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Habitat range shift and prediction of the potential future distribution of *Ricinodendron heudelotii* (Baill.) Heckel in Benin (West Africa)

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ABSTRACT

Ricinodendron heudelotii (Baill.) Heckel is an important nutraceutical reservoir. Its Sustainable exploitation requires information on its potential distribution in the current context of rapid population growth and climate change threats. This study aimed to map the suitable areas for its domestication and conservation under current and future climate conditions in Benin. Occurrence data were recorded and combined with the environmental layers of two climatic scenarios (optimistic RCP 4.5 and pessimistic RCP 8.5) following the biodiversity modelling approach (biomod2). Currently, about four percent (5082 Km^2) of the country's area mainly located in the sub-humid and the humid zones were potentially suitable for *R. heudelotii* distribution. Under future climatic conditions the potentially suitable areas were mainly in the sub-humid zone, but almost all the highly suitable areas located in the humid zone will become medium suitable areas by the years 2055 and 2085 horizons. This study shows that, whatever the future climatic scenarios, *R. heudelotii* will substantially maintain the size of its range across the country. These findings allow undertaking anticipated actions to better adapt to the potential effects of climate change and to better guide policies for the conservation and development of forest resources.

1. Introduction

Climate change is widespread, constant, and intensifying, and will undoubtedly be the main driver of ecological change in the coming decades [1]. This is a defining issue of our time, as its consequences are global in terms of impact and scale. In its 2021 report,

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the Intergovernmental Panel on Climate Change (IPCC) concludes that most natural systems will be affected at different intensities [2]. Terrestrial ecosystems must adapt to it and, like the fauna, the flora also migrates to new suitable habitats capable of offering the minimum of ecological comforts to be able to fully maintain the balance of its life cycle (reproduction, growth, and survival), in most cases, to higher latitudes or altitudes [3]. The conclusions of the IPCC, based on the more than 29 000 observational data series, from 75 studies, stated that a significant number of ecosystems (more than 89%) would be disturbed [4]. The impacts of climate change (ranging from shifting weather patterns, to rising sea levels) on the physical and biological systems threaten severely food production and increase the risk of natural catastrophes [2]. In addition to these, there are anthropogenic consequences, including changes in the spatial distribution of species [5].

Ricinodendron heudelotii (Baill.) Heckel (Euphorbiaceae) is a wild oil plant (WOP) with numerous virtues [6] and one of the rare species cultivated for its fruits in Benin republic [7,8]. Its stem is particularly used for cultural purposes (Guèlèdè mask), and its kernel and oil contain significantly higher physico-chemical properties and fatty acid profiles (87% unsaturated fatty acids, 190 mg KOH/g saponification value, and 160 g I_2/100 g Iodine value) [9]. This provides it excellent anti-cancerogenic, anti-mutagenic and anti-inflammatory activities [10]. Unfortunately, its populations are dramatically declining under anthropogenic pressures (with less than one tree counted per hectare), because of the main types of uses (collection of fruits and wood) [11]. Adult individuals are subjected to debarking and cutting for the exploitation of their wood in the manufacture of the Guèlèdè mask and urban construction [11]. This demonstrates the need for urgent actions for its sustainable exploitation.

R. heudelotii is widespread across sub-humid and humid zones in Benin. To date, its stands are mainly wilds and found in forest ecosystems (gallery, deciduous, and secondary forests) of central and southern Benin [7,8,12,13]. Thus, the species is likely susceptible to climate change, as most natural forests which are the primary sources of these products have either been lost or seriously degraded [11]. Actions towards preserving the remaining populations and reinforcing the protection of the remaining areas for its conservation are very needful. The sustainable management of these ecosystems, in the context of climate change, involves knowing the potential range of the species, as well as identifying the factors that condition it and the expected changes likely to affect it. In particular, it is necessary to explore the range of environmental conditions that suit *R. heudelotii* and to model its potential distribution.

Species Distribution Modeling (SDM) represents an important predictive tool in conservation ecology [14]. SDM began with the creation of the bioclimatic variables (BIOCLIM) packages in 1984 [15]. It consists of constructing a function of environmental parameters that predicts the probability of the species' presence, using occurrence data of the species and the values of certain parameters, mainly environmental, at the areas of observation of the species [16]. Several methods to model the distribution of species have been developed and used to address the major issues of understanding, describing, and predicting the potential range of a species, and identifying the factors that determine its distribution [14,17–19]. These methods differ according to the type of response they take into account, the way of weighting the observations and of incorporating the interactions, and their predictive capacity [15,16], and represent a relevant tool for the management and conservation of the environment and biodiversity.

In this study, the package "biomod2" [20] with ensemble approach was chosen to develop a predictive model that delineates suitable areas for *R. heudelotii* in Benin. This includes the ability to model the species distribution with several techniques, and test models with a wide range of approaches to pool the results of different algorithms so that the result of the ensemble outperforms individual models. The combination of the algorithms stabilizes the model and allows to generate more justified and reliable predictive maps, by reducing uncertainties and bias compared to the single model [20].

This study was undertaken to map suitable areas for the conservation and domestication of *R. heudelotii* under future climate scenarios, to understand the climate change effects on its comprehensive spatial distribution. Specifically, it focused on: (i) assessing the present-day distribution of *R. heudelotii* in Benin, and (ii) forecasting the future distribution under different climate scenarios.

Fig. 1. Global distribution of *R. heudelotii*.

2. Methodology

2.1. Study area

The study was conducted through the ten phytodistricts [21] across the three climatic zones of Benin, located between 6° N and 12°50′ N and 1° E and 3°40’ E in West-Africa and covers 114 763 km^2. The annual rainfall varies between 900 and 1300 mm and is bimodal in the humid zone but tends to be unimodal in the sub-humid and semi-arid zones. The mean monthly temperatures oscillate between 24 and 31 °C [21]. Benin has several inland waters among which the most important are Pendjari in the North-West (380 km), Couffo in South-East (170 km), Ouémé in the Southern and Central part (450 km), Mono in the Western part (100 km), Mekrou (410 km), Alibori (338 km), and Sota (250 km) for Niger River, and Zou (150 km) for Oueme river. Four major soil types with characteristic vegetation are distinguished throughout Benin [22]: (1) ferralitic soils covered by semi-deciduous forest, (2) ferruginous soils covered by dry forest, woodland, and savannah, (3) vertisol covered by dry semi-deciduous forest, and (4) hydromorphic soils covered by swamp and riparian forests. Figs. 1 and 2 illustrate the global occurrence data distribution of *R. heudelotii*, and its distribution in the studied area respectively.

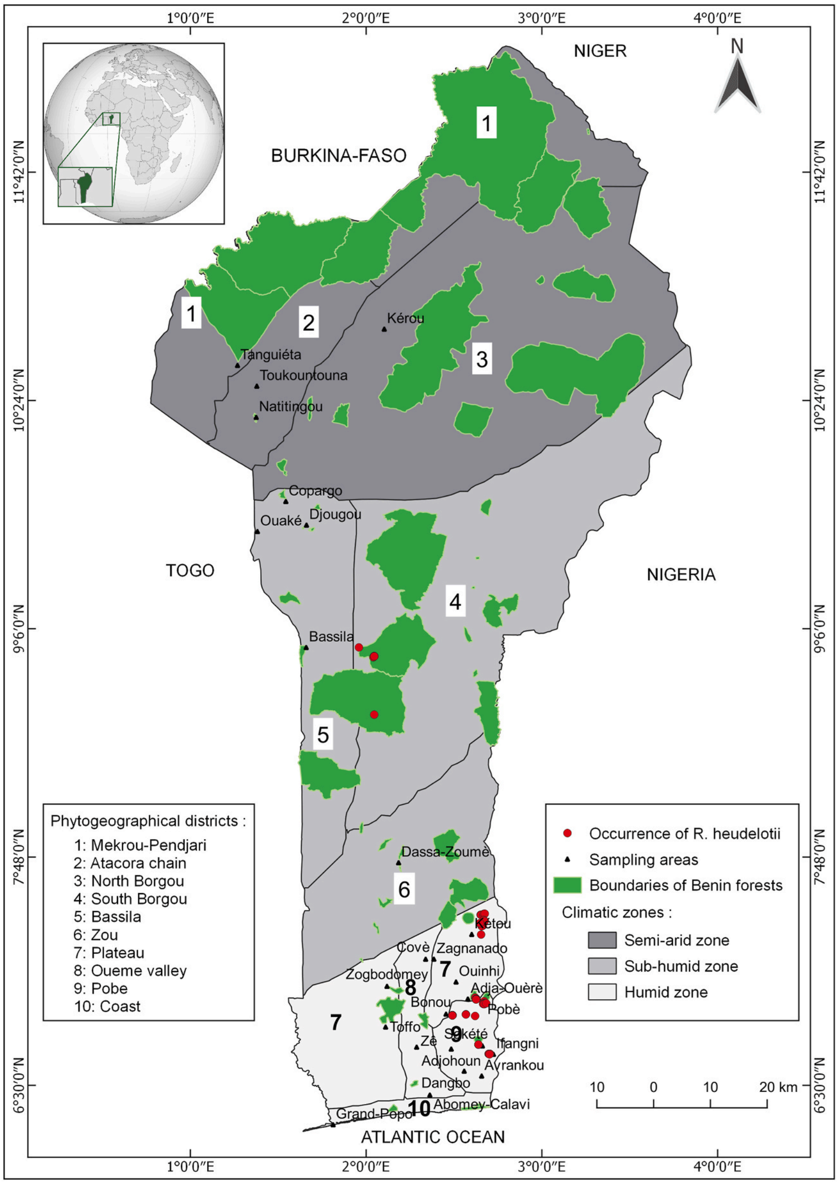

Fig. 2. Occurrence of *R. heudelotii* across its geographical distribution.

2.2. Sampling design

The natural habitats across protected areas (PA) and non-protected areas (nPA) of Benin were considered to assess the current and future suitable areas for *R. heudelotii*. *R. heudelotii* tree (Fig. 3) was naturally concentrated in the sub-humid and the humid zones in Benin [23]. Thus, the localities investigated are represented on the map (Fig. 2). Two perpendicular line transects (6 km length × 100 m width) were installed in each locality. A total of 54 transects were installed. They were arranged in the four directions (North-South and West-East) in each locality. Exceptionally, the transect was abandoned and another one was installed in the same locality in case of obstacles (houses, streams, etc.).

2.3. Data collection

Occurrence data (longitude and latitude) of presence points were collected on *R. heudelotii* trees, across its geographical distribution (130 occurrences). Additionally, all available occurrence data on the species were recorded (59 occurrences) and completed by available data on the online database Global Biodiversity Information Facility website (GBIF; www.gbif.org) to maximize the accuracy of modelling results by covering largely the region [24]. Prior to using the data for analysis, duplicate records and those with evident faults were removed, and a single occurrence per square kilometer or pixel was considered to reduce spatial autocorrelation using ArcGIS 10.4 [25] with SDMtoolbox 2.4 extension [26]. A total of 189 occurrence records were used for modelling (Fig. 2).

Environmental layers included data on climate, soils, elevation, land cover, and wetland. A total of 21 climatic data items relating to precipitation and temperature, for the present and the future, were retrieved with a resolution of 30 arcsec (1 km × 1 km) from the AfriClim database [27]. The climatic variables built under realistic Representative Concentration Pathways (RCP) 4.5 and 8.5 were used for projection in the future. RCP 4.5 is a realistic and optimistic climatic scenario (temperature is projected to rise above industrial level by at least 1.4 °C in West Africa by mid-21st century, with atmospheric CO_2 reaching 500 ppm), while RCP 8.5 is a realistic and pessimistic climatic scenario (temperature is projected to rise above industrial level by at least 2 °C in West Africa by mid-21st century, with atmospheric CO_2 reaching 550 ppm) [28]. Soil characteristics (www.isric.org) including bulk density ($kg.m^{-3}$), cation exchange capacity ($cmol.kg^{-1}$), clay content (%), organic carbon content ($g.kg^{-1}$), pH in H_2O, sand content (%) and silt content (%) were the parameters considered for six available horizons (0–5, 5–15, 15–30, 30–60, 60–100 and 100–200 cm), elevation and land cover data (www.globalmaps.github.io), and wetland distribution (www.cifor.org) were downloaded and adjusted at the same resolution (1 km × 1 km).

Fig. 3. *R. heudelotii* trees from Ketou District.

2.4. Data processing and model development process

Climatic and biophysical variables were projected to a similar projection system and subjected to a multicollinearity test (Variance Inflation Factor) using the packages “tidyverse” [29] and “usdm” [30]. Thus, we selected variables with low correlation coefficients ($r < |0.7|$) [31]. A total of 63 variables were removed due to multicollinearity, given the intrinsic ecological constraints to *R. heudelotii*, and the remaining three were used to train the algorithms: proportion of isothermality (Bio3), mean annual rainfall (Bio12), and soil sand content in percent for 22.5 cm depth (Sndppt_sd3) (Table 1). Variable importance was assessed using a function “get_variables_importance” in the package “biomod2” [20].

The package “biomod2” with ensemble approach [20] was used to develop a predictive model that delineates suitable areas for *R. heudelotii*. These are different modelling approaches designed to combine the results of different algorithms so that the overall result outperforms the individual models. General Boosted Models (GBM) [32], General Linear Models (GLM) [33], MAXimum ENTropy models (MAXENT.Phillips) [34], and Random Forest models (RF) [35] were the four algorithms out of the ten performed, used to develop the ensemble model because of their high accuracy. This step enables relatively simple models to be built for species distribution areas and the future state of biodiversity [36].

A pseudo-absence of the spore was generated with the Surface Range Envelope (SRE) model, as these models require both balanced present and absence records. The model was calibrated with 75% of occurrence data and the remaining points (25%) were used to test the model. To evaluate the performance of the model, the Area under the Relative Operating Characteristic Curve (a model is excellent if the AUC value is greater than or equal to 0.8), and the True Skill Statistic (a model is excellent if the TSS value is close to 1) [37] were used.

A gap analysis of suitable and priority habitats inside the protected areas network was performed by superimposing the distribution maps issued by modelling to the map of the network of protected areas of Benin using QGIS 2.18.25 software. The current and future geographic distribution of suitable habitats of *R. heudelotii* based on the logistic probability of occurrence (P) were also mapped. For this purpose, three habitat classes were defined: i-low suitable ($P \leq 0.3$), ii-medium suitable ($0.3 > P \leq 0.5$), and iii-high suitable areas ($P > 0.5$) [38,39]. The proportion of loss, stable, or gain areas was calculated and the trend was estimated. All analyses were performed using R-4.0.5 software [40].

3. Results

3.1. Model performance

Globally, the four algorithms showed good predictive powers (AUC = 0.867–0.991 and TSS = 0.686–0.949), and RF and GBM models were the best performing model algorithms with the highest values of AUC (0.991 and 0.984) and TSS (0.949 and 0.923) respectively whereas GLM models showed the lowest values of AUC (0.867) and TSS (0.686). Indeed, the ensemble model performance was excellent (AUC = 0.994 and TSS = 0.925), and correctly predicted 96.28% of *R. heudelotii* presences (sensitivity) and 96.18% of its absences (specificity). These values indicate the excellent performance of the ensemble model in predicting the spatio-temporal dynamics of *R. heudelotii* habitats in the study area (Fig. 4 and Table 2).

3.2. The relative importance of predictors

The relative contributions of isothermality (Bio3) and mean annual rainfall (Bio12) were high (40% and 34.01% respectively), showing their high influence on the discrimination of the habitats of *R. heudelotii.* In addition, the contribution of soil sand content in percent for 22.5 cm depth (Sndppt_sd3) is also important (25.99%). This indicates that the climatic and soil variables (Bio3, Bio12, and Sndppt_sd3) were the most important predictors of the habitats of *R. heudelotii* (Fig. 5).

3.3. Dynamics of the current and future distribution areas of R. heudelotii

The current and future distribution areas of *R. heudelotii* at both the country level and the protected areas revealed critical changes (Fig. 6a–e). Currently, the potential highly suitable areas for its distribution were confirmed in the sub-humid and humid zones in both protected areas and non-protected areas, mainly located in the North-East of the phytodistrict of Pobe (including Adja-Ouèrè, Adjohoun, Bonou, Ifangni, Pobè, and Sakété districts), center-North of the phytodistrict of Plateau (including Aplahoué, Kétou, Klouékanmey, Toffo, Za-Kpota, and Zogbodomey districts), South of the phytodistrict of Oueme valley in Abomey-Calavi district, and South and North-East of the phytodistrict of Zou in Covè, Djidja and Savè districts. The moderately suitable areas were mainly found in the phytodistrict of Bassila and South-Borgou, while the semi-arid zone represented the lowly suitable area (Fig. 6a). However, there

Table 1
Variance Inflation Factor of predictor variables.

Variable	Variance Inflation Factor (VIF)
Bio3	1.516
Bio12	1.372
Sndppt_sd3	1.065

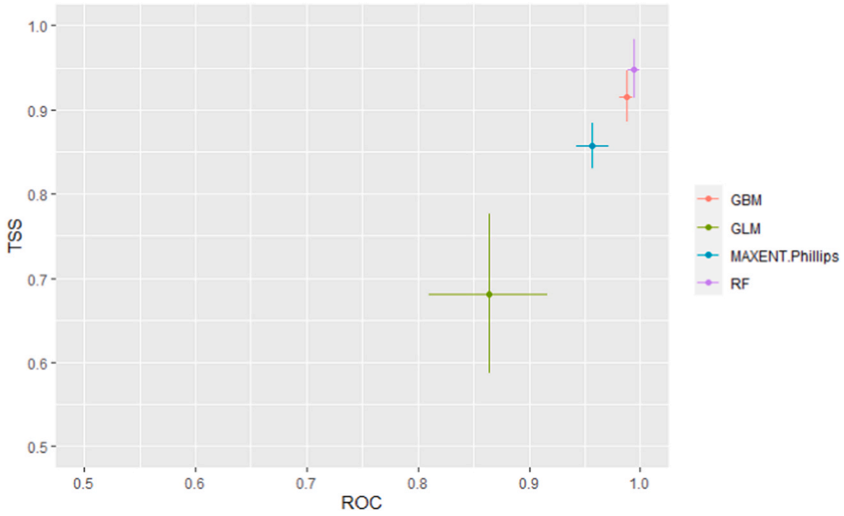

Fig. 4. Model performance comparison of the four model algorithms by the Area under the ROC Curve (AUC) and the True Skill Statistic (TSS) values. The points represent the mean estimates and the solid lines represent the 95% confidence intervals. GBM = General Boosted Models, GLM = General Linear Models, MAXENT. Phillips = MAXimum ENTropy models and RF = Random Forest models.

Table 2
Performance of ensemble model.

	Performance	Testing Data	Sensitivity (%)	Specificity (%)
TSS	0.925	512	96.28	96.18
AUC	0.994	497	96.81	95.78

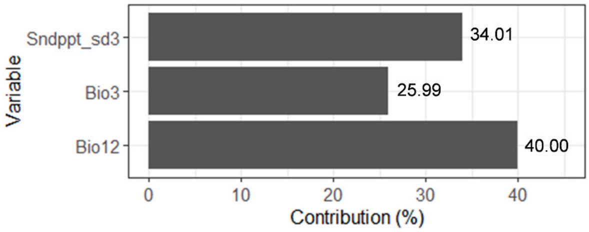

Fig. 5. Contribution of predictor variables to the ensemble model. Bio3 = Isothermality; Bio12 = Mean annual rainfall; Sndppt_sd3 = Soil sand content in percent for 22.5 cm depth.

was a significant influence of the future climatic scenarios (RCP 4.5 and RCP 8.5) on the distribution of the suitable areas of the species whether by years 2055 (Fig. 6b and c) or 2085 (Fig. 6d and e). Particularly, it was shown that almost all the highly suitable areas located in the humid zone will become moderately suitable areas for *R. heudelotii* distribution under future climatic scenarios. The potential future highly suitable areas were mainly located in the South-West of the sub-humid zone in both protected areas and non-protected areas, across Bantè, Dassa-zoumè, and Savalou districts (Fig. 6b–d). In addition, results showed the high sensitivity of the species to climate change within 30 years (Fig. 6b and c).

Results showed that the potential suitable areas for *R. heudelotii* distribution across Benin protected areas and non-protected areas were 5082 Km^2 (4.43% of the country's area). Accordingly, by the year 2055, the projections estimated the loss of the suitable areas to 3.30% of the country's area (3791 Km^2) for RCP 4.5 scenario and 3.46% (3970 Km^2) for the RCP 8.5. But, only 1.13% (RCP 4.5) and 0.97% (RCP 8.5) of the areas currently occupied, were predicted to remain occupied into the future. However, areas not occupied but predicted to be into the future were estimated at 4.44% (RCP 4.5) and 4.15% (RCP 8.5), showing that whatever the future climatic scenarios *R. heudelotii* will substantially maintain the size of its range across the country (Table 3). Trends were proportionally similar between time periods (by 2055 and 2085-time horizon) (Table 3).

4. Discussion

This study mapped the potential distribution of *R. heudelotii* under present-day and future climate conditions in Benin.

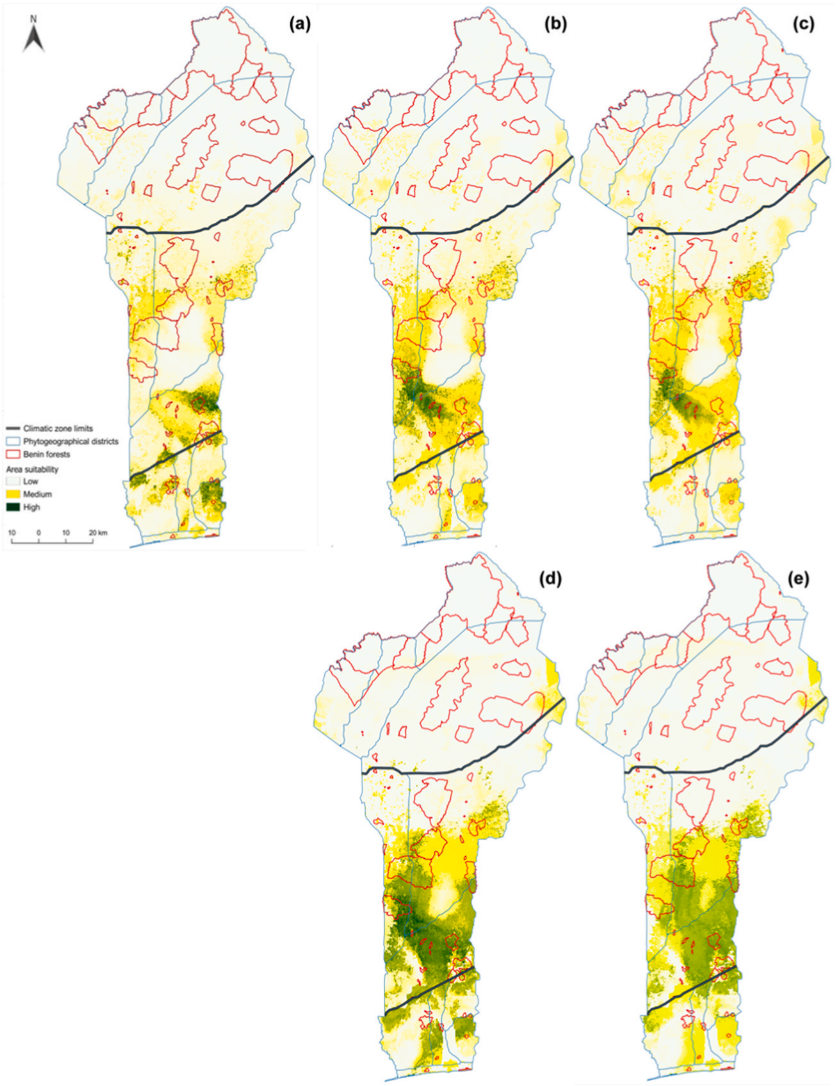

Fig. 6. Map of potential present-day distribution (a) and future suitable areas under RCP4.5 (b, d) and RCP8.5 (c, e) of *R. heudelotii* across Benin and protected areas network by the years 2055 and 2085 horizon respectively.

Table 3
Proportion of habitat loss, gain and stability under RCP4.5 and RCP8.5 across Benin by the years 2055 and 2085 horizon.

	Loss		Stable0		Stable1		Gain	
	Area (Km^2)	Proportion (%)	Area (Km^2)	Proportion (%)	Area (Km^2)	Proportion (%)	Area (Km^2)	Proportion (%)
Year-2055 horizon								
RCP4.5	3791	3.30	104 581	91.13	1291	1.13	5100	4.44
RCP8.5	3970	3.46	104 915	91.42	1112	0.97	4766	4.15
Year-2085 horizon								
RCP4.5	2057	1.79	101 002	88.01	2677	2.33	9027	7.87
RCP8.5	2979	2.60	103 973	90.60	1755	1.53	6056	5.28

Loss: areas currently occupied by *R. heudelotii* to be lost. Stable0: areas not currently occupied and not predicted to be. Stable1: areas currently occupied, and predicted to remain occupied into the future. Gain: areas not occupied but predicted to be into the future.

The combination of the four selected algorithms was excellent in predicting the spatio-temporal dynamics of *R. heudelotii* habitats. This finding confirms that the ensemble model stabilizes the four selected and allows to generate more justified and reliable predictive maps, by reducing uncertainties and bias compared to the single model [20]. The results indicated that the precipitation and temperature added to soil layers influenced significantly the prediction of the spatio-temporal dynamics of the suitable habitats of

R. heudelotii. The isothermality and mean annual rainfall were the most important climatic variables with a contribution greater than 74% for the modelling. It can however be deduced that these predictors discriminated highly the habitats of *R. heudelotii*, and confirms its preference for humid habitats benefiting from an annual rainfall greater than 1000 mm and fairly modest temperature [41]. Such results trends were reported for *Macrotyloma geocarpum* (Harms) Maréchal and Baudet [42], *Cochlospermum planchonii* Hook. f [43]. and *Borassus aethiopum* Mart [44]. The contribution of soil sand content in percent for 22.5 cm depth, known for its physiological action, was also important (25.99%) to predict the habitats of *R. heudelotii*. The species is mainly found on medium-textured, freely draining, or acidic soils from lower Senegal to Tanzania [45,46]. In particular, both ferrallitic soils and vertisol were the main soil types suitable for the distribution of the species (i.e., humid and sub-humid zones in Benin). These results confirm the fact that it is the direct parameters, such as temperature, precipitation, and soil, which most affect the distribution of species when the modelling concerns a large territory [47].

Climate is getting more significant in the study of plant population dynamics. Indeed, the current and future distribution areas of *R. heudelotii* were revealed critical. Currently, the potential suitable areas for its distribution were confirmed in the sub-humid and humid zones in both protected areas and non-protected areas, located in the North-East of the phytodistrict of Pobe, center-North of the phytodistrict of Plateau, South of the phytodistrict of Oueme valley, North-East of the phytodistrict of Zou, and center of the phytodistrict of Bassila and South-Borgou. While the semi-arid zone represented the lowly suitable area for its distribution. These results confirm that *R. heudelotii* is a characteristic species of the best-watered forest ecosystems of the country (i.e., gallery, deciduous, and secondary forests) and corroborate the previous studies in Refs. [8,12,13]. However, there was a significant influence of the future climatic scenarios (RCP 4.5 and RCP 8.5) on the distribution of suitable areas for the species. We found that its future suitable areas will probably migrate from its current areas located in the humid zone to the South-West of the sub-humid zone in both protected areas and non-protected areas. This indicates that the rising of temperature changes the range of many species, and will, unfortunately, lead to changes in the identity and abundance of plant species over the coming decades. This trend requires species to develop the capacity to adapt and tolerate high temperatures. Unlike other plants for which the situation seems to benefit from, such as *Balanites aegyptiaca* (L.) Delile and *Cochlospermum planchonii* [43], from a strong thermal preference, *R. heudelotii* will see its abundance decline and will lose ground like *Borassus aethiopum* [44,48] which are disappearing in places where they were present. We will probably see a change in the face of the flora of the country in the coming years. Indeed, sites with significant temperature variations will undergo a strong replacement of species over time, and the least heat-tolerant species giving way to the more tolerant. In general, as the climate warms, ranges migrate to higher latitudes or altitudes [3]. We can therefore clearly state that global warming is directly responsible for these rearrangements of wild flora. Accordingly, the loss area in the humid zone was considerably greater, indicating a significant reduction in the distribution area, therefore tends to move north, with consequences for humans. Faced with this phenomenon, the species can sometimes survive extinction by finding refuge in the few habitats with a favorable microclimate that remain. Otherwise, only human-assisted migration, including domestication/cultivation can save the species. Bringing the species out of the forest ecosystems to farmlands or home gardens will necessitate studying the appropriate ex-situ conditions [41]. Such studies would include the development of the technical routes for the seedlings' culture, the specific light conditions, nutrient requirements, storage conditions of seeds, and the use of proper vegetative propagation techniques.

The integrated approach of modelling and GIS used in this study is effective in predicting suitable areas for conservation and planning priority management actions [49,50]. This approach helps to refine the modelling process through powerful statistical approaches [50] to define the optimal conservation and domestication strategies for plant species. However, there are some limitations related to the models used, including the lack of ecological interaction parameters, the species-specific dispersal and dissemination factors, the plasticity of physiological limits, and anthropogenic pressures [51]. The predictive capacity of SDMs is generally limited by the number of predictors taken into account during their development [52]. For example, the addition of a dispersion filter is essential to correctly predict the presence of a species in an environment which seems favorable to it, but which it cannot colonize [53]. Moreover, SDMs absolutely do not consider the constraints due to the carrying capacity of a given environment, which determine the maximum number of individuals of the same species that can co-occur [54]. Finally, biotic interactions are not considered during spatial and temporal extrapolation, and species whose presence is predicted in a given environment can be excluded, through competitive exclusion for example [55]. Consequently, this study was only interested in the assessing the potential habitat suitability dynamics of the species, and in no way predicts its future presence.

Despite these, it should be noted that the findings of this study are important in the current context of climate change and represent a useful management tool for the sustainable conservation of *R. heudelotii* in Benin. Thus, only the fundamental concept of a niche representing the ranges of conditions and resources existing in a given area and potentially exploitable by a species was used, joining the previous study in Ref. [56]. Therefore, the primary issue here is its *in-situ* and *ex-situ* conservation in order to maintain the genetic potential available for sustainable exploitation.

5. Conclusion

The findings of this study showed that almost all the potential high suitable area located in the humid zone will become moderately suitable areas. However, the sub-humid zone will remain the potential high suitable areas for *R. heudelotii* conservation and domestication across both protected areas and non-protected areas by the years 2055 and 2085 in Benin. This species will migrate following its ecological requirements which are mainly linked to the isothermality (Bio3), mean annual rainfall (Bio12), and the soil sand content in percent for 22.5 cm depth (Sndppt_sd3). These findings are of public interest and decisive in the definition of priority actions for the development of economic activities linked to this species.

Author contribution statement

Guillaume Hounsou-Dindin; Rodrigue Idohou: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Paterne Agre; Achille Hounkpèvi: Contributed reagents, materials, analysis tools or data; Wrote the paper.

Aristide Cossi Adomou; Achille Ephrem Assogbadjo; Romain Glèlè Kakaï: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Data availability statement

The datasets generated during and/or analyzed during the present study are available from the authors upon request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:Guillaume Hounsou-Dindin reports financial support was provided by University of Abomey-Calavi. Guillaume Hounsou-Dindin reports financial support was provided by African-German Network of Excellence in Science.

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