index.

significantly higher accuracy compared with using only climatic predictors.

4.1.4. Accounting for spatial autocorrelation in the blocking strategy could improve the reliability of species modeling

The results showed that *random k-fold* cross-validation tends to be more performative than *k-fold blocked* cross-validation. Indeed, when the partitioning of the data was randomized, testing and training individuals that are spatially close may have similar characteristics (spatial autocorrelation). This probably led to overestimation of the predictive power of the models (Roberts et al., 2017). However, in this study, the difference in accuracy between both cross-validation approaches was not significant, showing that blocking methods could improve the reliability of the models by avoiding autocorrelation phenomena without significantly affecting the performance estimation. Roberts et al. (2017) showed that *k-fold blocked cv* can be much more appropriate than *random k-fold cv* in cases such as SDMs.

4.1.5. Each species is sensitive to a specific algorithm

SDM results are very sensitive to the algorithm used for the prediction (Senay and Worner, 2019), making the choice of the model type

crucial. In this paper, a comparative analysis of six algorithms showed that no single algorithm was the best for all species. This confirms previous studies on a wide range of SDMs showing that there is no single 'best' SDM algorithm for all circumstances (Elith et al., 2006; Norberg et al., 2019; Qiao et al., 2015). For a given case, it should be important to test different types of algorithms and modeling techniques to identify an adequate model. The results of this study showed the importance of benchmarking several modelling approaches. For example, although the Maxent model performed better for most species in this study, the benchmarking analysis showed that for the species *C. integrifolia* and *Z. mauritiana* in particular, the Domain and Bioclim models respectively should be used to obtain the best modelling results (see Table 3).

4.2. Deriving tree species diversity mapping from SDM predictions

Using SDM predictions to appreciate the spatial distribution of species richness is already known. (Kwon et al., 2018; Luo et al., 2020; Vila-Viçosa et al., 2020). Species richness is the number of species within a defined region (Moore, 2013). In this study, species richness index was computed by compiling species distribution maps then summing species presences at pixel scale (250 m × 250 m). The species richness index is a

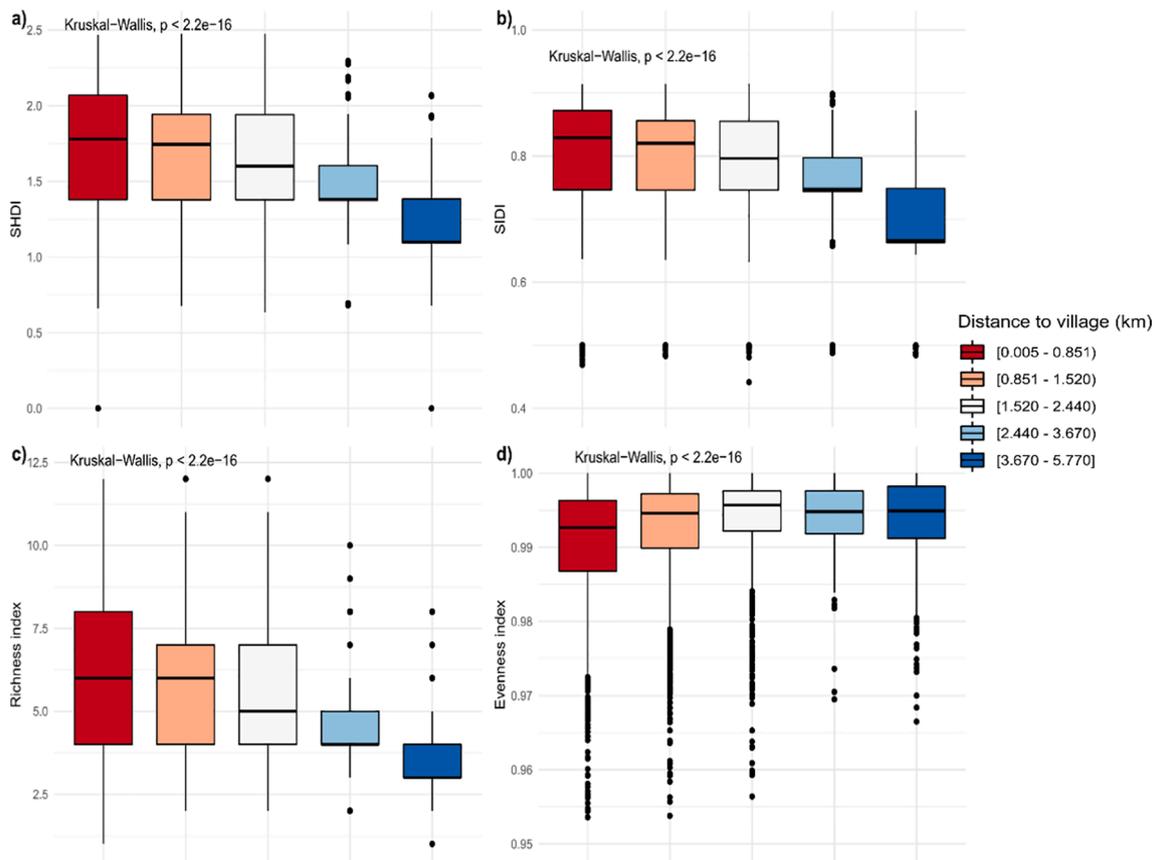


Fig. 8. Boxplots of tree species diversity values within DTV classes and Kruskal-Wallis one-way analysis of variance of the tree species diversity indices relative to distance to the village (DTV): a) SHDI, b) SIDI, c) richness, and d) Pielou's evenness index.

simple measure of diversity. Considering species distribution in addition to species richness strengthens the analysis and provides a better appreciation of diversity. Thus, the diversity indices of Shannon, Simpson and Pielou were computed on the basis of an assumption to complete the species richness index. The hypothesis is not verified in this study but it is strong and has been defended and discussed on the basis of previous studies. Also, it is very important to note that the Shannon and Simpson indices provided the same trends as the species richness index, i.e. even if the hypothesis is not proven the richness index alone, which was not based on the hypothesis, would have provided almost the same conclusions of this study.

The hypothesis assumes a significant correlation between the probabilities of occurrence of tree species and their relative abundances. Indeed, there is no denying that environmental factors affect the presence of tree species, their spatial distribution and their abundance. A significant correlation between environmental factors and the abundance of several tree species has been shown (Nguyen et al., 2015; Schwarz et al., 2003), suggesting a relationship between the probability of species presence derived from environmental predictors and species abundance. Therefore, SDM predictions could provide useful information to appreciate abundance distributions depending on environmental conditions (Gutiérrez et al., 2013; Van Couwenberghe et al., 2013; VanDerWal et al., 2009). Authors using only climate variables as predictors found this relationship to be weak or even neutral. They suggested integrating nonclimatic variables with climatic variables to better understand this relationship (Dallas and Hastings, 2018). Analyzing 243 vascular species at 10 996 French forest sites, Van Couwenberghe et al. (2013) reported a significant relationship between plant species abundances and the environmental conditions regarding variables of temperature, water balance and soil pH. In this study, we integrated different types of climatic and nonclimatic variables, including variables

of topographic and soil properties, which are both highly crucial for tree species presence and abundance (Nguyen et al., 2015). We also accounted for human impact knowing that factors other than environmental variables (Schwarz et al., 2003) could be needed for better predictions and characterization of spatial variation of tree species. The great significance of human influence predictors for SDMs has already been demonstrated (Bucklin et al., 2015). The integration of the different types of variables affecting the presence of trees increases the significance of the relationship between the species probability of presence predicted by the models and their abundance.

4.3. Spatial dynamics of tree species diversity in parklands

The results showed a significant negative correlation between the DTV and tree diversity, suggesting in this study a positive human impact on tree diversity (i.e., the closer to the village we are, the higher the tree diversity). These results are in contrast with the negative impact of the human footprint on species diversity that is commonly reported in studies on forest ecosystems (Vuyiya et al., 2014), showing that tree species diversity decreases linearly toward the village boundary (Popradit et al., 2015). The effects of human activities and presence on tree diversity are much less studied in African agroforestry systems. Nevertheless, a positive effect of village proximity on tree species diversity in agroforestry parklands was reported in this paper. Lelong et al. (2020) showed in the Senegalese Peanut Basin that tree species diversity is higher around villages. This positive effect could be linked to the many goods and services that people benefit from tree species (Sinare and Gordon, 2015), which they tend to sustain. In West Africa, agroforestry systems are highly anthropized, and the structure of tree diversity is mainly designed by people who select tree species generally for their contributions to their livelihoods (food, fodder, wood, medicine, and

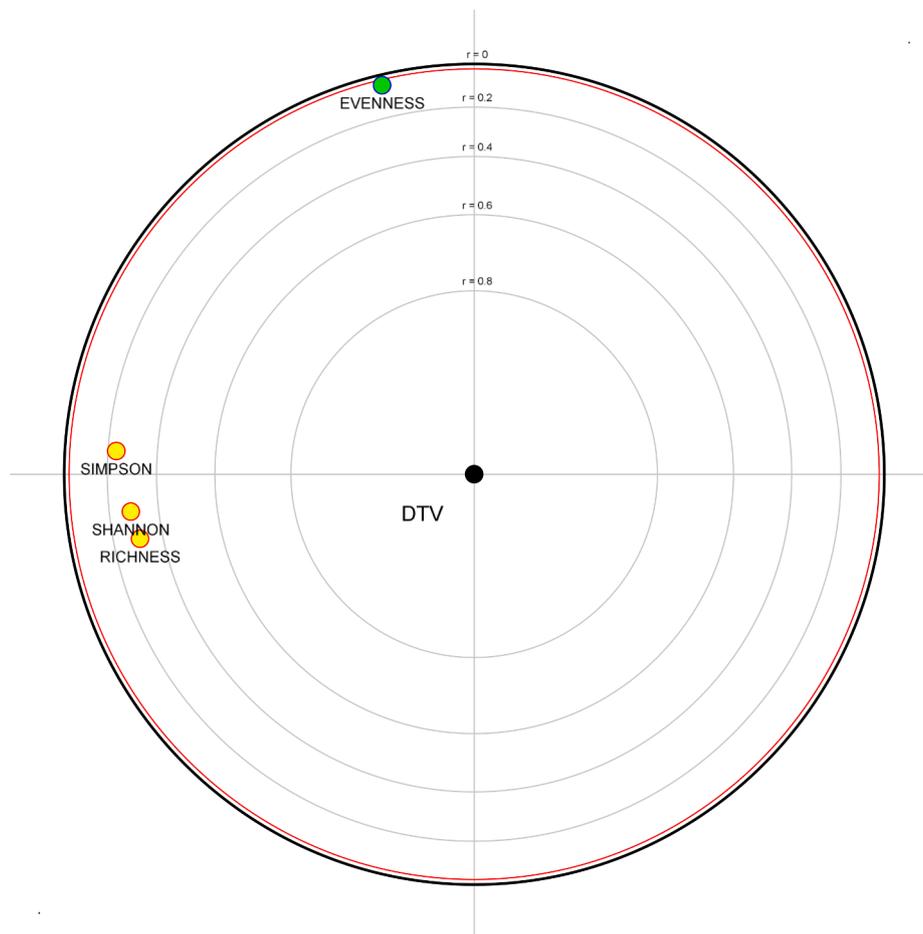


Fig. 9. Focused principal component analysis of the tree species diversity indices relative to distance to the village (DTV). The variables inside the red circle are significantly correlated with the focus variable (DTV). The colored dots (small circles) indicate whether this correlation is negative (yellow) or positive (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

soil fertility - Bayu, 2019; Sambou et al., 2017). The 8 species that the ecological niche factor analysis (ENFA) found to be sensitive to the DTV are all species that directly provide ecosystem goods and services to people. Almost all parts (roots, bark, fruit, wood and leaves) of *B. aegyptiaca* (Chothani and Vaghasiya, 2011), *T. indica* (Fandohan et al., 2010), *S. birrea* (Sene et al., 2018), *A. digitata* (Kébenzikato et al., 2015), *D. mespiliformis* (Ahmed and Mahmud, 2017), *B. aethiopum* (Salako et al., 2018) and *C. integrifolia* (Abah et al., 2019) are traditionally used for a wide range of human needs (medicine, food, handcraft, etc.). The last 7 species are particularly important sources of macro- and micronutrients required by rural communities and contribute significantly to improving the food security and nutrition of rural households (e.g., Chivandi et al., 2015; Félix et al., 2018; Ickowitz et al., 2014; Koffi et al., 2020). People obtain most of their staple food, fruits and drinks from indigenous trees (Gustad et al., 2004). For instance, fruit pulp of bearing trees such as *A. digitata* are consumed daily as juice called “booy” locally and is particularly rich in carbohydrates, vitamin C and minerals (Chadare et al., 2009). *A. digitata* is mainly planted in home fields so that their tenure is guaranteed for farmers (Koffi et al., 2020). *A. indica* is an evergreen species generally planted near and within villages due to its shadow cover. It also provides natural pesticides against insects or for pest control in agriculture (Schmutterer, 1990). Because of the many products and services provided by tree species, farmers have learned over generations to select and protect tree diversity according to their needs for subsistence, income and food security (Bayu, 2019). Indeed, the tree diversity associated with villages is particularly important for improving the resilience and food security of communities (Gustad et al., 2004).

Furthermore, the results also revealed a spatial dynamic of tree diversity that was higher in the southwestern part of the study area, gradually decreasing toward the northeast. The stratification of the landscape heterogeneity carried out by Ndao et al. (2021) in the same study area showed that in the southwestern part, the four landscape classes they identified are intermingled, and the area is more heterogeneous than the northeastern part (Fig. 10b). Many different studies have analyzed the relationship between environmental heterogeneity and species diversity, discovering positive, negative, hump-shaped or nonsignificant relationships (Allouche et al., 2012; Heidrich et al., 2020; Redon et al., 2014; Stein, 2016). Indeed, there is a level of environmental heterogeneity favorable to species diversity. In complex ecosystems with a high level of heterogeneity, especially in forests, the increase in landscape heterogeneity tends to reduce plant species richness. On the other hand, in environments with an intermediate level of complexity, landscape heterogeneity is more favorable to species diversity (Allouche et al., 2012; Redon et al., 2014; Yang et al., 2015). Especially in agricultural landscapes (intermediate complexity), landscape heterogeneity has a positive effect on the biodiversity of both plants and other groups of organisms (Alignier et al., 2020; Bo et al., 2016). In agroforestry systems, the spatial dynamics of biodiversity are significantly linked to the heterogeneity of the landscape, including the crop component and tree component. In particular, a greater level of tree diversity and the spatial distribution of trees are closely related to the complexity of agroforestry systems (Udawatta et al., 2019). It would therefore be important to account for landscape heterogeneity when planning biodiversity conservation measures (Harlio et al., 2019). The southwestern part is also characterized by the relative importance of

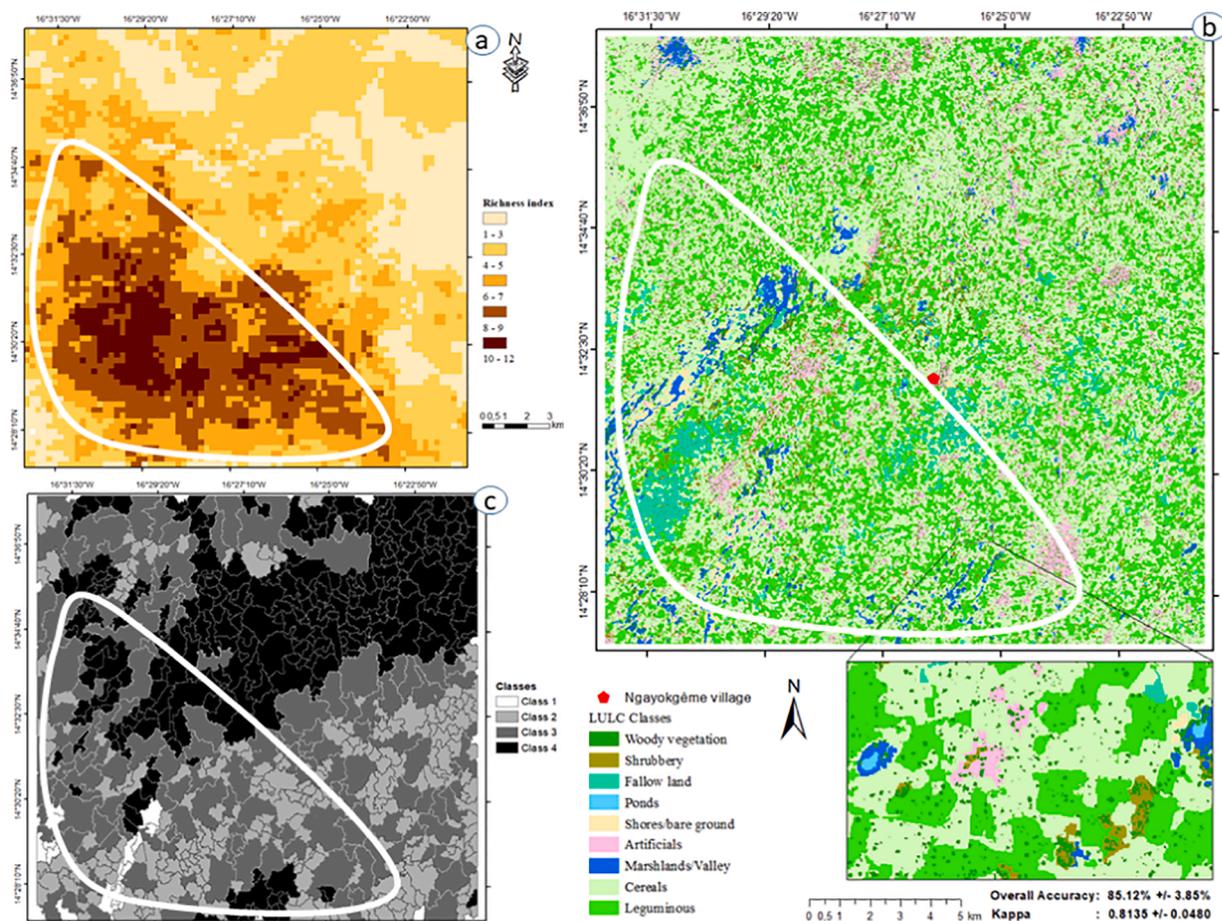


Fig. 10. Comparative view of the spatial dynamics of tree species diversity (a), stratification of landscape heterogeneity (b) and land use/land cover (c). b and c are obtained from Ndao et al., 2021. The white line delineation highlights the southwestern part of the study area.

small wetlands (numerous ponds, swamps, marshlands and ephemeral rivers – Fig. 10c – Ndao et al., 2021). This may partly drive the richness of tree species in this area. Indeed, in dry areas, the availability of water is decisive for the ecology of plants. It leads to gradients in tree diversity and structure around water bodies and wetlands (Douglas et al., 2018; de Terra et al., 2018).

5. Conclusion

Using SDMs, this paper proposed to shift from simple prediction of species distribution to quantitative analysis of the spatial distribution of species diversity. In short, tree diversity indices were computed and mapped from SDM predictions. Benchmarking several SDM algorithms, combination of variables and calibration approaches did not lead to identifying the best SDM technique for all species. But, this is crucial for each species to achieve its best prediction accuracy. It is also important but not necessary to integrate different environmental variables, including climate and nonclimate variables, to improve SDM performances.

The spatial analyses of the resulting diversity indices maps showed that the spatial dynamics of tree species diversity is closely related to socio-environmental conditions such as water availability, landscape heterogeneity or human impact. For instance, it was shown that, in contrast to forest ecosystems, human influence is rather favorable to sustaining tree diversity in the vicinity of villages in West African agroforestry systems.

Therefore, this study pointed out the importance of taking into account landscape and human impact factors for territorial planning and designing successful management strategies of Sahelian agroforestry

parklands to improve biodiversity conservation. It also proposed an interesting approach for monitoring tree diversity of Sahelian agroforestry parklands.in Senegal.

CRedit authorship contribution statement

Babacar Ndao: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Louise Leroux:** Methodology, Formal analysis, Software, Funding acquisition, Writing – original draft, Writing – review & editing. **Aboubacar Hema:** Data curation, Formal analysis, Methodology. **Abdoul Aziz Diouf:** Methodology, Writing – review & editing, Validation. **Agnès Bégué:** Writing – review & editing, Supervision, Validation. **Bienvenu Sambou:** Supervision, Project administration.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109443>.

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