



## Research article

# Predicting the potential impacts of climate change on the endangered *Caesalpinia bonduc* (L.) Roxb in Benin (West Africa)



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## ABSTRACT

*Caesalpinia bonduc* (L.) Roxb is a medicinal plant with high therapeutic values but declared extinct in the wild in Benin. This study explored the potential distribution and climatic suitability of the species under the present-day and future conditions in Benin, based on two Representative Concentration Pathways (RCP4.5 and RCP8.5) at the 2055-time horizon. The occurrence data were recorded in the distribution area of the species in Benin. These data were supplemented with those from the Global Biodiversity Information Facility (GBIF, [www.gbif.org](http://www.gbif.org)) website and the literature. A total of 23 environmental variables (15 bioclimatic data and 8 biophysical data) were used. The Bioclimatic variables for temperature and humidity were downloaded from Africlim site at 1 km resolution. The biophysical variables concern population, elevation, slope, landcover, wetland, distance to river, soil and distance to dwellings data that are downloaded respectively from DIVA-GIS, ISRIC and SEDAC website at different resolution. A correlation test has been applied to eliminate the highly correlated variables ( $r \geq 0.9$ ) using Pearson correlation coefficient. Species distribution modelling data were processed using five algorithms namely Random Forest (RF), Boosted Regression Trees (BRT), Maximum entropy (MAXENT), Generalized Linear Models (GLM) and Generalized Additive Models (GAM). The results showed that all models performed well with the area under the curve (AUC) values greater than 0.9. The RF, GLM, and GAM models predicted an increase in the suitable areas for the cultivation of the species. BRT and MaxEnt showed a substantial decrease in the suitable areas based on the two scenarios but this reduction is more observed with the MaxEnt model. These results show that climate change and human pressures will have significant effects on the distribution of *C. bonduc* throughout Benin. Sustainable management measures are necessary for *C. bonduc* and should be integrated in development policies to preserve the population of the species from total extinction in Benin.

## 1. Introduction

Biodiversity is a natural heritage and an invaluable resource for human survival (Gilani et al., 2020). It provides humans with useful biological resources in several forms, including medicine, food, wood, and firewood (Vihogbe et al., 2021; Avakoudjo et al., 2021). For instance, plant species are an essential component of biodiversity with high socio-cultural importance such as in traditional medicine (Qi et al., 2017). Among these plant species is *Caesalpinia bonduc* (L.) Roxb, a medicinal species with high therapeutic value and declared extinct in the wild in Benin, according to the Benin red list (Adomou, 2005; Neuenschwander et al., 2011). Currently, the species is only found in

agroforestry systems and home gardens (Lokonon et al., 2021) in Benin. It is a thorny shrub belonging to the Fabaceae family (Neuenschwander et al., 2011). Several studies have been carried out on its therapeutic values. The species is used to treat internal and external parasitosis (Sidi et al., 2018) and also problems related to intestinal worms, stomach aches, helminthic, menorrhagia, hepatitis, and malaria (Rakotonandrasana et al., 2017). In particular, medicine from this species has been reported to be an effective remedy for hernia, menstrual pain, and sexual weakness which are some of chronic challenges society is facing today (Assogbadjo et al., 2011). Recently, the studies on seed extraction showed that *C. bonduc* contains antioxidant properties that can be used to prevent the lipid peroxidation of the cell membrane and the management

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of polycystic ovary syndrome (Suhani et al., 2019; Meera et al., 2020; Sumithra et al., 2021; Kandasamy and Balasundaram, 2021).

Despite its multiple advantages, *C. bonduc* is under serious threat of extinction. Firstly, the species is subject to uncontrolled human activities through cultivation practices, exploitation of wood and Non-Timber Forest Products (Sinsin and Kampmann, 2010) coupled with intense harvesting and mutilation of organs (Mehta et al., 2020). In addition, the effects of climate change (Ma and Sun, 2018) pose another level of threat to the species through modification of annual mean temperature, annual precipitation, temperature seasonality, leading to extreme dry months. The climate plays a fundamental role in species distribution by modifying the life cycle by increasing or decreasing some variables of the species (temperature, precipitation, wind speed, etc.). These modifications can act directly on the ecology or lead to a reduction of the population or rather extinction of the species (IPCC, 2013). As a result, climate change represents an urgent and potentially irreversible threat to human societies, fauna and flora. According to the IPCC report (IPCC, 2019), human activities caused a planetary reheating of approximately 1 °C above the preindustrial levels, with a probable fork going from 0.8 °C to 1.2 °C. It is probably expected that the planetary reheating will reach 1.5 °C between the years 2030 and 2052 if it continues to increase at the current rate (IPCC, 2019). The increasing demand to predict the impact of global changes has pushed ecology towards a more predictive science (Evans et al., 2013; Thuiller et al., 2013). In this context, species distribution models (SDMs) have experienced a wide usage in recent decades. These models are based on the theory of the ecological niche, defined as the set of biotic and abiotic factors necessary for the survival and development of species at a given location (Hirzel and Le Lay, 2008). They statistically relate species occurrences to environmental variables to predict their potential distribution. These methods have become important tools for predicting suitable environmental conditions for species in space and time (Mallard, 2017). They are mostly based on the postulation of equilibrium conditions and the concept of the ecological niche (Gaudreau et al., 2015), and thus seek to reproduce environmental determinism of the species distribution at a given time (Bertrand, 2012). Several modelling algorithms exist in the literature with varying accuracies, but finding the best model in terms of predicting the potential distribution of a species remains a challenge (Yudaputra et al., 2019). As such, the use of a combination of algorithms seems to provide better accuracy in predictions than a single algorithm. Accordingly, in this study, the SDMs were applied based on the RF (Breiman, 2001), GLM (Guisan et al., 2002), MaxEnt (Phillips et al., 2006), BRT (Marmion et al., 2009), and GAM (Guisan et al., 2002) algorithms using the same setting.

To our knowledge, this is the first time that the impact of climate change on the distribution of *C. bonduc* has been assessed through the use of several modelling algorithms. Moreover, considering the status of the species in Benin, this study is important as it will make it possible to know the suitable habitats for the cultivation of the species. In addition, this study is a first step for the reintroduction of the species in the wild.

The study aimed (i) to examine how the models considered separately can predict the impacts of climate change on the distribution of the suitable habitats for *C. bonduc*, and (ii) to identify the important areas for its conservation and reintroduction in Benin. We explored the present-day distribution and the potential future impacts of climate on *C. bonduc* under RCP 4.5 and 8.5 at the 2055-time horizon. The results will help to define the possible strategies for the conservation of the species through the identification of areas with a high potential for domestication or reintroduction into the natural environment.

## 2. Material and methods

### 2.1. Study area

The study was performed in Benin (Figure 1). Benin is a West African country located between 6°30' and 12°30'N and 1° and 3°40' E. It covers a total area of 114,763 km<sup>2</sup> with a coastline of 125 km long and a crow

flies' distance of 700 km from the Atlantic to the Niger River in the north (Neuenschwander and Toko, 2011).

Benin is characterized by three climatic zones where the species occurs: Guineo-Congolian, Sudan-Guinean and Sudanian zones. In the Guinean zone, the rainfall regime is bimodal from April to June and from September to November, with a mean annual rainfall of 1200 mm. The mean temperature varies between 25 °C and 29 °C and the relative humidity between 69% and 97% (Assogbadjo et al., 2011, 2012). The soils are either deep ferrallitic, and of low fertility or alluvial and heavy clay soils. The vegetation in this zone has been strongly affected by various agricultural activities and now forms a mosaic of cultivated lands and small relic forest patches. The original vegetation was dense semi-deciduous forests and Guinean savannas. This zone represents about 10% of Benin and supports 60% of the country's inhabitants (Assogbadjo et al., 2011, 2012). The mean rainfall in the Sudan-Guinean zone is unimodal, from May to October, and lasts for about 113 days with total mean annual varying between 900 mm and 1110 mm. The annual temperature ranges from 25 °C to 29 °C, and the relative humidity from 31% to 98%. The soils in this zone are infertile mineral soils and ferruginous soils of variable fertility. The vegetation of the Sudano-Guinean transition zone is characterized by a mosaic of woodland, dry dense forests, tree and shrub savannas and gallery forests. In the Sudanian zone, the mean annual rainfall is often less than 1000 mm and the relative humidity varies from 18% during the harmattan period (December–February) to 99% in August. The temperature varies from 24 °C to 31 °C. The Sudanian zone has hydromorphic soils, well-drained soils, and lithosols. The vegetation of this zone is composed of savannas and gallery forests with trees of smaller size (Assogbadjo et al., 2014).

### 2.2. Data collection

#### 2.2.1. Occurrence data

Occurrence data on the species was obtained from three different sources, namely GBIF website ([www.gbif.org](http://www.gbif.org)), literature, and field investigations (Figure 2) across Benin. In total, 486 occurrences of *C. bonduc* were recorded, with 54.33%, 22.22% and 23.45% from the literature, GBIF site, and fieldwork respectively. Data were quality-controlled by removing duplicated records.

#### 2.2.2. Environmental data

Environmental data consists of bioclimatic and biophysical data. Data on current and future African climate was downloaded at a spatial resolution of 30 arcseconds (1 km at the equator) from the Africlim website ([www.africlim.org](http://www.africlim.org)). This dataset consists of 21 synthetic bioclimatic variables for temperature and humidity for the African region (Platts et al., 2015). Two representative concentrations pathways were considered for future projections at 2055-time horizon, RCP 4.5 and 8.5 (Platts et al., 2015). These scenarios were used as a priori since they predict a situation deemed more likely for Africa by 2055 (Williams et al., 2007).

Biophysical variables such as population, elevation, slope, Land cover, wetland, distance to river, soil and distance to dwellings at the scale of Benin were used to assess their contribution to the performance of the models. Elevation, vegetation cover, watercourse, population, and wetland data were downloaded from the DIVA-GIS website (<https://www.diva-gis.org/gdata>) whereas soil data were downloaded at a resolution of 30 arcseconds from the African Soil Profiles Database (<https://www.isric.org>) (Idohou et al., 2017). Human settlement data was extracted from the SEDAC website (<https://sedac.ciesin.columbia.edu/data/set/grump-v1-settlement-points/data-download>) and generated in ArcGIS via the Proximity-analysis tool to obtain distances related to waterways and dwellings. All these biophysical variables were primarily in different resolutions. As such, they were resampled to match the resolution of bioclimatic variables that is 30 arc second (1 km from equator).

To avoid bias in the results originating from variable multicollinearity, a correlation test was performed to eliminate the highly

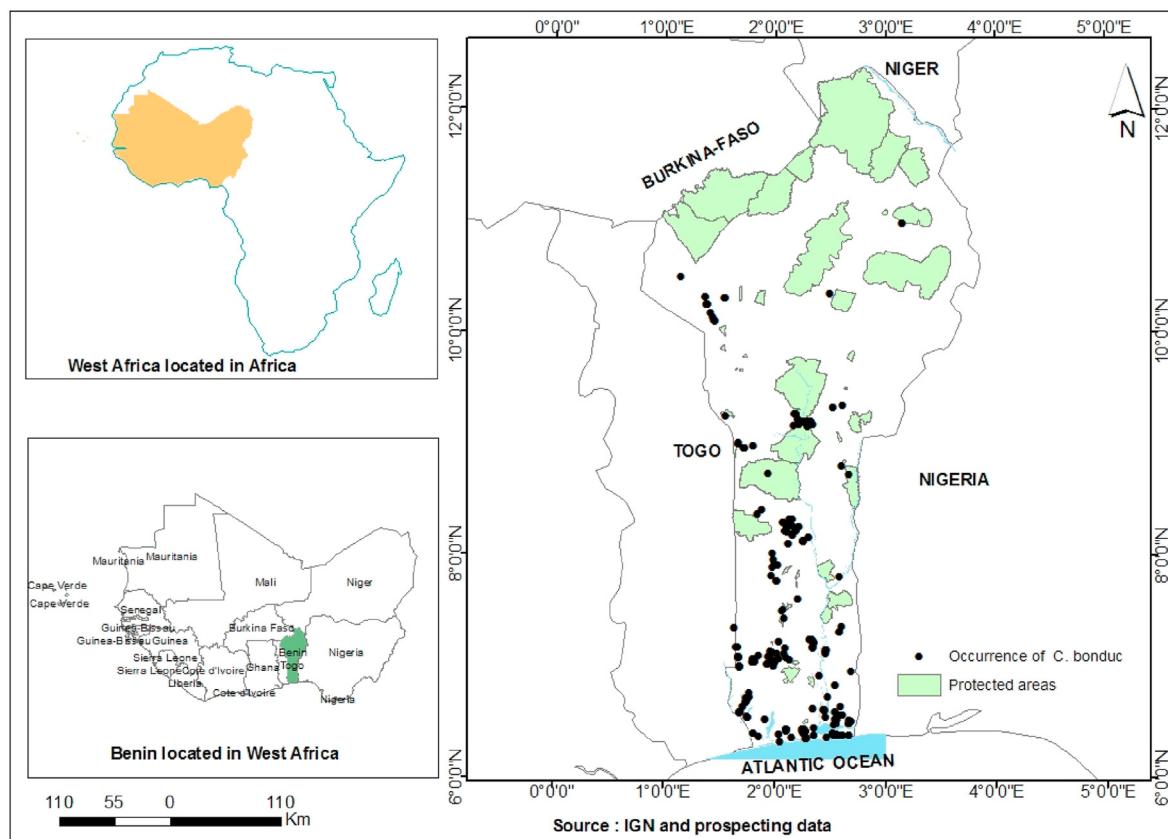


Figure 1. Geographic distribution of *C. bonduc* occurrences in Benin.

### 2.3. Model construction and evaluation

In this study, we adopted the approach of species distribution models using an SDM multi-model platform (Naimi and Araujo, 2016) implemented in the sdm 1.0-89 package performed in R 4.1.0 software (R Core Team, 2021). This platform allows the use of some well-known distribution models: Generalized Linear Model (GLM), Generalized Additive Model (GAM), Random Forest (RF), Maximum Entropy (MAXENT), and Boosted regression trees (BRT).

A variety of SDMs have been developed to predict species distributions under different climate scenarios. Four greenhouse gas concentration trajectories provided by the IPCC are used, Representative Concentration Pathway (RCP): RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.0. In 2100, the total radiative forcing values in the four scenarios stated would have attained  $2.6\text{W/m}^2$ ,  $4.5\text{W/m}^2$ ,  $6.0\text{W/m}^2$ , and  $8.5\text{W/m}^2$  over the value in the preindustrial period (Rogelj et al., 2012). Some of the commonly used SDMs include RF, BRT, GAM, GLM and MaxEnt (Table 1). These models are often applied individually and have proven to be efficient in predicting target species distributions under current, and also future climate scenarios (Rong et al., 2019). Among the existing models, some are based on regression technique and use the presence-absence data only. This includes GAM, RF, GLM and BRT (Table 1). On the other hand, MaxEnt (maximum entropy) has been widely used due to its advantages, including its ability to deal with incomplete data, small sample size, species presence data only (Table 1), both continuous and categorical environmental data, facilitate data collection and model interpretation, and for its prediction accuracy and reliability (Guo et al., 2017).

This study aims to assess the performance of the five models. SDMs assume that available presence locations represent a random (representative) sample in the geographical space, with no spatial dependencies



Figure 2. Picture showing the first author recording occurrence data of *C. bonduc* in northern Benin.

correlated variables ( $r \geq 0.9$ ) using the Pearson correlation coefficient. Thereafter, five variables (seasonality of precipitation (bio15), the precipitation of the driest quarter (bio17), the daytime mid-range (bio2), population and distance to dwellings (settlement distance) were retained for modelling based on their low correlation coefficient values.

**Table 1.** Characteristics of the species distribution model considered.

Methods	Procedure	Data type	Reference
Generalized Additive Model (GAM)	Regression analysis	Presence-Absence	Guisan et al. (2002)
Random Forest (RF)	Regression analysis	Presence-Absence	Breiman, 2001.
Generalized Linear Model (GLM)	Regression analysis	Presence-Absence	Lehmann et al. (2002)
Boosted regression trees (BRT)	Regression analysis	Presence-Absence	Elith et al. (2008)
MAXENT	Maximum Entropy	Presence/background	Phillips et al. (2006)

and bolstered by data-rich technologies, such as geographical information systems (GIS) (Elith et al., 2011). As all the five models do not use presence only data, samples of artificial absences (pseudo-absences) were created. In total, 1000 pseudo-absence points were randomly created. For evaluation, models were cross-validated with ten replications performed with 70% of the data for calibration and the remaining 30% for model evaluation. The accuracy of the models was assessed using the area under the curve (AUC) of the receiver operating characteristic (ROC) curve (Fielding and Bell, 1997) and the true skill statistics (TSS) (Allouche et al., 2006) with higher value indicating better performance. AUC values (0.5–0.7) correspond to low precision (0.7–0.9) correspond to good precision and those whose value is greater than 0.9 correspond to high precision (Swets, 1988). The TSS, also known as Hanssen Kuipers Discriminator compares the number of correct forecasts to that of a hypothetical set of perfect forecasts. The TSS is defined as the average of the net prediction success rate for presence and absence sites. Its values range from -1 to 1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche et al., 2006). This index is closely related to the arithmetic mean of sensitivity and specificity (Watling et al., 2015). The score of the different models against the metric values was then used to perform comparison studies of the performance of each model. Final models were built with the selected sets of variables for each procedure.

### 3. Results

#### 3.1. Performance of the models

The five models yielded good performance with significant AUC and TSS values (Table 2). The RF model yielded the best performance (AUC = 0.98; TSS = 0.9; Deviance = 0.29) after ten replications using the cross-validation method whereas GLM had the lowest performance (AUC = 0.93; TSS = 0.71; Deviance = 0.58).

#### 3.2. Variables contribution to the models

In total, five variables contributed to the models and the potential distribution of *C. bonduc*: seasonality of precipitation (bio15), the precipitation of the driest quarter (bio17), the daytime mid-range (bio2), human demography and distance from dwellings (sttlement\_dist). All the five variables under consideration contributed to the potential distribution of *C. bonduc* but in different proportions according to each model (Figure 3). The human demography variable mostly explained the potential distribution of *C. bonduc* considering RF and MaxEnt models.

#### 3.3. Present-day distribution for *Caesalpinia bonduc*

Highly suitable habitats for *C. bonduc* under the present-day conditions were observed using MaxEnt ( $20552.26 \text{ km}^2$  (representing 17.81 %)), while the other models (RF, BRT, GLM and GAM) produced more restricted distribution areas (Table 3). However, the highly suitable areas

**Table 2.** Performance of the models based on evaluation metrics.

METHODS	AUC	COR	TSS	DEVIANCIE
RF	0.98	0.89	0.9	0.29
BRT	0.97	0.84	0.86	0.59
MaxEnt	0.96	0.8	0.84	0.48
GLM	0.93	0.73	0.71	0.58
GAM	0.96	0.82	0.84	0.49

RF: Random Forest; GLM: Generalized Linear Model; GAM: Generalized Additive Model; MAXENT: Maximum Entropy; BRT: Boosted regression trees; COR: Correlation AUC: Received Operational Characteristics, TSS: True Skill Statistics.

for *C. bonduc* for all the five models were mainly located in southern Benin (Figure 4). Some areas around Bassila and Tchaourou were also highly suitable for the cultivation and restoration of the specie considering the BRT and GAM models.

#### 3.4. Future distribution for *Caesalpinia bonduc*

Future projections under the RCP 4.5 scenario showed that the most suitable areas for the species were more restrictive for the MaxEnt model compared to other models (Table 4). Thus, only  $780.05 \text{ km}^2$  (representing 0.67 %) of the habitats will be highly suitable for the species in the future. According to the same scenario, the Random Forest model predicted an increase of the highly suitable areas (Figure 5a), especially in the northwestern part of the country. For BRT (Figure 5b) and MaxEnt (Figure 5c), most of the highly suitable habitats of the species will be lost in the southern part of Benin and this decrease was more conspicuous for the MaxEnt model.

MaxEnt model remains more restrictive on highly suitable habitats for the distribution of *C. bonduc* under the RCP8.5 scenario. Approximately only  $815 \text{ km}^2$ , representing about 0.70 %, was predicted to become highly suitable for the cultivation of the species in the future (Table 5). On the contrary, Random Forest model predicted an increase in the highly suitable habitats for the species in northwestern Benin (Figure 6a). Unlike the MaxEnt model (Figure 6c), only a small part of south-eastern Benin will be highly suitable for the conservation of the species.

Among distribution models, RF, GLM and GAM predicted expansions in the future habitats for *C. bonduc* cultivation in Benin. On the contrary, the BRT and MaxEnt showed substantial decreases in the future projections of the distribution under the two climate scenarios, but this decrease was more drastic in the case of the MaxEnt.

Figure 7 represents the dynamic of habitats for *C. bonduc* according to the studied scenarios and the models used. MaxEnt and BRT predicted reduction in the highly suitable area based on the two future scenarios.

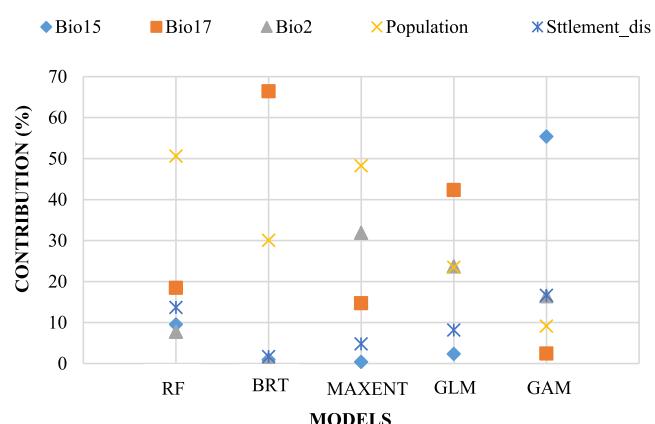


Figure 3. Contribution of the selected variables to the models. Bio15: Seasonality of precipitation, Bio 17: Precipitation of the driest quarter, Bio2: Daytime mid-range, Sttlement\_dis: Distance from dwellings.

**Table 3.** Variation of suitable areas (in km<sup>2</sup>) of the present-day distribution of habitat for *C. bonduc* in Benin.

	RF	BRT	MAXENT	GLM	GAM
Unsuitable area	86158.4 (74.68 %)	86506.29 (74.9 %)	68374.72 (59.27 %)	36159.53 (31.34 %)	72096.72 (62.49 %)
Less suitable area	18347.2 (15.9 %)	11865.91 (10.28 %)	26432.15 (22.91 %)	63645.37 (55.17 %)	27713.25 (24.02 %)
Highly suitable area	10853.5 (9.4 %)	16986.92 (14.72 %)	20552.26 (17.81 %)	15554.22 (13.48 %)	15549.17 (13.47 %)
Total	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)

#### 4. Discussion

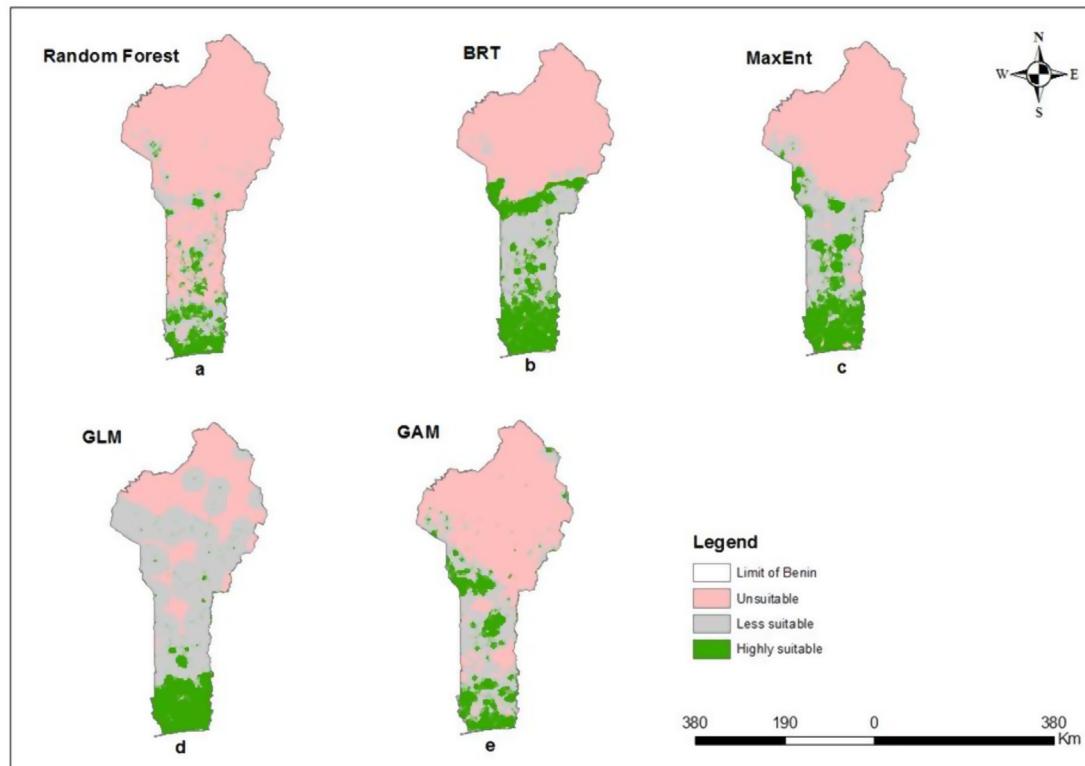
##### 4.1. Performance of the models

All the five models considered in this study showed good performance in predicting the potential distribution areas of *C. bonduc* since their AUC values were way above 0.9 (Swets, 1988) and the TSS values close to 1 (Watling et al., 2015). Specifically, the RF model was more precise in determining the distribution limits of the species followed by BRT, MaxEnt, GAM and GLM. This study suggests that modelling with the RF, BRT, MaxEnt, GAM and GLM can be applied with confidence to map the suitable habitats for *C. bonduc* in Benin. These results are similar to those of Kaky et al. (2020) in a comparative study of eight models including MaxEnt, RF, GLM and BRT on medicinal species in Egypt where the results showed that RF and MaxEnt were the best models. Similar results were obtained by Wang et al. (2012) comparing four distribution models (MaxEnt, GLM, GARP and DA) and by Yudaputra et al. (2019) comparing

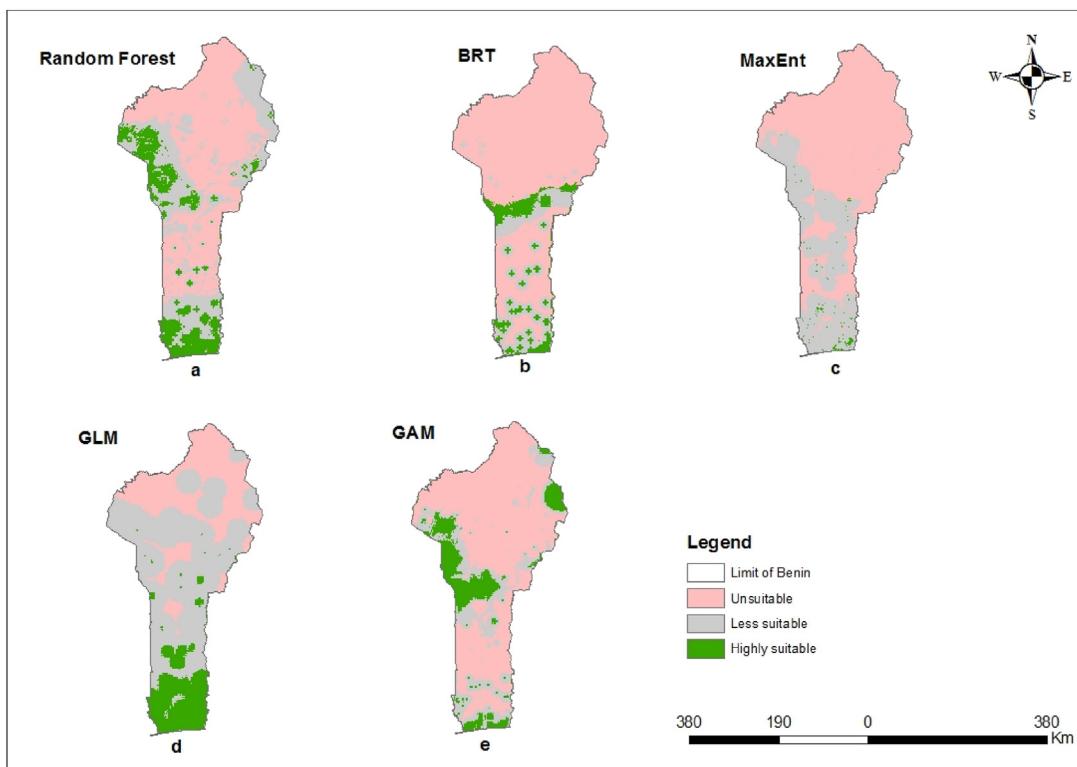
Bioclim, Domain, Glm, MaxEnt, Rf, and Svm on *Guettarda speciosa*. The choice of species distribution models has become an important subject within the scientific community. The use of species distribution models has increased in the last years (Kaky et al., 2020; Lastiri-Hernández et al., 2020; Gilani et al., 2020; Kunwar et al., 2020; Quintero et al., 2021). The results from these studies showed that the exactitude and the predictive power of a model depend initially on the type of the model, the choice of the environmental variables, the area of the distribution of the studied species, the sample size and the type of species (Kaky et al., 2020). In the literature, MaxEnt is often seen as the most robust in species distribution modeling due to its capacity to model presence-only data and small sample size (Abdelaala et al., 2019; Li et al., 2019; Kaky et al., 2020). However, in this study, the MaxEnt model appeared not to be the best based on the AUC value. Nevertheless, its predictive power is well appreciated in conservation studies (Idohou et al., 2017; Kaky et al., 2020). Contrary to this analysis, Guillera-Arroita et al. (2014) showed

**Table 4.** Variation of suitable areas (in km<sup>2</sup>) for *C. bonduc* distribution according to the RCP4.5

	RF	BRT	MAXENT	GLM	GAM
Unsuitable area	61204.54 (53.05 %)	89569.42 (77.64 %)	75831.76 (65.73 %)	34396.38 (29.81 %)	76868.74 (66.63 %)
Less suitable area	36733.17 (31.84 %)	16390.34 (14.20 %)	38747.32 (33.58 %)	63596.92 (55.12 %)	22695.62 (19.67 %)
Highly suitable area	17421.42 (15.10 %)	9399.36 (8.14 %)	780.05 (0.67 %)	17365.83 (15.05 %)	15794.77 (13.69 %)
Total	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)



**Figure 4.** Present-day distribution of the suitable habitats for *Caesalpinia bonduc*. a) Random Forest model; b) Boosted Regression Trees model; c) Maximum Entropy; d) Generalized Linear Model; e) Generalized Additive Model.



**Figure 5.** Suitable areas for *Caesalpinia bonduc* conservation according to the RCP4.5 scenario.

**Table 5.** Variation of suitable areas (in km<sup>2</sup>) for *C. bonduc* distribution according to the RCP8.5 scenario.

	RF	BRT	MAXENT	GLM	GAM
Unsuitable area	41297.23 (35.79 %)	85887.35 (74.45 %)	97493.77 (84.51 %)	34238.01 (29.67 %)	64577.46 (55.97 %)
Less suitable area	48045.6 (41.64 %)	16295.15 (14.12 %)	17050.77 (14.78 %)	62918.80 (54.54 %)	30755.58 (26.66 %)
Highly suitable area	26016.31 (22.55 %)	13176.63 (11.42 %)	814.59 (0.70 %)	18202.32 (15.77 %)	20026.09 (17.35 %)
Total	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)	115359.1 (100%)

that the methods based on the presence-absence data like GLM, GAM, RF and others can predict better the distribution of the species if the input data are well analyzed, even in the case of small sample size.

#### 4.2. Variables contribution to the models

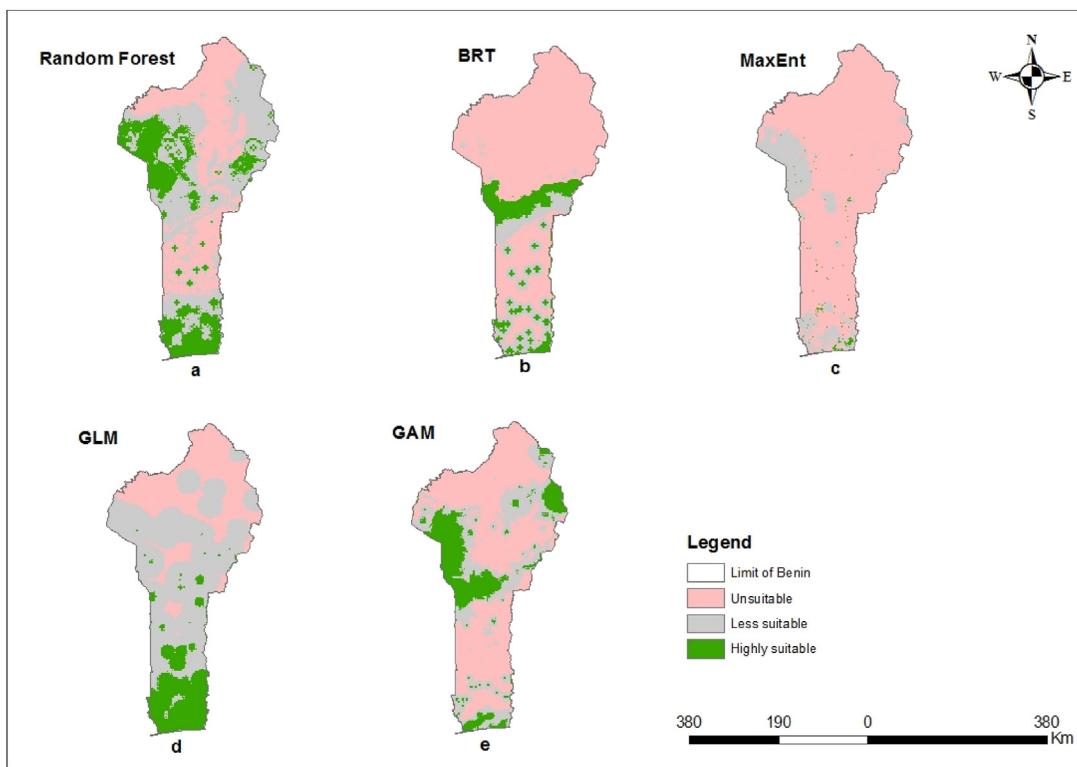
The distribution of *C. bonduc* is linked to different environmental conditions. The results from this study showed that precipitation of the driest quarter (bio17) contributed the most to the distribution of the species considering BRT and GLM models. In the case of RF and MaxEnt, it was the human demography that better influenced the distribution of the species. Only the precipitation seasonality (bio15) had a greater influence on the distribution of the species under GAM. Some of these variables were effective in modelling the suitable areas for *Borassus aethiopum* (Salako et al., 2018). Similar trends were obtained by Agbo et al. (2018) in the distribution of *Detarium microcarpum* where bio2 (daytime mid-range) and bio17 contributed to the distribution of the species. Compared to other studies on medicinal plants from Egypt, temperature is believed to be strongly responsible for the extinction of

medicinal species (Kaky and Gilbert, 2017). With regard to human demography and distance to dwellings, similar observations as in this study were also observed by Fatemi et al. (2018) on the distribution of *Juniperus excelsa*. In addition, the same results were obtained by Kaky et al. (2020) in their study of Egyptian medicinal plants. In the study, the contribution of the variable bio15 (Seasonality of precipitation) was very small for all the models used including MaxEnt, and RF. The difference between the five models related to the variable contribution is probably due to the specificity of each modelling procedure.

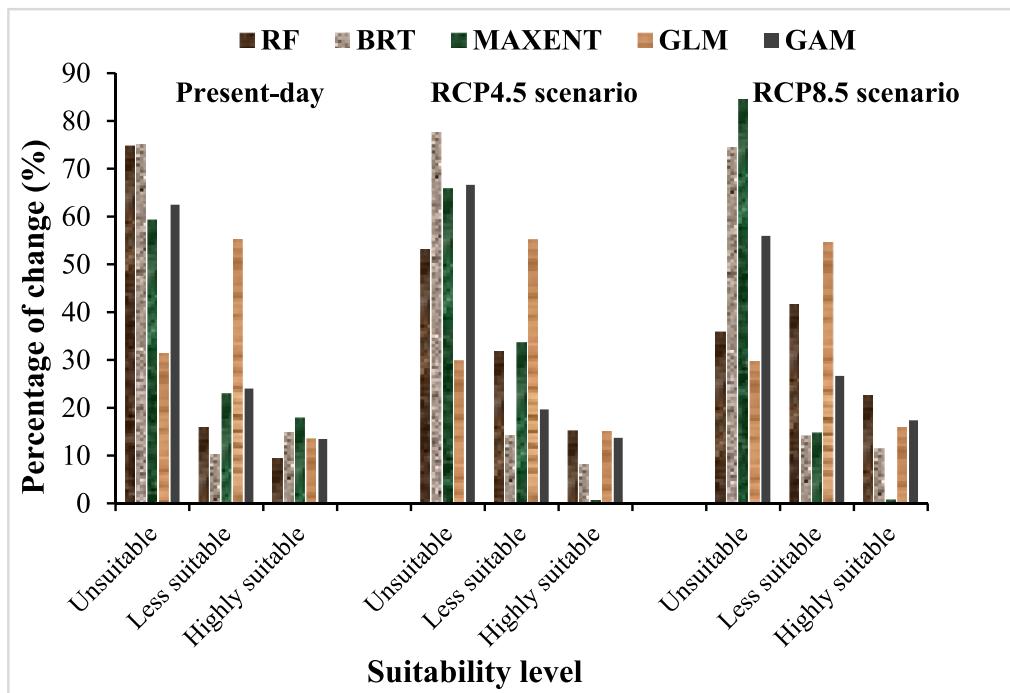
#### 4.3. Dynamics of the suitable areas to the species

The assessment of the impact of climate and global changes in the distribution of *C. bonduc* has shown great modification of highly suitable habitats from one model to another and from one scenario to another. The MaxEnt model was more restrictive in determining the impact of climate and global change although the RF model had the best performance in terms of AUC and TSS. This model showed a huge decrease in the highly suitable areas for the species, namely 0.68 and 0.71% respectively, under scenarios RCP4.5 and 8.5 against the current distribution of 17.82% of highly suitable habitats. This could be explained by the specificities of the MaxEnt model to give very good precision with small sample sizes (Anderson and Gonzalez, 2011). The results of these models thus showed that future environmental conditions will favor the production and conservation of *C. bonduc* according to the RF, GLM and GAM while decreases will be observed according to the BRT and more particularly with the MaxEnt.

The variations in distribution areas obtained from our results reaffirm those of many authors who have modeled the evolution of species distribution in the context of climate change (Martinez-Meyer et al., 2006; Bamba, 2010; Arouna, 2012; Tosso, 2013). However, this is contrary to the findings of Gbessso et al. (2013) on *Chrysophyllum albidum* or on *Parkia biglobosa* (Fachola et al., 2019) where climate change would favor an



**Figure 6.** Suitable areas for *Caesalpinia bonduc* conservation according to the RCP8.5 scenario.



**Figure 7.** Dynamic of habitats for *C. bonduc*.

increase in the distribution areas of these species according to the MaxEnt model.

#### 4.4. Sustainable management strategies for *Caesalpinia bonduc*

The management strategies of a species largely depend on the ecosystem in which it is found, where in situ or ex situ, and influenced by

the conservation status at the national level. In the case of *C. bonduc*, it is a species already extinct in the wild in Benin, for which imminent studies and actions are necessary in order to prevent it from total extinction (Neuenschwander et al., 2011). In other countries such as India (Balasubramanian et al., 2016), no formal conservation efforts have been undertaken with regard to this species despite the fact that it is declared endangered in the country. Knowing the threats to this species, some

authors have therefore made attempts on methods based on vegetative propagation including stem cutting (Krishnamurthy et al., 2013; Tiwari and Das, 2010) and tissue culture (Kumar et al., 2012; Sharma et al., 2009) with a view to restoring the endangered population of *C. bonduc*. The conservation of *C. bonduc* in home gardens and other places of conservation as suggested in this study constitutes an ex-situ conservation strategy intrinsically linked to the current status of the species. The strong market demand for the roots of the species has contributed to its extinction in the wild, leading to its presence only in fields where it is cultivated. It is important to strengthen and encourage local communities to cultivate this species in order to save it from total extinction in future. This same conservation strategy has been proposed by Codjia et al. (2018) for *Garcinia kola* in the districts of Adjara, Avrankou and Ifangni where the main threat to this species would be linked to the increased marketing of seeds for various uses. To conserve *C. bonduc*, the establishment of park in different municipalities is recommended and also the planting in gardens and the development of nurseries.

## 5. Conclusions and implications of the study

The results of this research revealed that future environmental conditions will significantly modify the distribution of *C. bonduc* regardless of the studied models. The contribution of the variables "population" and "distance from habitations" in the distribution of this species show the importance taking into account the human pressure in its conservation. Participatory conservation strategies may therefore not be effective without increasing the raising awareness of local communities for the restoration of this species and its associated traditional knowledge, uses, and practices. The modelling algorithms are important tools to inform decision making for the preservation of medicinal plants in particular and biodiversity in general. They allow anticipating variations that will be experienced in the distribution areas of the species and offer avenues for potential mitigation measures. Climate change and human pressures will have significant effects on the distribution of *C. bonduc* throughout Benin according to the models and scenarios studied. Conservation measures must be taken and integrated into sustainable development policies in order to enhance endogenous knowledge and guarantee future use of this species in Benin. In-depth studies on the biochemical aspect of the organs and the germination of the seeds are needed in order to find techniques for faster multiplication of this species.

## Declarations

### Author contribution statement

Hyacinthe Gbètoyénonmon Wouyou, Bruno Enagnon Lokonon, Rodrigue Idohou, Alban Gandonou Zossou-Akete: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Achille Ephrem Assogbadjo, Romain Glèlè Kakaï: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

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### Data availability statement

Data will be made available on request.

### Declaration of interests statement

The authors declare no conflict of interest.

### Additional information

No additional information is available for this paper.

## References

- Abdelaala, M., Foisa, M., Fenua, G., Bacchetta, G., 2019. Using MaxEnt modeling to predict the potential distribution of the endemic plant *Rosa arabica* Crép. in Egypt. Ecol. Inf. 50, 68–75.
- Adomou, A.C., 2005. Vegetation Patterns and Environmental Gradient in Benin: Implications for Biogeography and Conservation. Ph D thesis, Wageningen University, the Netherlands, p. 136.
- Agbo, R.I., Idohou, R., Vihotogbé, R., Missihoun, A.A., Dagba, R.A., Assogbadjo, A.E., Agbangla, C., 2018. Spatio-temporal dynamics of suitable habitats for *Detarium microcarpum* Guill. & Perr. (Caesalpiniaceae), a priority food tree species in Benin (West Africa). Model. Earth Syst. Environ. 5, 595–604.
- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43 (6), 1223–1232.
- Anderson, R.P., Gonzalez, J.I., 2011. Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with MaxEnt. Ecol. Model. 222 (15), 2796–2811.
- Arouna, O., 2012. Cartographie et modélisation prédictive des changements spatio-temporels de la végétation dans la commune de Djidja au Bénin: implications pour l'aménagement du territoire. Thèse de Doctorat Unique, Université d'Abomey-Calavi, Bénin, p. 246.
- Assogbadjo, A.E., Fandohan, B., Glèlè Kakaï, R., Kyndt, T., Hardy, O.J., Gheysen, G., Sinsin, B., 2012. Genetic evidence of the contribution of ethnic migrations to the propagation and persistence of the rare and declining scrambling shrub *Caesalpinia bonduc* L. Hum. Ecol. 40, 117–128.
- Assogbadjo, A.E., Glèlè Kakaï, R.L., Adjallala, F.H., Azihou, A.F., Vodouhé, G.F., Kyndt, T., JTC, Codjia, 2011. Ethnic differences in use value and use patterns of the threatened multipurpose scrambling shrub (*Caesalpinia bonduc* L.) in Benin. J. Med. Plants Res. 5 (9), 1549–1557.
- Assogbadjo, A.E., Sossa, B., Awessou, B., Noumonvi, R., Djagoun, S.C.A.M., Chadare, F.J., Padonou, E.A., Idohou, R., Salako, V., Mbairamadjé, J., 2014. Stratégie Nationale et plan d'actions de valorisation des Produits Forestiers Non Ligneux (PFNL) prioritaires du Bénin : cas des fruitiers sauvages, p. 143. Bénin.
- Avakoudjo, H.G.G., Idohou, R., Salako, K.V., Houenkpevi, A., Koné, M.W., Assogbadjo, A.E., 2021. Diversity in tree and fruit traits of *Strychnos spinosa* Lam. along a climatic gradient in Benin: a step towards domestication. Genet. Resour. Crop Evol.
- Balasubramanian, D., Arunachalam, K., Arunachalam, A., 2016. Dioecious *Caesalpinia bonduc* (L.) Roxb. Calls for conservation in burachapori wildlife sanctuary, Assam. Trop. Ecol. 57 (1), 119–124.
- Bamba, I., 2010. Anthropisation et dynamique spatiotemporelle de paysages forestiers en République démocratique du Congo. Thèse de doctorat, Université Libre de Bruxelles, Belgique, p. 189.
- Bertrand, R., 2012. Réponse spatio-temporelle de la végétation forestière au réchauffement climatique—Évaluation du remaniement de la végétation et caractérisation de l'effet des facteurs écologiques et géographiques le modulant à l'échelle de l'espèce et des communautés. AgroParisTech. Nancy, p. 312.
- Breiman, L., 2001. Random Forests. Statistics Department. University of California, Berkeley, CA 94720, p. 33.
- Codjia, S., Aoudji, A., Koura, K., Ganglo, J.C., 2018. Systèmes Agroforestiers à *Garcinia Kola* Heckel au Sud-Est du Bénin : distribution géographique, connaissances endogènes et retombées financières. Eur. Sci. J. 14 (12), 188.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813.
- Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists: statistical explanation of MaxEnt Divers. Distrib. 17 (1), 43–57.
- Evans, M.R., Bithell, M., Cornell, S.J., Dall, S.R.X., Díaz, S., Emmott, S., Ernande, B., Grimm, V., Hodgson, D.J., Lewis, S.L., Mace, G.M., Morecroft, M., Moustakas, A., Murphy, E., Newbold, T., Norris, K.J., Petchey, O., Smith, M., Travis, J.M.J., Benton, T.G., 2013. Predictive systems ecology. Proc. Biol. Sci. 280, 2013–1452.
- Fachola, O.B., Lougbegnon, O.T., Agossou, N., 2019. Modélisation de la niche écologique de *Parkia biglobosa* (Jacq.) au Sud et au Centre du Bénin (Afrique de l'Ouest). Rev. can. géogr. Trop. 6 (1), 19–25.
- Fatemi, S.S., Rahimi, M., Tarkesh, M., Ravanbakhsh, H., 2018. Predicting the impacts of climate change on the distribution of *Juniperus excelsa* M. Bieb. in the central and eastern Alborz Mountains, Iran. IForest 11, 643–650.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.
- Gaudreau, J., Perez, L., Legendre, P., 2015. Identification des variables expliquant la distribution spatiale d'oiseaux de la forêt boréale et modélisation de tendances futures : une approche multivariée.

- Gbéso, F.H.G., Tenté, B.H.A., Gouwakinnou, N.G., Sinsin, B.A., 2013. Influence des changements climatiques sur la distribution géographique de *Chrysophyllum albidum* G. Don (Sapotaceae) au Benin. Int. J. Biol. Chem. Sci. 7 (5), 2007–2018.
- Gilani, H., Goheer, A.M., Ahmad, H., Hussain, K., 2020. Under predicted climate change: distribution and ecological niche modelling of six native tree species in Gilgit-Baltistan, Pakistan. Ecol. Indicat. 111 (2020), 106049.
- Guillera-Arroita, G., Lahoz-Monfort, J., Elith, J., 2014. MaxEnt is not a presence absence method: a comment on Thibaud et al. Methods Ecol. Evol. 5, 1192–1197.
- Guisan, A., Edwards, J.T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157, 89–100.
- Guo, Y., Li, X., Zhao, Z., Wei, H., Gao, B., Gu, W., 2017. Prediction of the potential geographic distribution of the ectomycorrhizal mushroom *Tricholoma matsutake* under multiple climate change scenarios. Sci. Rep. 7, 46221.
- Hirzel, A., Le Lay, G., 2008. Habitat suitability modelling and niche theory. J. Appl. Ecol. 45, 1372–1381.
- Idhou, R., Peterson, A.T., Assogbadjo, A.E., Vihogbe, R.L., Padonou, E., Glèlè Kakai, R., 2017. Identification of potential areas for wild palm cultivation in the Republic of Benin through remote sensing and ecological niche modelling. Genet. Resour. Crop Evol. 64 (6), 1–11.
- IPCC, 2013. Changements climatiques 2013. Les éléments scientifiques Contribution du Groupe de travail I au cinquième Rapport d'évaluation du Groupe d'experts intergouvernemental sur l'évolution du climat. OMM, Suisse, p. 34.
- IPCC, 2019. Réchauffement planétaire de 1,5 °C, Rapport spécial du GIEC sur les conséquences d'un réchauffement planétaire de 1,5 °C par rapport aux niveaux préindustriels et les trajectoires associées d'émissions mondiales de gaz à effet de serre, dans le contexte du renforcement de la parade mondiale au changement climatique, du développement durable et de la lutte contre la pauvreté. OMM, Suisse, p. 110.
- Kaky, E., Gilbert, F., 2017. Predicting the distributions of Egypt's medicinal plants and their potential shifts under future climate change. PLoS One 12 (11), e0187714.
- Kaky, E., Nolan, V., Alatawi, A., Gilbert, F., 2020. A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: a case study with Egyptian medicinal plants. Ecol. Inf. 60, 101150.
- Kandasamy, V., Balasundaram, U., 2021. *Caesalpinia bonduc* (L.) Roxb. as a promising source of pharmacological compounds to treat Poly Cystic Ovary Syndrome (PCOS): a review. J. Ethnopharmacol. 279, 114375.
- Krishnamurthy, V., Mandle, L., Ticktin, T., Ganeshan, R., Saneesh, C.S., Varghese, A., 2013. Conservation status and effects of harvest on an endemic multipurpose cycad, *Cycas circinalis* L., Western Ghats, India. Trop. Ecol. 54, 309–320.
- Kumar, S.R.S., Krishnamurthy, V., Pradeepa, V.K., Kumar, K.G., Gnanesh, A.U., 2012. Direct and indirect method of plant regeneration from root explants of *Caesalpinia bonduc* (L.) Roxb. A threatened medicinal plant of Western Ghats. Indian J. Exp. Biol. 50, 910–917.
- Kunwar, R.M., Rimal, B., Sharma, H.P., Poudel, R.C., Pyakurel, D., Tiwari, A., Magar, S.T., Karki, G., Bhandari, G.S., Pandey, P., Bussmann, R.W., 2020. Distribution and habitat modeling of *Dactylorhiza hatagirea* (D. Don) soot, *Paris polypilla* Sm. And *Taxus* species in Nepal himalaya. J. Appl. Res. Med. Aromat. Plants.
- Lastiri-Hernández, M.A., Cruz-Cárdenas, G., Álvarez-Bernal, D., Vázquez-Sánchez, M., Bermúdez-Torres, K., 2020. Ecological niche modeling for halophyte species with possible anthropogenic use in agricultural saline soils. Environ. Model. Assess. 25 (3), 429–440.
- Lehmann, A., Overton, J.M., Leathwick, J.R., 2002. GRASP: generalized regression analysis and spatial prediction. Ecol. Model. 157 (2-3), 189–207.
- Li, J., Wu, J., Peng, K., Fan, G., Yu, H., Wang, W., He, Y., 2019. Simulating the effects of climate change across the distribution of two medicinal plants in the genus *Nardostachys*. PeerJ 7, 1–15 e6730.
- Lokonou, B.E., Sodoté, F.E., Glèlè Kakai, R., 2021. Use of local knowledge for contributing to the conservation of *Caesalpinia bonduc* (L.) Roxb in southern Benin (West Africa). Glob. Ecol. Conserv. 27, e01551.
- Ma, B., Sun, J., 2018. Predicting the distribution of *Stipa purpurea* across the Tibetan plateau via the MaxEnt model. BMC Ecol. 18, 10.
- Mallard, F., 2017. Programme les sentinelles du climat. Tome III : Cadre de la modélisation prédictive des réponses des espèces face aux changements climatiques en Nouvelle-Aquitaine. 1-90. C. Nature. Le Haillan, Gironde, France, p. 90.
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15, 59–69.
- Martinez-Meyer, E., Peterson, A.T., Servin, J.I., Kiff, L.F., 2006. Ecological niche modelling and prioritizing areas for species reintroductions. Oryx 40 (4), 411–418.
- Meera, B., Muralidharan, P., Hari, R., 2020. Antioxidant potential of *Caesalpinia Bonduc* seeds in the management of polycystic ovary syndrome (PCOS) using mifepristone induced rats model. J. Herbs, Spices, Med. Plants 27, 123–134.
- Mehta, P., Bisht, K., Sekar, K.C., 2020. Diversity of threatened medicinal plants of Indian himalayan region. Plant Biosyst. 1–37.
- Naimi, B., Araujo, M.B., 2016. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography 39, 368–375.
- Neuenschwander, P., Sinsin, B., Goergen, G., 2011. Protection de la Nature en Afrique de l'Ouest: une Liste Rouge pour le Bénin. In: Nature Conservation in West Africa: Red List for Benin. IITA, Ibadan.
- Neuenschwander, P., Toko, I., 2011. Bénin, milieu naturel et données socio-économiques. Benin, its natural environment and socio-economic data. In: Neuenschwander, P., Sinsin, B., Goergen, G. (Eds.), Protection de la nature en Afrique de l'Ouest: une liste rouge pour le Bénin. Nature conservation in West Africa: red list for Benin. IITA, Ibadan, pp. 7–13.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modelling of species geographic distributions. Ecol. Model. 190 (3-4), 231–259.
- Platts, J.P., Peter, A., Omeyen, P.A., Marchant, R., 2015. Africlim: high resolution climate projections for ecological applications in Africa. Afr. J. Ecol. 53, 103–108.
- Qi, Z., Rui, L., Yingying, G., Qian, Y., Xiaoqiang, G., Wenguo, W., 2017. Modelling impacts of climate change on the geographic distribution of medicinal plant *Fritillaria cirrhosa* D. Don. Plant Biosyst. 152, 349–355.
- Quintero, M.E., Rico, Y., Lira Noriega, A., Gonzalez, R.A., 2021. Molecular evidence and ecological niche modeling reveal an extensive hybrid zone among three *Bursera* species (section *Bullockia*). PLoS One 16 (11), e0260382.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rakotonandrasana, S.R., Rakotondrafara, A., Rakotondraona, R., Rasamison, V., Ratimbason, M., 2017. Plantes médicinales des formations végétales de la baie de Rigny- Antsiranana à Madagascar. Bois For. Trop. 331 (1), 55–65.
- Rogelj, J., Meinshausen, M., Knutti, R., 2012. Global warming under old and new scenarios using IPCC climate sensitivity range estimates. Nat. Clim. Change 2 (4), 248–253.
- Rong, Z., Zhao, C., Liu, J., Gao, Y., Zang, F., Guo, Z., Mao, Y., Wang, L., 2019. Modelling the effect of climate change on the potential distribution of qinghai spruce (*Picea crassifolia* Kom) in qilian mountains. Forests 10 (1), 62.
- Salako, K.V., Moreira, F., Gbedom, R.C., Tovissodé, F., Assogbadjo, A.E., Glèlè Kakai, R.L., 2018. Traditional knowledge and cultural importance of *Borassus aethiopum* Mart. In Benin: interacting effects of socio-demographic attributes and multi-scale abundance. J. Ethnobiol. Ethnomed. 14, 36.
- Sharma, G., Nautiyal, B.P., Nautiyal, A.R., 2009. Seedling emergence and survival in *Cinnamomum tamala* under varying micro-habitat conditions: conservation implications. Trop. Ecol. 50, 201–209.
- Sidi, I.Y.M.S., Olounlade, P.A., Dedebo, V.F.G.N., Alowanou, G.G., Azando, E.V.B., Hounzangbé-Adote, M.S., 2018. Diversité des espèces médicinales utilisées en médecine vétérinaire au Bénin. Rev. Elev. Med. Vet. Pays Trop. 74 (3), 167–175.
- Sinsin, B., Kampmann, D., 2010. Atlas de la Biodiversité de l'Afrique de l'Ouest. Tome I. Bénin, Cotonou & Frankfurt/Main, p. 726.
- Suhani, S., Bhat, K.M., Kumar, N., Padma, D., Pai, K.S.R., Choudhary, S., 2019. *Caesalpinia bonduc* Linn extracts exhibit hepatoprotective effect on HepG2 cells against paracetamol by up-regulating glutathione related genes. J. Krishna Inst. Med. Sci. Univ. 8 (2), 1–12.
- Sumithra, M., Chitra, V., Moka, M.K., Padaleeswaran, Ahamed, S., 2021. Anti-androgenic activity of *Caesalpinia bonduc* Linn androgen-induced polycystic ovarian syndrome rats. Int. J. Pharmacol. Res. 33 (55A), 220–227.
- Swets, J.A., 1988. Measuring the Accuracy of Diagnostic Systems. Laboratories Incorporated, Cambridge, pp. 1285–1293.
- Thuiller, W., Münkemüller, T., Lavergne, S., Mouillet, D., Mouquet, N., Schifflers, K., Gravel, D., 2013. A road map for integrating eco-evolutionary processes into biodiversity models. Ecol. Lett. 16 (1), 94–105.
- Tiwari, R.K.S., Das, K., 2010. Effect of stem cuttings and hormonal pre-treatment on propagation of *Embelia tjeriam* and *Caesalpinia bonduc*, two important medicinal plant species. J. Med. Plants Res. 4, 1577–1583.
- Tozzo, F.D., 2013. Modélisation de la distribution de six espèces d'arbres multi-usages en Afrique et évaluation de l'effet des changements climatiques changements climatiques. Master complémentaire en sciences et gestion de l'environnement dans les pays en développement. Communauté française de Belgique, p. 78.
- Vihogbe, R., Idhou, R., Vianou, A., Spies, P., Salako, V., Assogbadjo, A., Glèlè Kakai, R., 2021. Abundance and effects of climate change on geographical distribution of *monidia whitei* (hook. f.) skeels (apocynaceae) in the Dahomey gap (West Africa). Afr. J. Ecol. 59 (4), 924–933.
- Wang, W.C., Lo, N.J., Chang, W.I., Huang, K.Y., 2012. Modelling spatial distribution of a rare and endangered plant species (*Brainea insignis*) in central Taiwan. Int. Arch. Photogramm. Remote Sens. XXXIX-B7, 241–246.
- Watling, J.I., Brandt, L.A., Bucklin, D.N., Fujisaki, I., Mazzotti, F.J., Romañach, S.S., Speroterra, C., 2015. Performance metrics and variance partitioning reveal sources of uncertainty in species distribution models. Ecol. Model. 309, 48–59.
- Williams, B., Leung, G., Maiato, H., Wong, A., Li, Z.X., Williams, E.V., Kirkpatrick, C., Aquadro, C.F., Rieder, C.L., Goldberg, M.L., 2007. Mitch a rapidly evolving component of the Ndc80 kinetochore complex required for correct chromosome segregation in *Drosophila*. J. Cell Sci. 120 (20), 3522–3533.
- Yudaputra, A., Pujiastuti, I., Cropper Jr., W.P., 2019. Comparing six different species distribution models with several subsets of environmental variables: predicting the potential current distribution of zebra *Guettarda speciosa* in Indonesia. Biodiversitas 20, 2321–2328.