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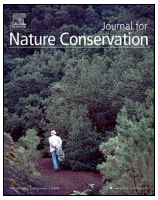

Climate change aggravates anthropogenic threats of the endangered savanna tree *Pterocarpus erinaceus* (Fabaceae) in Burkina Faso

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ABSTRACT

Species distribution modelling is gaining popularity due to significant habitat shifts in many plant and animal species caused by climate change. This issue is particularly pressing for species that provide significant ecosystem goods and services. A prominent case is the valuable African rosewood tree (*Pterocarpus erinaceus*) that is threatened in sub-Saharan Africa, while its present distribution, habitat requirements and the impact of climate change are not fully understood. This native species naturally occurs in various savanna types, but anthropogenic interventions have considerably reduced its natural populations in the past decades. In this study, ensemble modelling was used to predict the current and future distribution potential of the species in Burkina Faso. Fifty-four environmental variables were selected to describe its distribution in the years 2050 and 2070 based on the greenhouse gas concentration trajectories RCP4.5 and 8.5, and the general circulation models CNRM-CM5 and HadGEM2-CC. A network of protected areas in Burkina Faso was also included to assess how many of the suitable habitats may contribute to the conservation of the species. The factors isothermality (31%), minimum temperature of coldest month (31%), pH in H_2O at horizon 0–5 cm (11%), silt content at horizon 60–100 cm (9.2%) and precipitation of warmest quarter (8%) were the most influential distribution drivers for the species. Under current climate conditions, potentially highly suitable habitats cover an area of 129,695 km^2, i.e., 47% of Burkina Faso. The projected distribution under RCP4.5 and 8.5 showed that this area will decrease, and that the decline of the species will be pronounced. The two models used in this study, forecast a habitat loss of up to 61% for *P. erinaceus*. Hence, development and implementation of a conservation programme are required to save the species in its native range. This study will help land managers prioritise areas for protection of the species, and avoid introducing it to inappropriate areas unless suitable conditions are artificially created through the management options applied.

1. Introduction

Understanding species requirements and their relationships with environmental gradients is a crucial issue in ecological research and conservation of ecosystems. This is particularly important for mitigating and adapting to climate change. According to the latest report released by the IPCC (6th Assessment), it is unequivocal that human influence has warmed the atmosphere, ocean and land (Ting and Ying 2021), and the

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average temperature has increased by 0.8 °C since the year 1800, as caused by greenhouse gas emissions. Climate change is also expected to change the frequency and distribution of precipitation which will affect plant growth. Changed climatic factors are also known to significantly impact plant recruitment, phenology, and soil properties (Nord and Lynch 2009). Pursuing the objective to reduce adverse effects of climate change on ecosystems and their functioning, conservation strategies largely depend on modelling species distribution to identify suitable habitats where important species can exist. This is particularly urgent in semi-arid regions that are more prone to negative effects of climate change. Several other environmental factors can influence the distribution of tree species (Dimobe et al. 2018, 2020). Therefore, to effectively model distributions of such species, it is important to distinguish natural factors from anthropogenic factors (e.g., climate change, pollution, unsustainable land use) by using reliable models capable of predicting future species distribution scenarios.

In the past 20 years, the use of statistical tools such as Species Distribution Models (SDM) or Ecological Niche Models (ENM) has allowed researchers to make great advances in the field, with hundreds of scientific publications (Guisan et al. 2017). SDMs have been shown to be an important tool for predicting geographic distribution by relating species distribution to environmental variables (Miller 2010, Dimobe et al. 2020, Lompo et al. 2021). Applications include conservation planning, potential invasion ranges or temporal predictions. SDMs have been successfully applied to a variety of terrestrial and marine organisms (Adjonou et al. 2020) The accuracy of SDM predictions varies from algorithm to algorithm, although the Maxent algorithm is most commonly used (Qiao et al. 2015, Monsimet et al. 2020). This variation in the accuracy can be mitigated with ensemble models, which combine algorithms and produce more consensual predictions (Araújo and New 2007). Of course, input data also affect predictions, and while most SDMs use only climatic variables, the inclusion of other variables such as land use could improve predictions (Monsimet et al. 2020).

Here, we aim to understand the potential effects of climate change on the regional species distribution of the sub-Saharan tree *Pterocarpus erinaceus* that is considered a widespread legume with high socio-economic, cultural and ecological values (Alaba et al. 2020). Its utilisation as fodder (leaves), medicine (bark, roots, leaves), timber and fuelwood has substantially increased in the past decades, with negative effects on its natural populations (Banla et al. 2019). Thus, its populations are now ageing, with many individuals negatively affected by livestock and chronic pruning as well as poor regeneration. A marked decline of its natural populations has been reported in several countries (Adjonou et al. 2010, Akpona et al. 2017, Banla et al. 2019, Houehanou et al. 2013, Nacoulma et al. 2011, Ouédraogo et al. 2006, Rabiou et al. 2019). Due to its overexploitation of its wood, the species is considered globally endangered (CITES 2018, IUCN 2018) and has been recently registered within Annex II of the CITES (CITES 2018).

In Western Africa, the cultural importance of *P. erinaceus*, its multiple uses, and persistent anthropogenic pressure have put the species high on the research agenda (Akpona et al. 2017, Banla et al. 2019, Glèlè Kakaï et al. 2009, Nacoulma et al. 2011, Ouédraogo et al. 2006, Rabiou et al. 2019). The species provides a timber much sought after by Burkinabè artisans for making musical instruments such as the balafon and the djembe (Ouédraogo et al. 2006; Thiombiano et al. 2012). Individuals in fields, fallow land or classified forests are also heavily pruned to feed livestock. The leaves are sold as fodder in urban centres in Burkina Faso, Niger and Mali (Ayantunde et al. 2014, Bayala et al. 2014). Moreover, there are many uses in traditional medicine (Ouédraogo et al. 2006a, Arbain et al. 2021). The resulting strong pressure, combined with climate change, low seed production and slow growth, makes this species one of the most threatened trees in Burkina Faso. Due to habitat loss and human activities, the population of *P. erinaceus* has sharply declined over the past decades in Western Africa and especially in Burkina Faso (Adjonou et al. 2020). It is, in fact, locally extinct in several regions of Burkina Faso and Niger (Sokpon et al. 2006). The species is classified as critically endangered by the Burkinabe government, included in Appendix I listed species of the Convention on International Trade in Endangered Species of wild fauna and flora (CITIES) and listed as “CR” in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. The genus *Pterocarpus* comprises numerous species, which are economically important (e.g., timber) and which are becoming increasingly endangered as is the case with Mukula (*P. tinctorius*) in Central and Southern Africa. In addition to local anthropogenic exploitation, climate change may have a significant effect on the potential range of the species (Busby et al. 2012) and can be considered as an additional threat (Adjonou et al. 2020). However, without knowing the climatic preferences and potential geographical distribution of the species, it is difficult to develop a management strategy and practical measures for conservation and cultivation. Therefore, assessing whether climate change will affect the regional suitability of habitats of this species is worth investigating because of its economic and ecological values. Since the ecological requirements of *P. erinaceus* have not been sufficiently investigated so far (Adjonou et al. 2020), little is known about which areas should be prioritized for afforestation using *P. erinaceus*, considering climate change.

Thus, we modelled the potential current and future distribution of the species using Burkina Faso as a representative study country within its range. This information is important to understand whether potential connectivity between patches of occurrence is insufficient for gene flow between the remaining populations of *P. erinaceus*. We believe that by describing future climatically suitable areas for the species, we could strengthen conservation efforts, to create ecological corridors by identifying climatic refuge areas and promoting creation and maintenance of new or existing protected areas. The results will allow researchers to identify suitable future habitats, and help, manage and cultivate the species.

2. Material and method

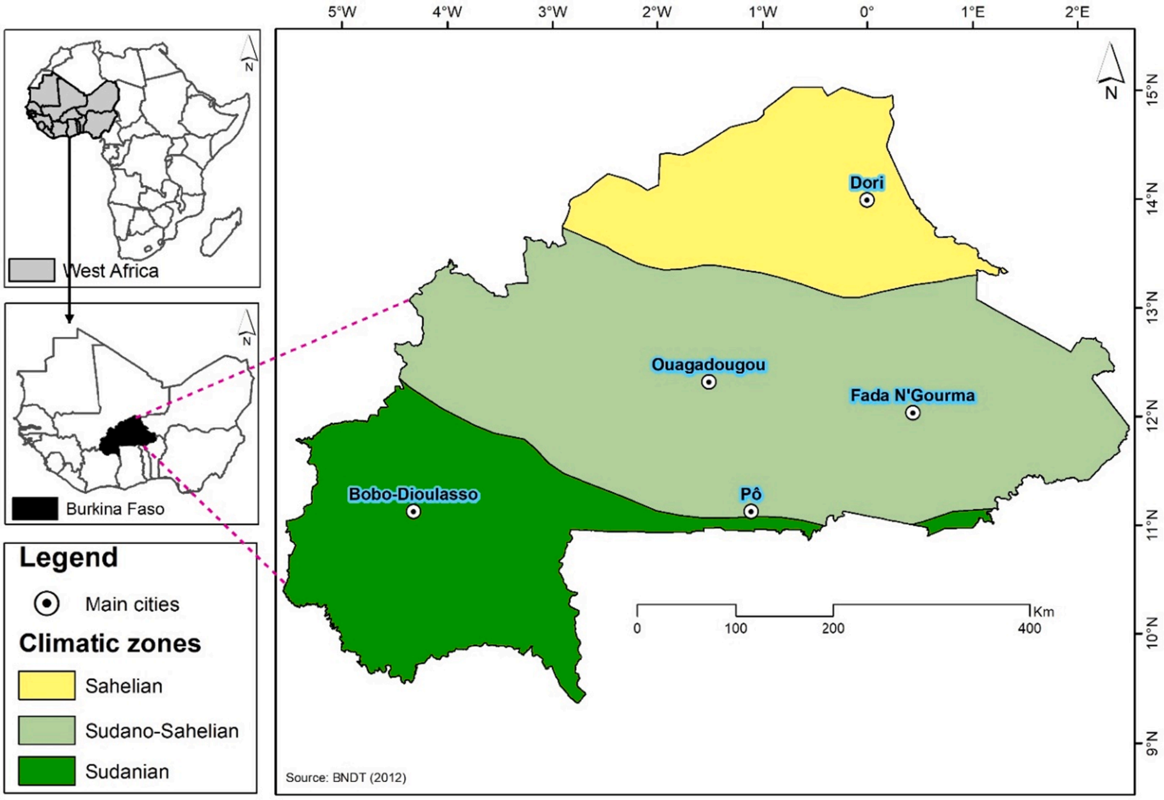
2.1. Study area

The study was conducted in Burkina Faso, a landlocked country in West Africa (Fig. 1). The country covers an area of 274,200 km^2 between 9 and 15°N and 6°W–3°E and is inhabited by well over 17 million people (INSD 2007). Most of the Burkinabe population (77.3 %) lives in rural areas and is therefore dependent on multipurpose trees. Biogeographically, the country extends from the Sahelian zone in the North to the Sudanian zone in the South (Schmidt et al. 2005). Located between sub-arid and sub-humid zones, Burkina Faso shows variable environmental conditions where natural resources are distributed along a climate gradient, while being locally mediated by geological and soil properties (Thiombiano and Kampmann 2010). Based on the Köppen-Geiger climate classification, Burkina Faso covers a broad bioclimatic gradient from a tropical savanna climate (ca.1000 mm year^{-1}) to an arid climate (ca. 300 mm year^{-1}) (Heubes et al. 2013).

The country’s climate leads to a correspondingly broad gradient in plant diversity and composition of taxonomic and functional groups. Plant diversity is high in the South and decreases continuously towards the North (Schmidt et al. 2005, 2011). In Burkina Faso, shifting cultivation with fallows combined with the deliberate retention of specific trees, such as the shea butter tree (*Vitellaria paradoxa*), create species-rich agroforestry systems (Augusseau et al. 2006).

2.2. Study species and occurrence records

P. erinaceus Poir. called ’Vène’ or ’Palissandre du Sénégal’ (in French), ’African rosewood’ or ’barkwood’ (in English), ’Bu natombu’ (in Gulmancema), ’Balan yiri’ (in Dioula), ’Noeka’ (in Mooré), and ’Bani’ or ’Banuhi’ (in Fulfulde), belongs to the Fabaceae (subfamily Faboideae; habitus in Fig. S1). It reaches 12–15 m in height and 5–90 cm in diameter at breast height (DBH). The species is distributed in Africa



Source: BNDT (2012)

Fig. 1. Location of the study area in Burkina Faso.

from Senegal to Cameroon and the Central African Republic. In Burkina Faso, the species mainly has a Sudanian distribution but is also encountered in the Sahelian zone (Arbonnier 2002, Nacoulma 2012, Ouédraogo et al. 2006). The species is found in dry Sudano-Guinean forests and savannas up to 400 m altitude, in areas with an annual rainfall of 700–1800 mm year^{-1}, a dry season of 4–6 months and an average annual temperature of 19–32 °C. It occurs on all soil types, but prefers light–medium acid to neutral, freely draining soils. It can survive annual bush fires.

2.3. Distribution data and environmental variables

Occurrence data of *P. erinaceus* were gathered from extensive field surveys in Burkina Faso from January 2014 to June 2021 and from Global Biodiversity Information Facility (GBIF, https://www.gbif.org, https://doi.org/10.15468/dl.n6nsvl). Our raw dataset initially counted 2141 occurrence records. After discarding erroneous and duplicate records, we selected only one occurrence point in each model grid to reduce the spatial autocorrelation of presence records (i.e., more than one presence record in one environmental grid cell with a 30 arc-second spatial resolution, ca. 1 km^2 at the equator) through a spatial thinning method provided by Boria et al. (2014), and 820 occurrence datasets finally remained for model construction (Fig. S2).

The spatial extent of analysis was 5°N to 30°N and 18°W to 15°E. This latter includes the entire latitudinal distribution of *P. erinaceus* and a large part of its longitudinal distribution, an important means of minimizing bias in model projections (Barbet-Massin et al. 2010). A total of 54 environmental variables were selected to be the candidate-predicting variables for the distribution of suitable habitats according to other SDM studies (Guidigan et al. 2018, Dimobe et al. 2020) and the biological relevance to distribution. Nineteen bioclimatic variables representing current and future climate conditions were downloaded from CHELSA (Climatologies at High resolution for the Earth's Land Surface Areas, https://www.chelsa-climate.org), a database that provides climatic data derived from monthly temperature and precipitation collected from weather stations around the world, and interpolated onto a surface of a 1-km^2 spatial resolution (Karger et al. 2017). Current distributions were based on mean climatology (1973–2013). Three terrain variables, i.e., slope, aspect, and elevation, were extracted from the 30-m resolution Shuttle Radar Topographic Mission (SRTM) Digital Elevation Model (DEM). The terrain variables were computed using the System for Automated Geoscientific Analysis (SAGA) software.

As soil provides physical environmental support to plant species and remains an important factor for the geographic distribution of plant species not only in the tropics (Linder et al. 2005), six soil variables were also obtained with 1-km^2 resolution from the Harmonized World Soil Database, version 1.2 (FAO/IIASA/ISRIC/ISSCAS/JRC 2012). They include cation exchange capacity (Cec, cmol/kg) at different horizons: 0–5 cm (Cec1), 5–15 cm (Cec2), 15–30 cm (Cec3), 30–60 cm (Cec4), 60–100 cm (Cec5); clay content (Clay, %) at different horizons: 0–5 cm (Clay1), 5–15 cm (Clay2), 15–30 cm (Clay3), 30–60 cm (Clay4), 60–100 cm (Clay5); soil organic carbon content (SOC, g/kg) at different horizons: 0–5 cm (SOC1), 5–15 cm (SOC2), 15–30 cm (SOC3), 30–60 cm (SOC4), 60–100 cm (SOC5); pH in H_2O (pH) at different horizons: 0–5 cm (pH1), 5–15 cm (pH2), 15–30 cm (pH3), 30–60 cm (pH4), 60–100 cm (pH5); sand content (Sand, %) at different horizons: 0–5 cm (Sand1), 5–15 cm (Sand2), 15–30 cm (Sand3), 30–60 cm (Sand4), 60–100 cm (Sand5); and silt content (Silt, %) at different horizons: 0–5 cm (Silt1), 5–15 cm (Silt2), 15–30 cm (Silt3), 30–60 cm (Silt4), 60–100 cm (Silt5). Furthermore, Normalised Difference Vegetation Index (NDVI) and Human Footprint Index (HFI) were used. The HFI cumulates different proxies of human pressure on the environment, such as the number of built environments, croplands, pasture lands, population density, nightlights, railways, major roadways and navigable waterways (Venter et al. 2016). We used MODIS data for NDVI (MOD13C2, Didan 2015).

The terrain variables were resampled at 1-km^2 resolution using the bilinear interpolation method. The environmental variables were then clipped to fit the West African ecoregion through R statistical software using the package '*raster*', '*rgdal*' and '*sp*'. These variables were tested by Pearson correlation coefficient and principal component analyses.

For reducing the uncertainty in model prediction, we applied two different global climate models (GCMs): CNRM-CM5 and HadGEM2-CC which are widely used in West Africa. Climate change scenarios were averaged for two 30-year periods: 2040–2069 ('2050 s'), and 2070–2099 ('2070 s'). Each GCM was tested under future greenhouse gas concentration trajectories, called Representative Concentration Pathways (RCPs). Here, to assess the potential impacts of climate change on the distribution of the species in Burkina Faso, we considered two RCPs for climate change, namely the RCP 4.5 and RCP 8.5. The RCP 4.5 reflects a scenario where temperatures are predicted to increase by approximately 2–3 °C as global average by the end of the 21st century, while under a pessimistic situation, such as RCP 8.5, temperatures will continue to increase even beyond 2100, reaching a level of around 4.8 °C compared with pre-industrial conditions, or 4 °C relative to 1986–2005.

To limit multicollinearity effects among the 54 environmental variables, we evaluated pairwise Pearson's correlations among predictor variables and selected only variables with $r < |0.7|$, selecting the ones with higher biological importance. We retained twelve variables (Fig. 3), i.e., isothermality (BIO3), minimum temperature of the coldest month (BIO6), mean temperature of the wettest quarter (BIO8), mean temperature of the driest quarter (BIO9), precipitation of the wettest month (BIO13), precipitation of warmest quarter (BIO18), cation exchange capacity at horizon 0–5 cm (Cec1), clay content at horizon 5–10 cm (Clay2), human footprint index (HFI), soil organic carbon content at horizon 60–100 cm (SOC 5), pH in H_2O at horizon 0–5 cm (pH1) and silt content at horizon 60–100 cm (Silt 5).

2.4. Species distribution modelling and evaluation

All analyses were performed using the R language for statistical computing (R Core Team 2020). Modelling was conducted using the '*sdm*' package (Naimi and Araújo 2016). Five algorithms were run: generalized additive models (GAM), multivariate adaptive regression splines (MARS), Support Vector Machine (SVM), random forest (RF), based on classification trees (Breiman 2001) and maximum entropy (MaxEnt). These algorithms have been frequently used in SDMs to develop ensemble models. The default implementations in the '*sdm*' package were used (Naimi and Araújo 2016). The data were presence-only, and pseudo-absence data were generated using the default settings of the '*sdm*' package (see Naimi and Araújo 2016) by randomly sampling 1000 locations for the species across the study area. We combined the outputs of the algorithms following the ensemble forecasting approach (Araújo and New 2007). Ensemble forecasting is a method to reduce uncertainty in species distribution models (SDMs), balancing the accuracy and robustness of SDM models via committee averaging (Araújo and New 2007).

We evaluated the predictive performance of the models using repeated split-sample tests: we split the data repeatedly into 70 % training and 30 % test data. Model parametrization was conducted with the training data, and resulting models were used to predict the test data. To avoid bias from splitting the data, each algorithm was run ten times, totalizing 50 model runs. We built the consensus models with all of the data available since removing presence information adversely affects the model projections (Araújo et al. 2005).

The ensemble modelling performance was assessed using (i) a threshold-independent statistic – the area under the curve (AUC) (Fielding and Bell 1997), which calculates the model's probability to rank a randomly chosen species presence site higher than a randomly chosen absence site, and (ii) a threshold-dependent statistic – the true skills statistic (TSS) (Allouche et al. 2006). TSS varies from −1 to +1, where +1 indicates perfect agreement between predictions and observations and values of 0 or less indicate agreement not being better than random classification (Landis and Koch 1977). AUC varies from 0 to 1, and an AUC value close to 0.5 indicates that the model did not perform better than random. In contrast, a value close to 1 indicates perfect and more accurate prediction (Thuiller et al. 2009). Using the committee-averaged method, algorithms with a TSS score greater than 0.6 and an AUC score greater than 0.8 were selected for the development of ensemble models.

The probabilistic output was converted to presence/absence using the mean of the predicted probabilities of species occurrences as the threshold to determine the species range. The reasoning for this threshold is the fact that it maximizes the agreement between observed and predicted distributions. For the habitat suitability class maps, we categorized the final logistic output into the following classes: (i) lowly suitable (0.00–0.46), (ii) moderately suitable (0.46–0.70), and (iii) highly suitable (0.70–1.00) using the spatial analysis toolset in ArcGIS® (ArcMap 10.5) software by Esri.

To assess the effectiveness of protected areas to conserve the species, we first overlapped current and future habitat suitability maps within the protected area polygons. Second, we computed the area (in km^2) colonized by the species within the protected areas using the spatial analysis tools in ArcGIS. Third, we calculated the percentages of potential habitat suitability within protected areas.

3. Results

3.1. Model performance

All model algorithms met the guideline of mean AUC values greater than 0.8 and mean TSS values greater than 0.6 (Fig. S3). Of the five algorithms used, the RF algorithm outperformed the rest. The ensemble model also showed good accuracy with a mean AUC of 0.853 and TSS of 0.674, indicating the high capability of the models used in accurately modelling the distribution of *P. erinaceus*. This result shows that the five algorithms selected for the modelling could be used to predict the spatial distribution of the species under current and future climate conditions.

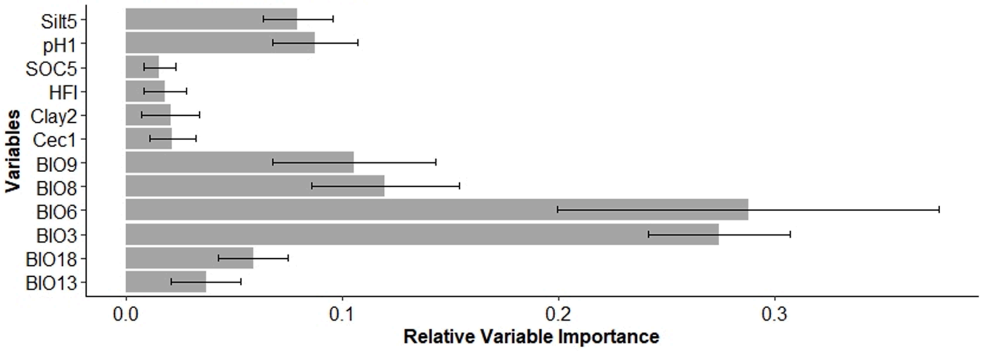


Fig. 2. Variable importance for twelve less correlated climatic and soil variables of the ensemble species distribution model for *Pterocarpus erinaceus*. BIO 3 = isothermality, BIO 6 = min temperature of coldest month, BIO 8 = mean temperature of wettest Quarter, BIO 9 = mean temperature of driest quarter, BIO 13 = precipitation of wettest month, BIO18 = precipitation of warmest quarter, Cec1 = cation exchange capacity at horizon 0–5 cm, Clay2 = clay content at horizon 5–10 cm, HFI = human footprint index, SOC5 = soil organic carbon content at horizon 60–100 cm, pH1 = pH in H_2O at horizon 0–5 cm, and Silt5 = silt content at horizon 60–100 cm.

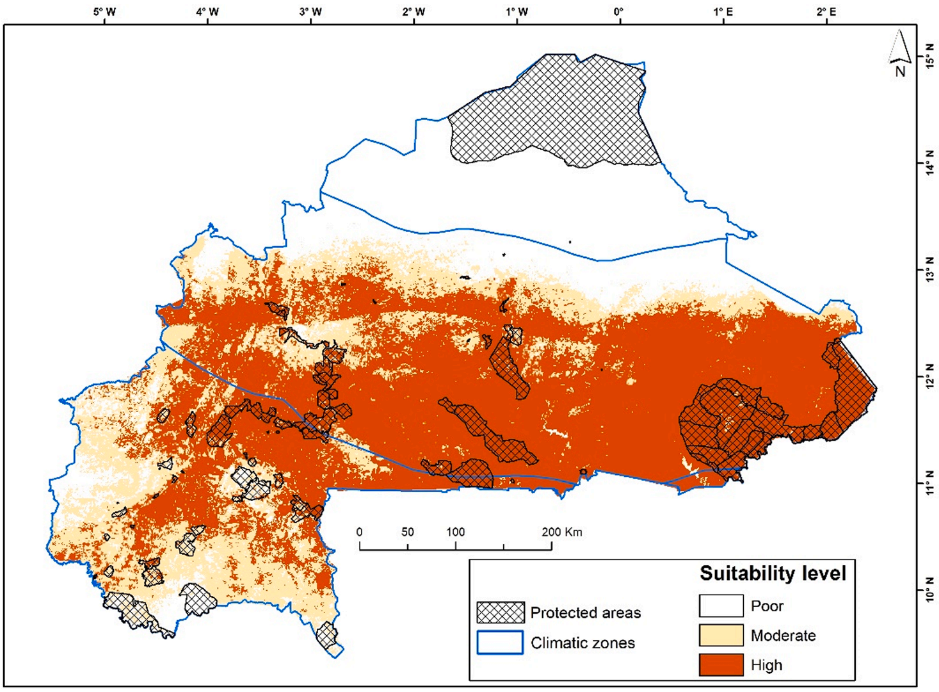


Fig. 3. Areas potentially suitable for *Pterocarpus erinaceus* in Burkina Faso under current climate.

3.2. *Influencing predictor variables*

The response curves from the ensemble models to the twelve selected environmental variables showed that the probability of *P. erinaceus* occurrence increases with an increase in isothermality (BIO3), minimum temperature of the coldest month (BIO6), mean temperature of the wettest quarter (BIO8), mean temperature of the driest quarter (BIO9), precipitation of the wettest month (BIO13), precipitation of warmest quarter (BIO18), human footprint index (HFI), pH in H_2O at horizon 0–5 cm (pH1), and silt content at horizon 60–100 cm (Silt 5), and starts dropping when the optimum condition or the humped relationship has been reached (Fig. S4). Such observation indicates that these environmental variables influenced the area of habitat suitability at a certain range only. Cation exchange capacity at horizon 0–5 cm (Cec1) and soil organic carbon content at horizon 60–100 cm (SOC 5) negatively influenced the prediction (Fig. S4). However, of the twelve environmental variables used for the model establishment, BIO3 (30.8%), BIO6 (30.7%), pH1 (11.1%), Silt 5 (9.2%) and BIO18 (8.1%) showed high relative importance (Fig. 2). For the above variables, their accumulation rate reached 89.9%, indicating that those factors exerted a vital part on the distribution of *P. erinaceus* in Burkina Faso.

3.3. *Potential current distribution*

By visual inspection of the current potential distribution of *P. erinaceus* based on occurrence points, it becomes clear that the Sudano-Sahelian climatic zone has large suitable areas compared with the two other zones in Burkina Faso (Fig. 3). The highly suitable habitats (indicated in dark orange) of *P. erinaceus* cover 47.3% (129,695 km^2) of the country's total area and are confined to Sudanian and Sudano-Sahelian climate zones. Moderately suitable habitats (area indicated in light orange), which cover 20.8% of the country's total area, were mainly located in the Southwest and the Sudano-Sahel zone. The poor habitats (area indicated in white) (82,754 km^2; 30.2%) are mainly located in the Sahel zone and in patches in the Southwest of the country.

3.4. *Vulnerability of Pterocarpus erinaceus to climate change*

The predictions of habitats suitable for *P. erinaceus* in the years 2050 and 2070, according to CNRM-CM5 and HadGEM2-CC models under RCP 4.5 and RCP 8.5 are shown in Fig. 4. The results revealed that all future climate scenarios (RCP 4.5 and 8.5) would lead to a decrease in the extent of highly suitable habitats across the study area.

Our analysis resulted in a decrease of highly suitable habitat areas (dark orange) in 2050 by 2.5% (HadGEM2-CC) up to 5.4% (CNRM-CM5) under RCP 4.5 (Table 1). These habitats were converted into poor (white) and moderate habitats (light orange). The CNRM-CM5 model predicts an important loss of suitable habitats and a high conversion rate from highly suitable to poor (4.0%) and moderate (19.7%) habitats relative to the HadGEM2-CC model (Table 1). Conversely, with RCP 8.5 HadGEM2-CC predicts a greater loss of highly suitable habitat for the species than does CNRM-CM5. Similarly, by 2070 a considerable decrease of highly suitable habitats by 26.8% (CNRM-CM5) to 28.2% (HadGEM2-CC) is expected under RCP 8.5 and by 22.6% (HadGEM2-CC) to 24.3% (CNRM-CM5) under RCP 4.5. The poor (white) and moderately suitable habitats (light orange) showed an increase for both future scenarios of the years 2050 and 2070 (Table 1, Fig. 4), whereas, in RCP 8.5, the predicted loss of highly suitable habitats was greater compared with RCP 4.5. The predicted loss in highly suitable habitat increased from 9.6% to 26.8% (CNRM-CM5) and from 13.9% to 28.2% (HadGEM2-CC) for the year 2050 and 2070, respectively (Table 1).

3.5. *Protected area network effectiveness in the conservation of Pterocarpus erinaceus*

Roughly 54% of the area covered by Burkina Faso's national network of protected areas is currently considered highly suitable for the conservation of *P. erinaceus*. Under all scenarios, the area with climatic conditions suitable for *P. erinaceus* within the protected areas is forecasted to decline by 2050 and 2070. According to the HadGEM2-CC model projections, 45% of this area will remain highly suitable for the conservation of the species by 2050 (RCP4.5), representing a loss of 55% of highly suitable habitats (Fig. 5b). The CNRM-CM5 model predicts a higher conversion (a reduction of more than 60%) of habitats highly

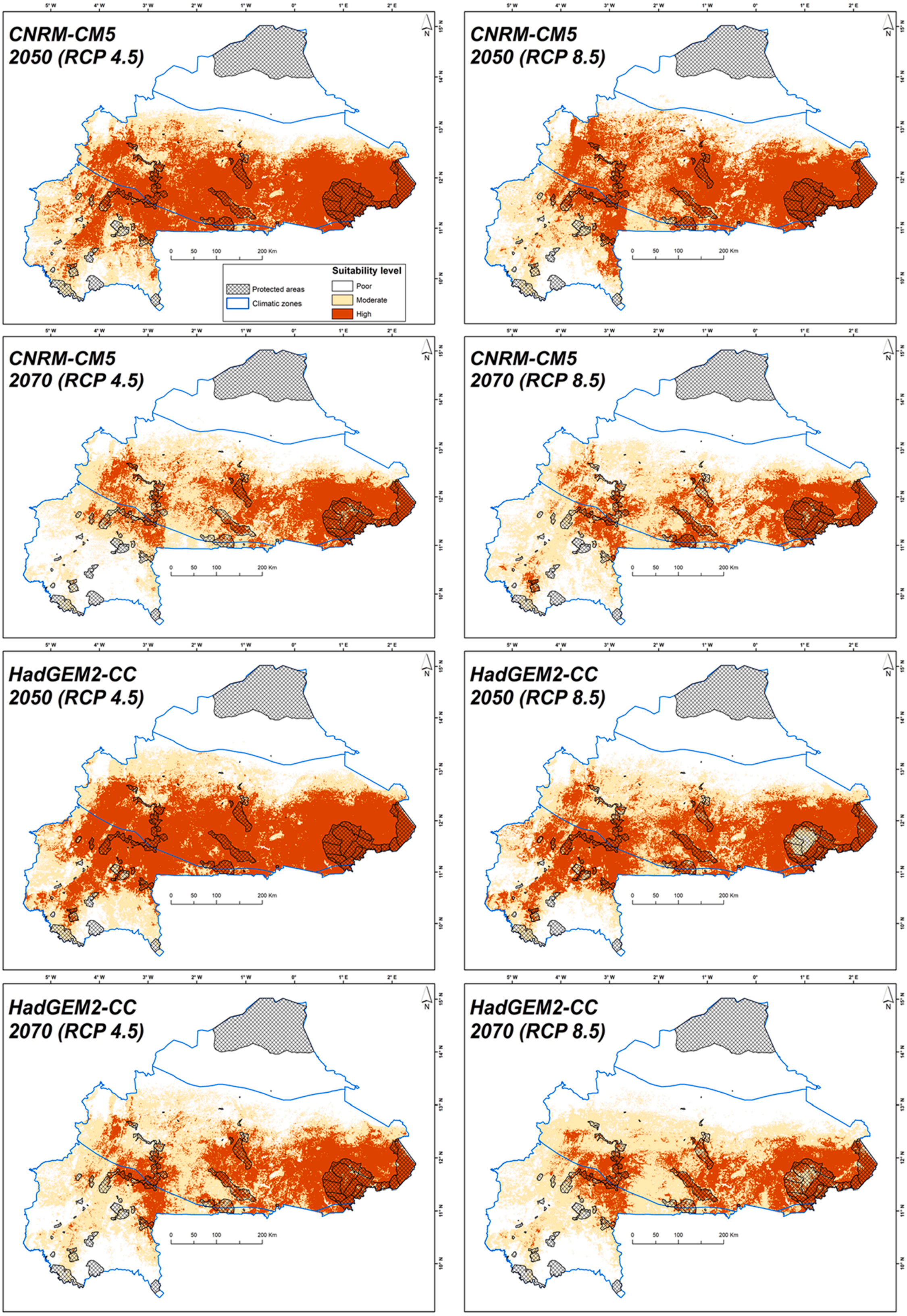


Fig. 4. Future potential distribution of *Pterocarpus erinaceus* under the general circulation models CNRM-CM5 (upper panels) and HadGEM2-CC (lower panels) for 2050 and 2070 in Burkina Faso.

Table 1
Current and future distribution of *Pterocarpus erinaceus* in Burkina Faso, based on CNRM-CM5 (upper panels) and HadGEM2-CC (lower panels) models.

	Current		CNRM-CM5				HadGEM2-CC			
			RCP 4.5		RCP 8.5		RCP 4.5		RCP 8.5	
Habitats	Area (km^2)	(%)	Area (km^2)	Trend* (%)	Area (km^2)	Trend* (%)	Area* (km^2)	Trend* (%)	Area (km^2)	Trend* (%)
2050										
Poor	82,754	30.7	86,089	+1.2	93,862	+4.1	82,878	+0.04	106,802	+8.9
Moderate	56,965	21.1	68,195	+4.2	71,740	+5.5	63,523	+2.4	70,448	+5.0
High	129,695	48.1	115,131	−5.4	103,812	−9.6	123,012	−2.5	92,165	−13.9
2070										
Poor	82,754	30.2	123,278	+15.0	123,541	+15.1	115,107	+12.0	125,476	+16.0
Moderate	56,965	20.8	82,020	+9.3	88,478	+11.7	85,523	+10.6	90,242	+12.4
High	129,695	47.3	64,117	−24.3	57,396	−26.8	68,784	–22.6	53,697	−28.2

*: Positive percentages indicate gain, and negative ones indicate loss.

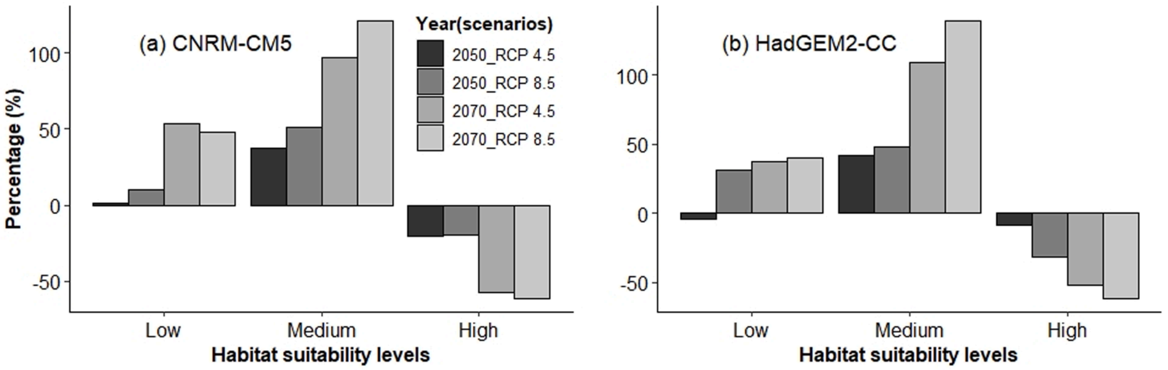


Fig. 5. Area change of habitat suitability levels for *Pterocarpus erinaceus* based on the general circulation models CNRM-CM5 and HadGEM2-CC within the protected areas network in Burkina Faso by the years 2050 and 2070 (Low: lowly suitable (0.00–0.46), medium: moderately suitable (0.46–0.70), high: highly suitable habitats (0.70–1.00)).

suitable for the conservation of the species into poor and moderately suitable habitats (Fig. 5a). Furthermore, for the year 2070, our analysis revealed a decrease of highly suitable habitats by 57.7% (RCP 4.5) to 61.1% (RCP 8.5) for the CNRM-CM5 model and by 51.6% (RCP 4.5) to 61.2% (RCP 8.5) for the HadGEM2-CC model.

In the country's protected areas, there is also a conversion of a portion of habitats currently very favourable for the conservation of the species into poor and moderately suitable habitats. For instance, in 2050, the area of poorly suitable habitats showed a marginal increase by 1.6% (RCP4.5) to 9.9% (RCP8.5) for the CNRM-CM5 model (Fig. 5a). According to the HadGEM2-CC model, the poorly suitable habitat area showed a marginal decrease of 3.9% (RCP4.5) and a considerable increase of 31.0% (RCP8.5) (Fig. 5b). Similarly, in 2070 modelling results show a considerable increase in moderately suitable habitat area by 97.1% (RCP4.5) to 121.2% (RCP8.5) for the CNRM-CM5 model (Fig. 5a) and by 109.1% (RCP4.5) to 139.4% (RCP8.5) for the HadGEM2-CC model (Fig. 5b). Overall, HadGEM2-CC predicted a strong decrease of highly suitable habitats under RCP 8.5 in 2050 and 2070 at the expense of an increase in moderately suitable habitats, while CNRM-CM5 predicted a strong decrease under RCP 4.5. The magnitude of change differed according to the scenarios, with RCP 8.5 inducing very large changes (Fig. 5a, b). The current results show that the protected areas in Burkina Faso do not effectively protect the species.

4. Discussion

Pterocarpus erinaceus is a valuable savanna tree in Burkina Faso. However, little was known about its potential distribution and the impacts of climate change under different scenarios on this species. This study is the first to explore in detail both the current and future distribution of potentially suitable habitats of this species in Burkina Faso. It provides an important link for developing strategies and plans for sustainable use and management of this species with high socio-economic value.

4.1. Performance of the models

The ensemble models produced higher AUC values than individual models, confirming the advantage of using the former to predict species occurrence. TSS values greater than 0.6 indicate excellent predictive power. The algorithms used in this study showed good to very good precision in habitat prediction for the species, according to the scale used by Thuiller et al. (2009), with the highest values corresponding to the RF model. Surprisingly, Maxent is ranked fourth among the five algorithms in terms of model performance (see Fig. S2) after RF, SVM and GAM even though it is one of the most widely used and accurate methods for predicting species distribution (Elith et al. 2006, Dimobe et al. 2020, Lompo et al. 2021). These results show that all algorithms used here have proven to be extremely effective in predicting suitable habitats corroborating the findings of past work with a variety of species (Kaky et al. 2020, Ahmed et al. 2021).

4.2. Variables used in the models

In an attempt to determine which environmental factors shape and maintain the geographic distribution of the species in terms of evolution and ecology, our results suggest isothermality (30.8%), minimum temperature of the coldest month (30.7%), pH in H_2O at horizon 0–5 cm (11.1%), silt content at horizon 60–100 cm (9.2%) and precipitation of the warmest quarter (8.1%). These results do not only reflect the importance of climate and soil conditions to the distribution of *P. erinaceus*, but also extend this observation to semi-arid savanna ecosystems. The first striking result is the effect of silt content (Silt5) on the distribution of the species, reflecting the importance of this textural element on tree growth as it promotes water retention and reduced air circulation (O'Geen 2013, Bünemann et al. 2018, Sanchez 2019).

Further, we found precipitation (BIO18) and temperature (BIO3 and BIO6) contributing to the models, indicating a balanced influence of these variables on species distribution. This balanced influence of environmental factors is consistent with the idea that in the (sub)tropical zone, both water availability and temperature regime are important factors in controlling species occurrence patterns mediated by intrinsic species growth and leaf traits (Wagner et al. 2012, Bauman et al. 2022). Tolerance to a particular temperature range is one of the most important traits used to explain the geographic distribution of a species (Gonzalez et al. 2012, Adji et al. 2021). *P. erinaceus* generally grows in warm and humid regions with a mean annual temperature and rainfall of ca. 37 °C and 600 mm/year, respectively (K. Dimobe, unpubl. data), and this finding is consistent with the known climatic preferences of the species (Segla et al. 2020). Temperature fluctuations affected the distribution of *P. erinaceus* by influencing germination, water uptake, photosynthesis, transpiration, respiration, reproduction and growth (Ouédraogo et al., 2006). Like temperature, precipitation (here BIO18) directly affects growth and morphology, phenology, and plant biomass accumulation of *P. erinaceus* (Segla et al. 2020). Plant height, biomass accumulation and seed production of *P. erinaceus* decreased with lower rainfall (Banla et al. 2019).

4.3. Current and future distribution

According to our results, habitats suitable for *P. erinaceus* cover about 47.3% of the Burkinabé territory, under rainfed conditions, especially in the Sudanian and Sudano-Sahelian zones. This confirms previous observations on the niche of *P. erinaceus* in Burkina Faso (Dimobe 2017). These zones offer the species a dry season characterised by the dry north-eastern 'harmattan' wind and a great reduction in the hygrometry it would need for good fruit ripening and yield.

The modelling results vary according to the model used, the type of scenario considered, and the species. The CNRM-CM5 and HadGEM2-CC models predict a strong reduction of the areas suitable for cultivation of the species in Burkina Faso. The poor habitats are found in the country's extreme North, mainly in the Sahelian zone. Obviously, this result seems to confirm that the environmental conditions, particularly the high temperature and low rainfall in the Sahelian zone, do not correspond to the climatic niche of this species.

This finding is in line with the results of Thuiller et al. (2008), who worked on predicting the impacts of global changes on the distribution of plant species. As for the conservation of this species, the potential distribution of its favourable habitats could help to identify areas allowing for its maintenance in the framework of reintroduction programmes. The models considered here predict a significant regression of habitats favourable for *P. erinaceus* thus agreeing with what has been widely reported in the literature (Araújo and New 2007, Agwu et al. 2020, Dimobe et al. 2020, Lompo et al. 2021). These variations can depend on many factors such as the variables used, the modelling technique, the process applied in the construction of a model or the uncertainties in the climate scenarios that may influence the model outputs.

The regressive trends noted in the habitats suitable for *P. erinaceus* suggest that climate change (i.e., increasing temperature and decreasing rainfall) will have a negative impact on the distribution of the habitats of this species, which is already threatened with extinction in Burkina Faso due to over-exploitation. This also confirms the hypothesis that climate change could modify the species' range as proven by several studies (Hannah et al. 2002, van Zonneveld et al. 2009, Dimobe et al. 2020). The decrease of suitable habitat areas in 2050 and 2070 could be related to the predicted shift towards a somewhat drier climate (i.e., higher temperatures and lower rainfall) even the opposite may happen according to Lyam et al. (2022). Although *P. erinaceus* is sensitive to precipitation changes, a combination of both precipitation-related bioclimatic variables (BIO18) and temperature (BIO3 and BIO6) greatly affected its distribution. This was illustrated by the significant loss of highly suitable habitats, which decreased by ca. 27 and 28 % in 2070 for CNRM-CM5 and HadGEM2-ES under RCP 8.5, respectively, in response to changes in both BIO3, BIO6 and BIO18. A decline of habitats highly suitable for *P. erinaceus*, whose range is already small, should be seriously considered in trying to conserve the species.

Thus, concerted efforts are required to protect this species under the scenarios of rainfall decrease and temperature increase. The model output of *P. erinaceus* showed that the decrease of suitable habitat areas was more pronounced for the pessimistic scenario (RCP 8.5) than for the RCP4.5. Dimobe et al., (2020) predicted similar adaptation results for *Vitellaria paradoxa* in Burkina Faso in response to climate change using the MaxEnt approach, while the studies by Guidigan et al., (2018) reported an opposite trend in Benin. A similar study by Lompo et al., (2018) showed a decrease of suitable habitat of *Ximenia americana* in Burkina Faso by 2050. Many studies mainly showed a significant loss of suitable habitat under climate change scenarios for tree species in West Africa (Fandohan et al. 2013, Dimobe et al. 2020, Lompo et al. 2021). Beyond models and variables considered, the difference might also stem from scales with the latest being more local and Lyam et al. (2022) who investigated the whole continent.

In summary, both models (CNRM-CM5 and HadGEM2-CC) predict a significant decrease of habitats where local populations or ecotypes of *P. erinaceus* will keep on regenerating by 2050 and 2070. However, in a large number of tropical species, adjustment of reproductive physiology to climatic conditions has been observed (Yadav and Yadav 2008, Pittock 2009). Thus, as far as the tolerance limits of ecological factors allow, local ecotypes of *P. erinaceus* may be able to adjust to changes.

4.4. Implication for conservation planning

In general, plants have only two options in facing future climate conditions in the absence of any human actions: either adapting *in situ* or dispersing, following their climate niche (Robiansyah and Hajar 2017). Failure in adopting to at least one of these two strategies results in extinction. *In situ* conservation in protected areas is one of the most effective conservation strategies. In the case of *P. erinaceus*, a decrease by 21–61% is projected under CNRM-CM5 and 8–61.2% under HadGEM2-CC in highly suitable habitats, thus drastically restricting its adaptive capacity within the country. This will likely exacerbate the adverse effects of habitat destruction due to anthropogenic actions or natural disastrous events. The fate of the species in protected areas will therefore be linked to the fate of these habitats and its ability to withstand extremes in temperature and rainfall. Despite the reduction in highly favourable habitats predicted by both models, neither model predicted a failure of the national protected area network to provide highly favourable habitats for the species by 2050 and 2070.

Modelling results can be used to classify natural habitats for *P. erinaceus* as being at low or high risk under changing climate conditions in Burkina Faso to support conservation planning. The findings of our models can be tailored to suit conservation guidelines for *P. erinaceus* in the country by identifying critically vulnerable habitats and potential climatically suitable habitats where regeneration should be facilitated to restore forests. For instance, *P. erinaceus* afforestation activities should be concentrated in climatically suitable habitats, and more should be done for the natural regeneration of this species in the habitats that will not be suitable under future climate conditions. Outside the actual reserve networks, pruning and thinning techniques, and active restoration practices, could be used for the sustainable management of the species (Bayala et al. 2022). Against this background, future studies might focus more strongly on the sustainable yield that can be realised with the species under different climate and soil conditions. In addition, given its multiple uses, including *N*-fixation and being a good nectar plant for honeybees, it could be well integrated into new agroforestry approaches.

Habitats of the species are fragmented due to human activities. According to Myers et al. (2000) and Ganzhorn (2003), habitat loss and fragmentation are among the greatest threats to biodiversity worldwide, particularly in tropical ecosystems. They reduce habitat area, quality and connectivity for many wild species with potentially dramatic consequences for population viability. Under these circumstances, actions for promoting gene flow of the African rosewood are likely to promote other threatened species, including species with less sensitive breeding strategies. Due to the decrease of suitable habitats for the species, understanding the role of habitat connectivity between spatially structured and declining populations is necessary to develop effective conservation measures that promote genetic variation and population viability. Assuming that there are several populations (small and large) of the species in the study area, if gene flow is very low, genetic diversity in the small populations will erode due to genetic drift and inbreeding, making the populations prone to extinction.

So, to allow for sufficient gene flow in the remaining populations, controlled pollination and seedling transplants should be considered as the next step to increase the numbers of individuals within the smaller populations, and enable the *in-situ* conservation of genetic resources. However, as pollen moves beyond the distance up to which trees are most closely related, there is only limited biparental inbreeding. Extensive long-distance pollen dispersal, scattered remnant populations and spatially isolated trees play vital roles in maintaining genetic diversity, connectivity, and low genetic differentiation between populations, reducing the risk of inbreeding and local extinction. Efforts that promote habitat connectivity enhancement, require information about functional connectivity and genetic variability of populations. In addition to connecting habitats, preservation of genetically diverse populations (genetic pool and polymorphism) is also a conservation strategy. Pollen dispersal is still possible today among most savanna patches for this species. Above all, the main threat to *Pterocarpus* spp. in Western Africa should be addressed, which is being cut and shipped to China. If that (and too much pruning for fodder) can be effectively stopped, the species will do fine in the Sudanian zone.

5. Conclusions

Based on our findings and previous biological data, the distribution of *P. erinaceus* is primarily influenced by the effects of isothermality, silt, pH, minimum temperature of the coldest month and precipitation of warmest quarter. Our findings suggest that the Sudanian and Sudano-Sahel climatic zones are currently ideal for *P. erinaceus* growth. Under climate change scenarios, *P. erinaceus'* climatic niche will be geographically reduced toward the Southeast of Burkina Faso. The study provides a quantitative view of the risks associated with regional climate change that could affect the conservation and cultivation of *P. erinaceus*. Furthermore, the methods proposed in this study could be used to quantify the current and future distribution of other threatened and endangered plant species, provide baseline information for reconnaissance surveys, and improve efforts for conservation and restoration of valuable timber trees.

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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Supporting information to be added here

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2022.126299.

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