Received: 14 April 2024 | Revised: 16 October 2024 | Accepted: 5 December 2024

DOI: 10.1002/ppp3.10630

Plants People Planet PPP Open Access

RESEARCH ARTICLE

Towards the sustainability of African sandalwood: Understanding the distribution and environmental requirements

Jane Gachambi Mwangi[1] | Salisu Mohammed[2] | Kabir Mustapha Umar[3] | Jeremy Haggar[4] | Truly Santika[4]

[1]Department of Natural Resources, Faculty of Environment and Resources Development, Egerton University, Kenya

[2]Department of Geography, Faculty of Earth and Environmental Science, Bayero University, Kano, Nigeria

[3]Centre for Dryland Agriculture, Bayero University, Kano, Nigeria

[4]Natural Resources Institute (NRI), University of Greenwich, Chatham Maritime, ME4 4TB, UK

Correspondence
Jane Gachambi Mwangi, Department of Natural Resources, Faculty of Environment and Resources Development, Egerton University, Kenya.
Email: mwangijane35@gmail.com

Funding information
RSIF-PASET program (Regional Scholarship and Innovation Fund - Partnership for Skills in Applied Sciences, Engineering and Technology)

Societal Impact Statement

African sandalwood (*Osyris lanceolata*) leaves, roots, barks, fruits, and woods are used for multiple purposes throughout Asia, Africa, and Europe. The species is threatened in several eastern African countries. To improve the species' management and conservation, a habitat suitability study was undertaken in its at-risk region in eastern Africa and extended to southern and horn of Africa due to its continuous distribution. African sandalwood continues to face intense human pressure and needs to be prioritized in terms of sustainable management practices. The plant's significant human importance necessitates inclusive conservation measures in all three habitat regions in Africa to safeguard it.

Summary

- African sandalwood (*Osyris lanceolata*) is a versatile plant with significant economic and societal importance. It is threatened in several countries in Africa due to overexploitation. The lack of knowledge about the plant's ecology and environmental requirements complicates the species' long-term management.
- We sought to address this issue by providing a novel understanding of the environmental factors that influence the occurrence of African sandalwood and its potential distribution. Using publicly available occurrence records from 1950 to 2021 and field data, we examined the species' habitat requirements in eastern, southern, and horn of Africa regions. We applied the Generalized Additive Models to link the plant's occurrence data to 12 environmental variables reflecting climatic, physiographic, and edaphic characteristics, while controlling for the biases that arise from publicly gathered occurrence records.
- Our findings revealed that the plant's habitat requirements vary among the three regions investigated. While climatic factors are essential in all three regions, physiographic aspects are mainly important for the eastern and southern populations, while edaphic variables were pertinent exclusively in southern region. Areas suitable and optimal for the plant were estimated to comprise 674,700 km^2 (17.3% of

total land area) in eastern Africa, 267,750 km^2 (25.6%) in the horn of Africa, and 716,300 km^2 (13.9%) in southern Africa.

- More than two-thirds of these areas are located on unprotected lands, highlighting the importance of community involvement for a sustainable management of the species. Our results on the potential geographical distribution of African sandalwood are crucial to guide more targeted conservation and recovery efforts.

KEYWORDS
abiotic, anthropogenic, conservation, habitat modelling, management, *Osyris lanceolata*

1 | INTRODUCTION

African sandalwood (*Osyris lanceolata*) is a multi-stemmed, evergreen hardy shrub or small tree from *Santalaceae* family (Maundu & Tengnäs, 2005). It has high socioeconomic, ecological, and cultural importance across its distribution range (Těšitel et al., 2021). The plant's leaves, roots, barks, fruits, and woods are used by people in Asia, Africa, and Europe for different purposes, including for medicine, cosmetics, and ornaments (Teixeira Da Silva et al., 2016). The plant's high economic value, diverse uses, and demands from the global market, combined with its slow growth in the wild, have contributed to population decline (CITES, 2013; Mwangi et al., 2023). The International Union for Conservation of Nature (IUCN) classifies it as threatened in some countries in eastern Africa, including Kenya, Tanzania, Uganda, South Sudan, Rwanda, and Burundi, but not elsewhere (Wilson, 2018). It is also classified as endangered in these eastern African states, under Appendix 11 of the Convention on International Trade in Endangered Species (CITES) of Wild Fauna and Flora (CITES,). Several field reports from eastern Africa indicate that the plant's population continues to decline (FSSD-MWE, 2022; Khayota et al., 2021), and it is predicted that it will vanish in the wild in this region by 2040 (Thomson, 2020). Other studies have also documented a dwindling condition in non-endangered places in southern Africa (Semenya & Maroyi, 2019).

African sandalwood thrives in a variety of orographic environments and is greatly impacted by human activities. Despite this, little is known about its ecological and anthropogenic range, as well as the heterogeneity of its habitat (Mugula et al., 2021; Mwangi et al., 2023). Numerous studies have been undertaken to explain the biological and localized ecological characteristics of the plant to inform conservation planning (Díaz-Barradas et al., 2023; Mwang'ingo et al., 2003). Several studies have also examined the species in relation to its protection and management (Mwang'ingo et al., 2003; Ochanda, 2009), genetic diversity (Mugula et al., 2023; Mwang'ingo et al., 2008), socioeconomic benefits (Mwangi et al., 2021), and illicit trade at domestic and international level (Bunei, 2017). However, there is still a paucity of knowledge on the climatic, physiographic, and edaphic elements that might influence the plant's occurrence across its native distributional range. There is a dearth of knowledge about the species' potential distribution, thus rendering it hard to determine the optimal locations for in-situ and ex-situ conservation (Mugula et al., 2021; Mwangi et al., 2023).

Previous research has shown that regression-based species habitat modelling are a cost-effective, timely, robust, and relatively accurate method for mapping and estimating the distribution of an endangered species over large spatial areas, as well as identifying abiotic and climate effects on their distribution (Morales et al., 2023). It can also assess how anthropogenic stressors, including deforestation and overexploitation, affect a species (Jefferson et al., 2023). Species habitat modelling methodology offers a useful way for evaluating the African sandalwood's current geographical range and improving knowledge of the complex factors controlling the plant's distribution. This approach can help guide a more targeted conservation strategy to ensure the plant's survival in the wild. Nonetheless, no research has been conducted on the species using this methodology.

In this study, we aimed to provide a novel assessment of the complex environmental factors that influence the geographical distribution of African sandalwood and identify suitable areas for conservation. We used species occurrence records obtained from a variety of sources, including public records, government reports, and field surveys. More specifically, we sought to address two objectives: (1) to employ the species habitat modelling approach to ascertain the impacts of climatic, physiographic, and edaphic factors on the plant's occurrences, while accounting for sampling bias associated with public records; (2) estimate the species' potential habitats and evaluate them in terms of land protection status to infer the extent of community participation. We carried out separate habitat modelling for the three regions of the plant's distribution range in Africa (Figure 1). This is to account for the differences in climatic conditions among the three regions, particularly seasonal rainfall patterns (Figure 2). Drawing from the habitat modelling results, we recommend actions to enhance the species' in situ and ex situ conservation management. Our study will assist in guiding ongoing conservation efforts for this critically endangered species in eastern Africa, as well as build a better knowledge of the species and its long-term conservation strategies throughout Africa.

2 | METHODS

2.1 | Study area

Our study area spans between longitudes 10° E and 50° E and latitudes 35° S and 20° N (Figure 1). This area corresponds to the range of the

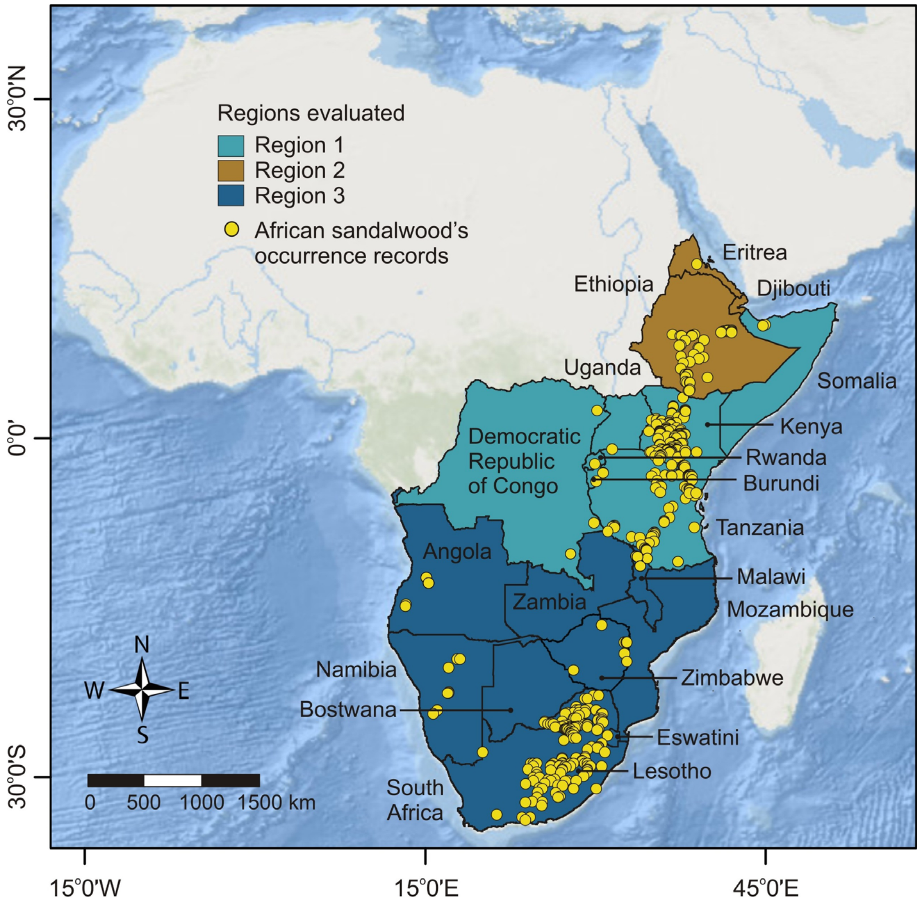

FIGURE 1 The locations of reported African sandalwood (*Osyris lanceolata*) across three regions, each with distinct climatic characteristics, including region 1 (comprising most eastern African countries), region 2 (mainly the horn of Africa), and region 3 (southern African countries).

African sandalwood, according to the species' occurrence data recorded in the GBIF (Global Biodiversity Information Facility) database (downloaded on June 23, 2023). The plant distribution range exhibits significant variation in precipitation patterns, which can be broadly categorized into three patterns that align with distinct geographical differences (Figures 1 and 2). Region 1 typically experiences two major rainy seasons: long rains from March to June and short rains from October to December (Figure 2a). It includes the eastern African nations of Kenya, Rwanda, Burundi, Tanzania, and Uganda, as well as the westward and eastward adjacent countries of Democratic Republic of Congo and Somalia, covering a total land area of 3,901,800 km^2 (Figure 1). Region 2 also has two rainy seasons, but the timing and intensity differs from that of region 1. Here, rainy seasons generally last from April to May and July to September (Figure 2b). This region includes the horn of African countries of Eritrea, Ethiopia, and Djibouti, covering 1,045,850 km^2 of land area (Figure 1). The Intertropical Convergence Zone (ITCZ), which migrates periodically, influences precipitation patterns in regions 1 and 2 (Omay et al., 2023). Region 3 only has one rainy season lasting from November to March (Figure 2c). This region encompasses southern African states of Angola, Zambia, Malawi, Mozambique, Namibia, Botswana, Zimbabwe, Mozambique, South Africa, Lesotho, and Eswatini, spanning a total land area of 5,169,825 km^2 (Figure 1). The precipitation in region 3 is influenced by various factors, including the El Niño Southern Oscillation (ENSO), the Southern Annular Mode, the South Indian Ocean Dipole, and the Botswana High (Thoithi et al., 2021).

Regions 1 and 2, located in eastern and horn of Africa, as well as Democratic Republic of Congo, support a diverse range of habitats, including the arid plains of northern Kenya and the rainforests and alpine moorlands of Africa's two tallest mountains (Mount Kenya in Kenya and Mount Kilimanjaro in Tanzania). These regions are characterized by complex topography, with elevations ranging from below sea level to the highest points of Mount Kilimanjaro (5,895 m a.s.l) in Tanzania and Mount Kenya (5,199 m) in Kenya. Region 3, which lies in southern part of Africa, exhibits more variability in climate, including tropical, subtropical, and temperate zones. This region includes ecosystems such as savannas, woodlands, semi-deserts (such as the Kalahari Desert), Mediterranean-like shrublands (such as the Fynbos biome), and temperate forests. Considering the unique climatic and environmental attributes of the three regions essential to support plant survival, we shall henceforth define region 1, 2, and 3 as broadly representing eastern Africa, the horn of Africa, and southern Africa habitats, respectively (Figure 1).

2.2 | Data

2.2.1 | Species occurrence data

The species occurrence records were mainly downloaded from the GBIF, an open access network for species occurrence records globally (GBIF, 2023), using the rgbif package in R (Chamberlain et al., 2022).

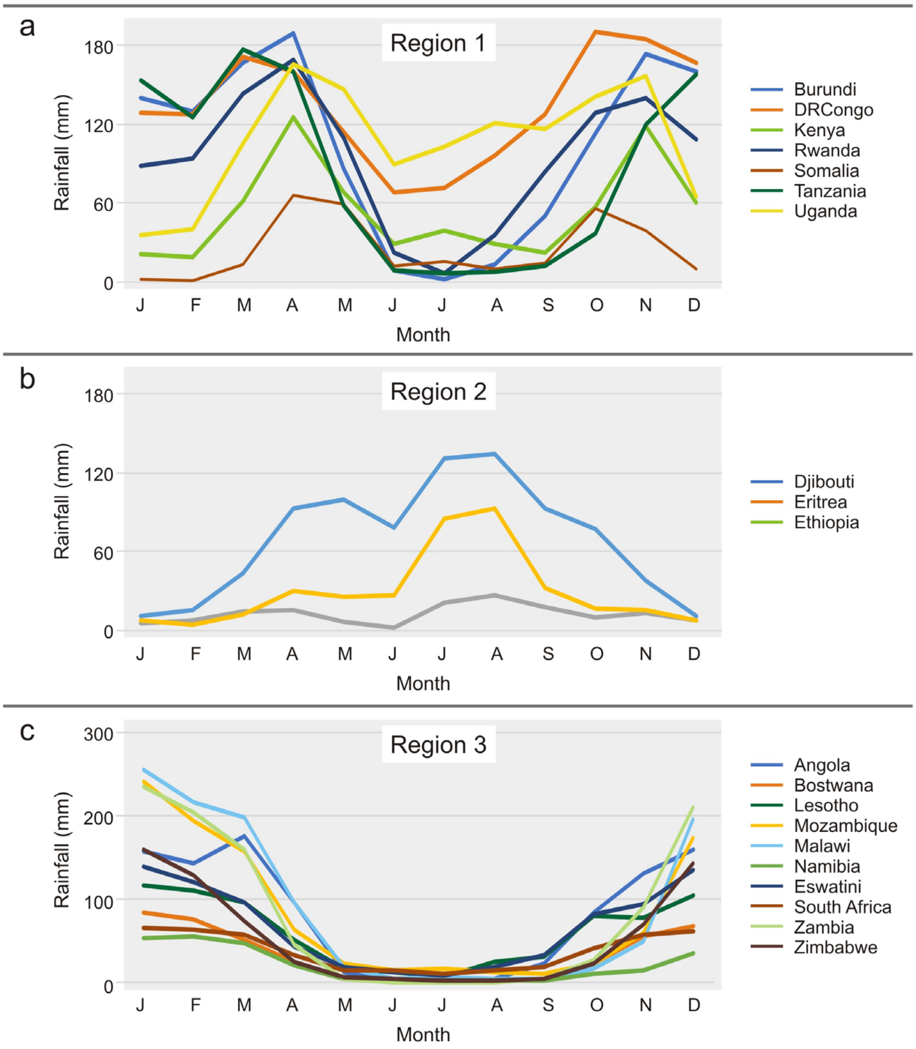

FIGURE 2 Long-term seasonal rainfall patterns, i.e., the timing of dry and rainy months, in three regions of the African sandalwood distribution range, namely region 1 (mostly eastern African countries), region 2 (mainly the horn of Africa), and region 3 (southern African countries). Given the differences in seasonal rainfall patterns, we performed independent habitat modeling to suit the plant distribution in each region.

Other sources of occurrence data were from published articles (Bekele et al., 2019; Mugula et al., 2023; Mwang'ingo et al., 2003), government reports (Mukonyi et al., 2012), herbarium specimens from the National Museums of Kenya for countries in eastern Africa and few countries in southern Africa (Zambia, Zimbabwe, Malawi, South Africa), and ecological field surveys for Kenya carried out in 2021 by the author (J.G.M) (Table S1).

To improve the quality and accuracy of the datasets and the contextual information for the models, only downloaded occurrence records with geographic coordinates were used and duplicated records were deleted. These records were then projected onto the map using Google Earth and pre-checked whether the projected locations corresponded to the collection site description using the leaflet package in R. All the downloaded nongeoreferenced records with locality description were individually georeferenced.

The species occurrence records were spatially thinned with a 5-km distance using the spThin package for R (Aiello-Lammens et al., 2015) to reduce the effects of spatial bias (Araújo et al., 2019). This filtering method helps in keeping the highest possible number of localities by ensuring that only one unique presence record is retained within the 5 km grid cell. After filtering, the species were required to have more than 30 occurrence records, which is generally considered sufficient to build accurate distribution models (van Proosdij et al., 2016). The final species occurrence global dataset for use in model included 409 occurrence records, comprising 172 records for southern Africa, 44 records for the horn of Africa, and 193 records for eastern Africa.

2.2.2 | Spatial datasets

A total of 12 environmental and human-related sampling variables were used to build the species habitat models. The environmental spatial data were chosen based on a thorough examination of the literature on the ecology and biology of African sandalwood across the world, as well as expert knowledge (Mwangi et al., 2023). These data can be broadly classified into three categories: (i) climatic, (ii) physiographic, and (iii) edaphic. Human-related variables were used to account for potential sampling biases arising from the use of publicly collected species occurrence records. Besides these environmental and human-related sampling variables, we used data on the extent of protected areas to estimate the extent of suitable

TABLE 1 List of spatial datasets/variables used in this study.

Variable	Units	Spatial resolution	Data sources
Climatic variables			
Mean annual temperature	°C	1 km	CHELSA (Karger et al., 2017)
Long-term wet season rainfall	km/month	0.05°	CHIRPS v2.0 (Funk et al., 2015)
Long-term dry season rainfall	km/month	0.05°	CHIRPS v2.0 (Funk et al., 2015)
Physiographic variables			
Elevation	m a.s.l	90 m	SRTM (https://earthexplorer.usgs.gov/)
Slope	Degrees		SRTM (https://earthexplorer.usgs.gov/)
Edaphic variables			
Clay content (<0.002 mm)	%	250 m	SoilGrds (Hengl et al. 2021)
Silt content (0.002–0.05 mm)	%	250 m	SoilGrds (Hengl et al. 2021)
Soil organic carbon	g/kg	250 m	SoilGrds (Hengl et al. 2021)
Soil pH		250 m	SoilGrds (Hengl et al. 2021)
Human-related sampling variables			
Population density (2020)	Persons/km^2	1 km	Gridded Population of World (GPWv4) (CIESIN, 2022)
Distance to the cities	km		Global Gazetteer Version 2.3
Other			
Protected area network			WDPA (World Database on Protected Areas)

habitat that are on protected land. All these variables are listed in Table 1.

We incorporated climatic data such as long-term precipitation and temperature. These datasets were chosen because few existing local studies revealed that the African sandalwood's vegetative and reproductive phenological phases follow distinct patterns between the dry (and warm) and wet (and cooler) years (Mwang'ingo et al., 2008; Rodríguez-Gallego & Navarro, 2015). This implies that long-term precipitation and temperature are required during the plant's long growth life cycles. Long-term mean monthly precipitation records were obtained from the CHIRPs (Climate Hazards Group Infrared Precipitation with Station data) database, which has a 5 km spatial resolution (Funk et al., 2015). The data was used to derive the mean monthly precipitation for both the wettest and driest seasons. Long-term mean annual temperature data were acquired from the CHELSA database with a spatial resolution of 1 km (Karger et al., 2017).

We incorporated physiographic information including elevation and slope. The African sandalwood requires a specialized microclimate niche that includes rocky outcrops, hilly terrain, and extremely steep regions that enable it to grow and propagate. These habitats are found in dry upland and riverine forests, forest edges, riverbanks, lowland bush, and arid and semi-arid lands (ASALs), which are extremely vulnerable because they are not protected and are located on communal or private lands (FSSD-MWE, 2022; Khayota et al., 2021; Orwa et al., 2009). Elevation data were based on the digital elevation model SRTM (Shuttle Radar Topography Mission) with a 90 m and were obtained from the United States Geological Surveys' Earth Explorer (USGS). Based on the data, we derived the slope variable for further analysis.

We included edaphic information such as soil pH in water, soil organic carbon (SOC), and the content of sand, clay, and silt in soil. African sandalwood is reported to grow in isolated groups with certain edaphic conditions. It may be found in a variety of soil types, including sandy clay loam, clay, sandy loam, clay, rocky loam, and sandy loam in various ecological zones (Gathara et al., 2022; Khayota et al., 2021; Mwang'ingo et al., 2003). Raster maps of these five soil constituents were derived from the SoilGrids database at a resolution of 250 m (Hengl et al., 2021).

To account for potential sampling bias associated with publicly collected species records, we included proxies for human activities, including human population density in 2020 and distance to large cities. The list of major cities across the study regions was obtained from the Gazetteer Version 2.3 (https://www.fallingrain.com/world/), while data on human population density were acquired from the Gridded Population of the World (GPW) v4 (CIESIN, 2022). Additionally, we obtained data on protected area network across the three regions from the WDPA (World Database on Protected Areas), a database with the most comprehensive list on terrestrial and marine protected areas globally (UNEP-WCMC, 2019).

2.3 | Analysis

We carried out independent analyses for the three regions of African sandalwood: the eastern, southern, and horn of Africa. This was considered given marked variations in long-term precipitation across the three regions that could affect the ecosystem structure and land productivity. In Figure 3, we summarized the three main analysis phases conducted in this study, including (1) *data preparation*, which includes data cleaning and processing; (2) *species habitat modelling*, which comprises building the species habitat model based on relevant datasets,

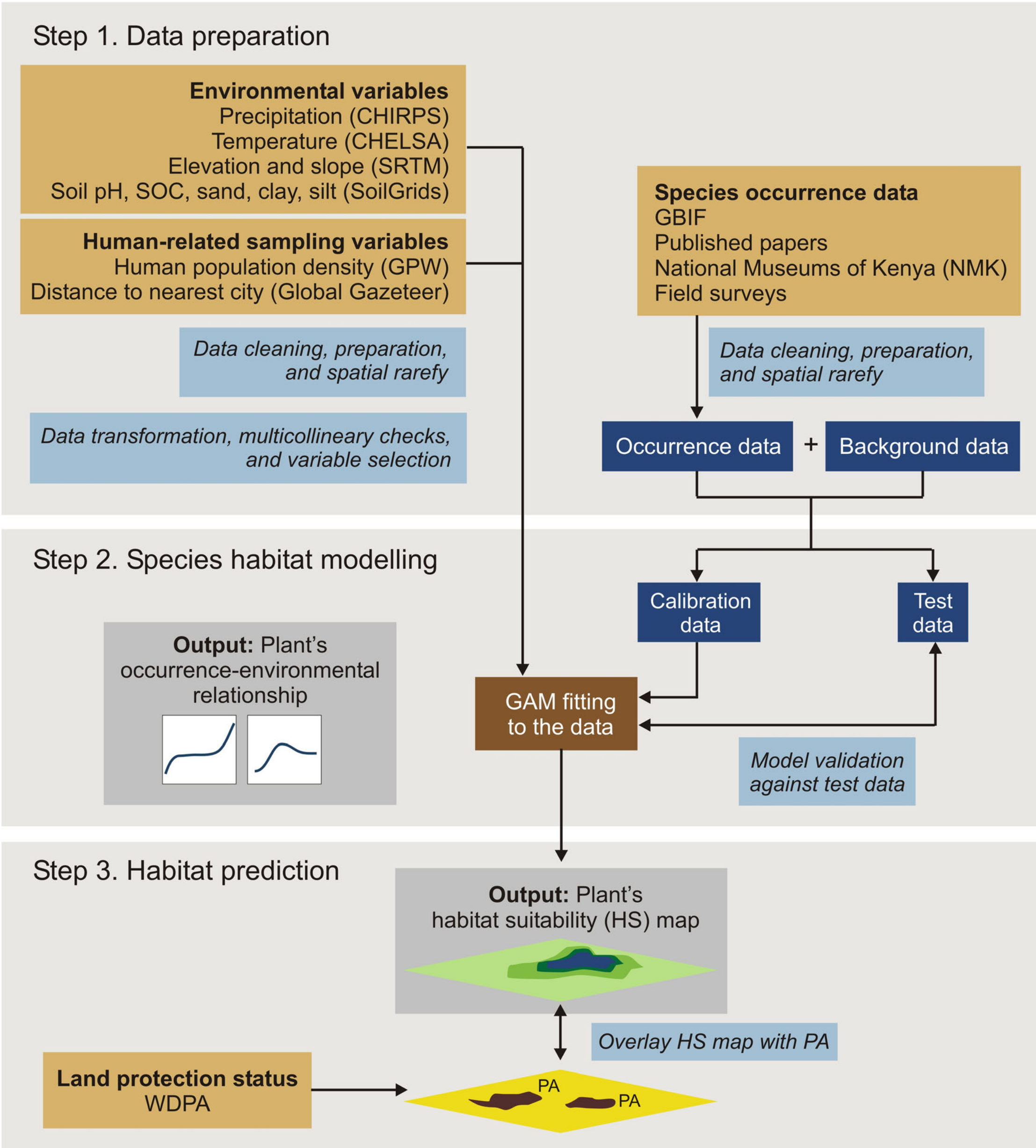

FIGURE 3 Analysis framework undertaken in this study, which broadly included three phases of analysis: (1) data preparation, which includes data cleaning and processing; (2) species habitat modelling, which comprises constructing the species habitat model based on relevant data, analyzing the relationship between species and environment, and evaluating the accuracy of the models; and (3) habitat prediction, which comprises generating the species habitat suitability maps based on the habitat model and identifying suitable areas on protected versus nonprotected land.

analyzing the relationship between species and environment, and evaluating the accuracy of the models; and (3) *habitat prediction*, which comprises generating the species habitat suitability maps based on the habitat model and identifying suitable areas on protected versus nonprotected land.

2.3.1 | Data preparation

We employed fishnet grids with a spatial resolution of 5 km as our analytical unit. All 15 environmental and sampling-related predictors were resampled to meet this resolution. To contrast the current species presence data points, background points or pseudo-absence data were randomly chosen over the study area, similar to the method employed by Barbet-Massin and Jetz (2014). This method provides for an equal balance of presence and absence. The pseudo-absences were constructed since our data did not include real absences obtained in the field during the ecological surveys. Furthermore, real absences can include unproven assumptions, thus potentially yield less accurate models than those that used pseudo-absences (Zaniewski et al., 2002).

Prior to habitat modelling, all predictor variables with strongly skewed distributions were transformed logarithmically or square-rooted. These include variable rainfall during the dry season for regions 1 and 3 (eastern and southern Africa), slope for the three regions, and population density and distance to nearest city for the three regions. Variable transformation is useful in habitat modelling as it helps to capture nonlinear relationships, stabilize variance, and improve model fit. Pearson's correlation coefficient (*r*) was then employed to analyze the pair correlation among all these transformed predictors. If two variables were significantly correlated ($|r| > 0.7$), we retained one of them, choosing those that have frequently been recognized in the literature as being of ecological and biological relevance (Fourcade et al., 2018).

2.3.2 | Species habitat modelling

The species occurrence and background data were first partitioned by randomly selecting a subset of 75% of the data for model calibration and 25% for evaluation (Thuiller et al., 2009). We used the generalized additive models (GAMs) to fit the species and environmental data. Given the relatively small number of occurrence records available for the species, GAM was deemed the most appropriate methodology in comparison to the more popular machine learning methods. The GAM approach offers an effective compromise between flexibility and performance while maintaining a high level of interpretability.

Given that each region had a distinct mixture of uncorrelated predictors, we built three independent GAMs for each. The model for eastern Africa, horn of Africa, and southern Africa can be written in the following order:

$$\text{Logit}(p) = \propto + f_1(TEMP) + f_2(DRY) + f_3(WET) + f_4(SLOPE) + f_5(CLAY) + f_6(SILT) + f_7(POP) + f_8(CITY) \tag{1}$$

$$\text{Logit}(g) = \gamma + f_1(TEMP) + f_2(DRY) + f_3(WET) + f_4(SLOPE) + f_5(CLAY) + f_6(CITY) \tag{2}$$

$$\text{Logit}(q) = \beta + f_1(TEMP) + f_2(DRY) + f_3(WET) + f_4(ELEV) + f_5(SLOPE) + f_6(CLAY) + f_7(POP) + f_8(CITY) \tag{3}$$

where *p*, *g*, and *q* denote the probability of species occurrence for each of the three regions. *TEMP* denotes the climatic variable mean annual temperature, and *DRY* and *WET* denote the precipitation during the dry and wet season, respectively. *ELEV* and *SLOPE* denote the physiographic variable elevation and slope, respectively. *CLAY* and *SILT* denote the edaphic variable clay and silt content in soil. *POP* denotes the sampling-related predictor human population density, whereas *CITY* denotes the distance to nearest city.

We used the mgcv package in R to fit the GAM to the data (Wood, 2011). Smoothing spline function was used in the GAM model fitting. The impact of a variable in influencing the distribution of African sandalwood was assessed by calculating the percentage loss in model performance when the corresponding variable was removed, as indicated by the value of the model's Akaike information criterion (AIC) (Searcy & Shaffer, 2016).

The accuracy of the models was assessed using independent test datasets. We used both threshold-independent and threshold-dependent metrics implemented in the dismo and Presence Absence packages in R. The threshold-independent measure comprises the AUC (area under the curve receiver operating characteristic), while the threshold-dependent measure includes TSS (true skill statistic), sensitivity, and specificity. The AUC value ranges from 0 to 1, with AUC >0.8 indicating good performance (Janitza et al., 2013). TSS ranges between −1 and 1, with value >0.75 indicating good performance. Sensitivity measures the proportion of correctly predicted presences, while specificity quantifies the proportion of correctly predicted absences. For the threshold-dependent measures, we employed a 0.5 cutoff value, a commonly utilized threshold in the literature.

2.3.3 | Habitat prediction

The species habitat suitability maps were generated by projecting each GAM to the three study regions, accounting for the climatic, physiographic, and edaphic components while omitting human-related sampling variables from the calculation. These maps range from 0 to 1, with higher values indicating a more suitable environment for the species to occur. These maps were then categorized into four suitability classes signifying increasing levels of habitat suitability or likelihood for the species to occur, including (i) not suitable, (ii) less suitable, (iii) suitable, and (iv) optimal. This categorization was achieved based on natural breaks (jenks) classification technique (Chun et al., 2016).

After the species habitat suitability maps have been generated, we overlaid them with the spatial layer of protected area network. This include different forms of protection according to the International Union for Conservation of Nature (IUCN) classification, ranging from strict protected area (Category Ia) to areas where resources can be utilized sustainably (Category VI). The extent of suitable and optimal habitat for the plants that are located on protected land were then estimated.

3 | RESULTS

3.1 | African sandalwood's occurrences with respect to environmental factors

The models of African sandalwood occurrence performed well, with the three regions exhibited AUC values greater than 0.87, sensitivity and specificity greater than 0.86, and TSS greater than 0.75 (Table S2). The species occurrence data that were gathered by the public appears to be biased due to proximity to human activities, notably in the eastern and the horn of Africa regions (regions 1 and 2) (Figure 4; Table S3). For data from the horn of Africa (region 2),

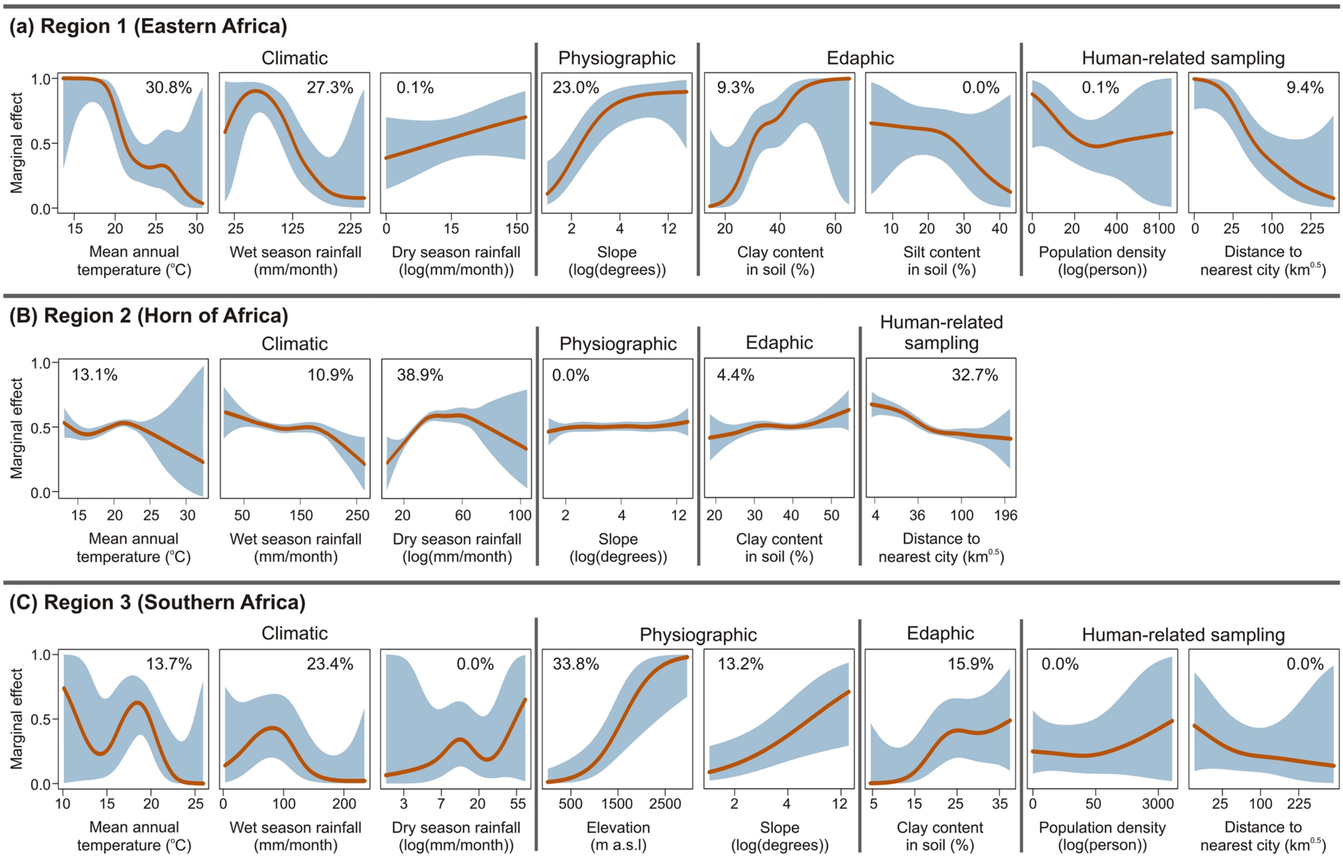

FIGURE 4 Marginal effects of the relevant predictors on the occurrence of African sandalwood estimated by the generalized additive models (GAMs), for (a) eastern Africa (region 1), (b) horn of Africa (region 2), and (c) southern Africa regions (region 3). The list of predictors for each region is shown in Equations 1, 2, and 3. The shaded blue area indicates the 95% confidence interval.

proximity to the nearest city explained 32.7% of the total variation. In the eastern region (region 1), human-related sampling bias was moderate, with proximity to the nearest city accounting for 9.4% of the total variation in the data.

The plant's distribution was found to be subject to regional environmental variations. For the eastern population (region 1), climatic and physiographic aspects were the most important predictors of species occurrence. Mean annual temperature, wet season precipitation, and slope were responsible for 30.8%, 27.2%, and 23% of the overall variation in the data, respectively (Figure 4; Table S3). The species' occurrence rate decreased with rising mean annual temperature (optimum at 15–20°C) and wet season rainfall (optimum at 0–100 mm/month) but increased with increasing slope (optimum at >5°) (Figure 4a). Climate variables were the only factors that had a significant impact on the occurrence of species in the horn of Africa (region 2). Here, the mean annual temperature and the volume of rainfall during the dry season explained 38.9% and 13.1% of the total variation in the data, respectively (Figure 4; Table S3). The rate of occurrence of the species rose with increasing amount of rainfall during the dry season (optimum at >40 mm/month), but it declined with increasing mean annual temperature (optimum at <20°C) (Figure 4b). Climatic, physiographic, and edaphic variables all had a significant impact on the southern region's population (region 3). Elevation, wet season rainfall, clay content, mean annual temperature, and slope were responsible for 33.8%, 23.4%, 15.9%, 13.7%, and 13.2% of total data variation, respectively (Figure 4; Table S3). The species' occurrence rate rose with increasing elevation, slope, and clay content. However, the species occurrence rate varied nonlinearly along the wet season rainfall and mean temperature gradients, with the species habitat optimum at an intermediate range of wet season rainfall of 50–100 mm/month and mean temperature of 18–22°C (Figure 4c).

3.2 | African sandalwood's suitable habitats and land protection status

The GAM analysis for region 1 (comprising eastern African countries and the Democratic Republic of Congo and Somalia) suggested that the area under suitable condition for the plant to survive and reproduce was estimated to be 226,950 km^2, and those under optimal condition was 447,750 km^2, respectively (Figure 5, Table 2). Suitable condition refers to an area where the species has a moderate probability of occurrence, whereas optimal condition signifies an area where the species has a high likelihood of occurrence and hence may be of greater conservation concern. For the population in region 2 (comprising the horn of African countries), the GAM analysis estimated 41,850

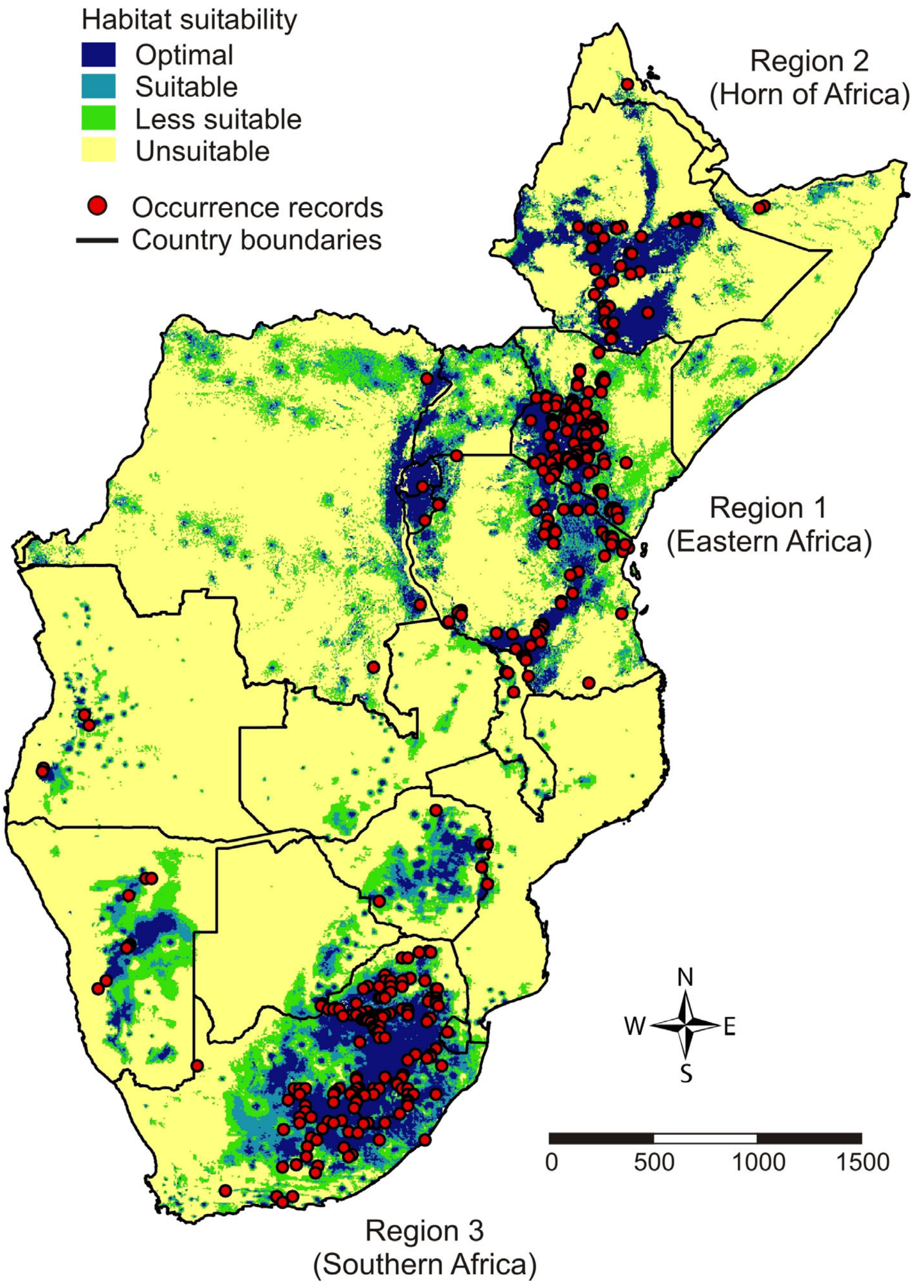

FIGURE 5 Habitat suitability maps of the African sandalwood generated by generalized additive models (GAMs) for eastern Africa, the horn of Africa, and southern Africa region.

and 225,900 km^2 to be suitable and optimal, respectively. The GAM analysis estimated that 581,450 km^2 were suitable and 134,850 km^2 were optimal for the species in region 3 (southern African countries). The total area suitable and optimal for the species' occurrence, therefore accounted for 17.30%, 13.86%, and 25.60% of the land area in the region 1, region 2, and region 3, respectively. Some localities identified as suitable for the plant to survive in each region is outlined in Table S4.

Of those areas considered suitable or optimal for the plant's survival in Africa (Figure 5), 16.16% have some form of protection ranging from strict protected area (IUCN Category Ia) to sustainably managed area (Category VI) (Table 2). Plant habitats in regions 1 and 2 encompassing eastern and the horn of Africa regions appear to be better protected than their counterparts in region 3 (southern Africa). Protected land covers 21.74% and 28.44% of plant-suitable habitats in regions 1 and 2, respectively, but only 6.31% of habitats in region 3. Nonetheless, more than two-thirds of suitable and optimal environments exist on unprotected lands, indicating that anthropogenic pressure might be significant.

4 | DISCUSSION

Climatic variables, including rainfall and temperature, was found to play an important role on determining the likelihood of African sandalwood occurrence across the three regions evaluated. Precipitation, especially during the wet season, affects the time of accessible water and its storage across soil layers, hence influencing the distribution of

Habitat suitability by region	Total area km² (% land area)		Area protected km² (% suitability class)	
Region 1, eastern Africa (total land area 3,901,800 km²)				
Unsuitable	2,160,200	55.36%	376,525	17.43%
Less suitable	1,066,900	27.34%	158,575	14.86%
Suitable	226,950	5.82%	49,475	21.80%
Optimal	447,750	11.48%	97,175	21.70%
Total suitable and optimal	674,700	17.30%	146,650	21.74%
Region 2, horn of Africa (total land area 1,045,850 km²)				
Unsuitable	708,275	67.72%	115,175	16.26%
Less suitable	69,825	6.68%	15,175	21.73%
Suitable	41,850	4.00%	9,675	23.12%
Optimal	225,900	21.60%	66,475	29.43%
Total suitable and optimal	267,750	25.60%	76,150	28.44%
Region 3, southern Africa (total land area 5,169,825 km²)				
Unsuitable	4,062,425	78.58%	1,142,000	28.11%
Less suitable	391,100	7.57%	32,400	8.28%
Suitable	581,450	11.25%	32,250	5.55%
Optimal	134,850	2.61%	12,975	9.62%
Total suitable and optimal	716,300	13.86%	45,225	6.31%

TABLE 2 Total area predicted to be unsuitable, less suitable, suitable, and optimal for the habitats of African sandalwood in eastern Africa (region 1), the horn of Africa (region 2), and southern Africa (region 3).

plant species based on rooting patterns (Lauenroth et al., 2014). Several local studies have revealed that the Africa sandalwood's vegetative and reproductive phases follow distinct patterns between the dry (warm) and wet (cool) years (Mwang'ingo et al., 2008; Rodríguez-Gallego & Navarro, 2015). This implies that rainfall throughout the wet season is vital for plant growth, development, and potential propagation. Because the plant grows in habitat-specific places where it is exposed to a variety of disturbances such as fire and herbivory, rainfall during the wet season is crucial for sprouting and coppicing. In a southern African savanna, resprout growth rates were observed to be higher during the wet than the dry season (Sebata, 2017). During the wet season, resprouts benefit from better mobilization of stored energy reserves and higher photosynthetic rates. Moreover, because the plant has mechanical dormancy and recalcitrant seeds (i.e. seeds require ambient temperatures for survival, therefore cannot be viable for more than 1 year) (Kamondo et al., 2021), the timing of the rain season and seed dissemination is vital, as advance regeneration is more significant than seed bank (Bazzar, 1991).

Temperature directly limits species ranges due to plant physiological thermal tolerances, and it interacts with precipitation to determine ecosystem water inputs (Allington et al., 2013; Bradford & Lauenroth, 2006). Temperature also has a direct impact on plant physiological processes, growth rates, phenology, and overall plant performance. Due to the temperature variations, the plants have evolved diverse mechanisms to cope with variations and maximize their growth potential (Kefford et al., 2022). The estimated temperature range we found for the eastern, southern, and the horn of Africa populations supports prior studies on the suitable range of 14–22°C for the plant to grow (Orwa et al., 2009). The range also falls between the 19–29°C temperature limit for *Santalum album* in southern India, a plant that is a member of the *Santalaceae* family (Rajan & Jayalakshmi, 2017) and highly beneficial for medicinal, cosmetic and cultural purposes (Khan et al., 2021).

Physiographic variables, particularly slope, had a major role in determining the occurrence of Africa's populations in eastern and southern Africa. Several studies have reported that slope is significant for the growth of sandalwoods (Padmanabha, 2003; Strohbach, 2012). For example, *S. album* was reported to occur in steep, well-drained locations with a 45° slope; the steepness of the terrain was thought to be crucial in preventing waterlogging conditions (Padmanabha, 2003). The steepness of the slope found in our study agrees with the reported occurrences of African sandalwood at a slope of 6° in Auas mountains, Lichtenstein mountains, Eros mountains, upper slope of Gamsberg mountain in Namibia (Strohbach, 2012). Edaphic variables, particularly clay content, also had a major role in determining the probability of African sandalwood's occurrence in eastern and southern Africa. This agrees with many studies which have reported higher clay contents where the plant occurs (Gathara et al., 2022). However, the plant has also been observed to grow in different soil types, including sand, clay red soils, laterite loam, and black-cotton soil, provided they are well drained. Even very poor and rocky soils have been reported to support its growth (Maundu & Tengnäs, 2005), as well as good, drained soils with humic friable clays (Orwa et al., 2009).

The current study identified potential sites that could serve as habitats for in situ and ex situ conservation and reintroduction of African sandalwood into the wild. Coppice management, through tending the existing rootstocks or coppices, may be a sensible solution to assist regeneration, as the plant is more of a sprouter than a seeder (Mwang'ingo et al., 2008). This can be done during the rainy season to improve the survival chances of the plantings (Sebata, 2017). As our analysis further shows that optimal habitats for Africa sandalwood are primarily found on unprotected areas, community participation in the species' conservation and management may be crucial (Borrow & Pathak, 2004). In communal and private lands, which are not under government control, community-based management may help sensitize and encourage the local community to actively participate in tending the plant's remnants through coppice management (Mwangi et al., 2023; NMK, 2019). Reforms to national legislation governing local communities' rights to engage in sustainable harvesting and propagation programs, as well as the distribution of benefits from these programs, could offer a path forward.

Our habitat suitability maps, while the first of their kind for this species, can be enhanced by including landscape characteristics such as vegetation cover. Accounting for social and economic variables could also help us better comprehend the impact of anthropogenic pressure and market-driven commerce on the plant's distribution change. Several studies on other species have included such variables in the evaluation, such as predicting the change in distribution of medicinal plants (Groner et al., 2022) and parasitic weeds (Mudereri et al., 2020), demonstrating the viability of such an approach. Notwithstanding, our map, particularly those in at-risk region of eastern Africa, can be used to advise government biodiversity conservation agencies and nongovernmental organizations on the locations of reclamation efforts for the species' deteriorated habitat. The maps can further provide critical baseline information to support national conservation and management initiatives in the three African regions across the plant's distribution range.

AUTHOR CONTRIBUTIONS

J.G.M. conceptualized the research, conducted the fieldwork, performed data analysis and interpretation, wrote the original manuscript draft, performed visualization, and validated and verified results. S.M., K.M.U., and J.H. reviewed and edited the manuscript and carried out supervision. T.S. conceptualized the research, performed data analysis and interpretation, performed visualization, validated and verified results, reviewed and edited the manuscript, and carried out supervision.

ACKNOWLEDGEMENTS

This study was supported by the RSIF-PASET program (Regional Scholarship and Innovation Fund - Partnership for Skills in Applied Sciences, Engineering and Technology). Research permit for collecting additional data for the species' locations in eastern Africa was obtained from NACOSTI (National Commission for Science, Technology, and Innovation) (Permit number: NACOSTI/P/23/23015).

CONFLICT OF INTEREST STATEMENT

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 STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Jane Gachambi Mwangi https://orcid.org/0000-0003-0341-7170
Kabir Mustapha Umar https://orcid.org/0000-0001-9170-3243
Jeremy Haggar https://orcid.org/0000-0002-4682-4879
Truly Santika https://orcid.org/0000-0002-3125-9467

REFERENCES

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, *38*(5), 541–545. https://doi.org/10.1111/ecog.01132

Allington, G. R. H., Koons, D. N., Morgan Ernest, S. K., Schutzenhofer, M. R., & Valone, T. J. (2013). Niche opportunities and invasion dynamics in a desert annual community. *Ecology Letters*, *16*(2), 158–166. https://doi.org/10.1111/ele.12023

Araújo, M. B., Anderson, R. P., Barbosa, A. M., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, *5*(1), eaat4858. https://doi.org/10.1126/sciadv.aat4858

Barbet-Massin, M., & Jetz, W. (2014). A 40-year, continent-wide, multispecies assessment of relevant climate predictors for species distribution modelling. *Diversity and Distributions*, *20*, 1285–1295. https://doi.org/10.1111/ddi.12229

Bazzar, F. A. (1991). Regeneration of tropical forest: Physiological response of pioneer and secondary specie. In A. Gomez-Pompa, T. C. Whitmore, & M. Hadley (Eds.), *Rainforest regeneration and management* (pp. 91–118). UNESCO and the Parthenon Publishing Group.

Bekele, T., Seifu, A., & Ayenew, A. (2019). Status of *Osyris quadripartita* in Borena and west Guji zones, Oromia region, Ethiopia. *Biodiversity International Journal*, *3*(2), 79–83. https://doi.org/10.15406/bij.2019.03.00131

Borrow, E., & Pathak, N. (2004). Conserving "unprotected" protected areas–communities can and do conserve areas of all sorts. The Protected Landscape Approach Linking Nature. Culture and Community, Gland, Switzerland and Cambridge, UK, 65–80.

Bradford, J. B., & Lauenroth, W. K. (2006). Controls over invasion of Bromus tectorum: The importance of climate, soil, disturbance, and seed availability. *Journal of Vegetation Science*, *17*(6), 693–704. https://doi.org/10.1111/j.1654-1103.2006.tb02493.x

Bunei, E. K. (2017). The hunt for the precious wood illegal trade of sandalwood as an international criminal enterprise in Kenya. *Society and Business Review*, *12*(1), 63–76. https://doi.org/10.1108/SBR-04-2016-0025

Chamberlain S., Barve V., Mcglinn D., Oldoni D., Desmet P., Geffert L., Ram K. (2022). Rgbif: Interface to the global biodiversity information facility API. R Package Version 3.7.0. https://CRAN.R-project.org/package=rgbif

Chun, Y., Koo, H. & Griffith, D.A. (2016). A comparison of optimal map classification methods incorporating uncertainty information. In Proceedings of the Spatial Accuracy, Avignon, France, 20–22 April 2016 pp. 177–181.

CIESIN (Center for International Earth Science Information Network). (2022). Documentation for the Gridded Population of the World, Version 4 (GPWv4), Revision 11 Data Sets. In *Palisades NY: NASA socioeconomic data and applications center (SEDAC)*. University. https://doi.org/10.7927/H45Q4T5F Accessed 23/06/2023

CITES (Convention on International Trade in Endangered Species). (2013). Inclusion of east African sandalwood Osyris lanceolata in appendix II. In convention on international trade in endangered species of wild Fauna and Flora (Issue 1832).

Díaz-Barradas, M. C., Valera, J., Esquivias, M. P., & Zunzunegui, M. (2023). The hemi-parasitic shrub Osyris lanceolata (Santalaceae) does not disturb the ecophysiology of its hosts. *Flora*, *303*, 152277. https://doi.org/10.1016/j.flora.2023.152277

Fourcade, Y., Besnard, A. G., & Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, *27*(2), 245–256. https://doi.org/10.1111/geb.12684

FSSD-MWE (Forest Sector Support Development- Ministry of Water and Environment). (2022). CITES Tree Species Programme (CTSP): Non-Detriment Findings Report on Osyris lanceolata for Uganda. Government of Uganda. https://cites-tsp.org/sites/default/files/project_files/2023-03/CTSPNDF_Ug_report_August_2022-min.pdf

Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., Husak, G., Rowland, J., Harrison, L., Hoell, A., & Michaelsen, J. (2015). The climate hazards infrared precipitation with stations - a new environmental record for monitoring extremes. *Scientific Data*, *2*(1), 1–21. https://doi.org/10.1038/sdata.2015.66

Gathara, M., Kamondo, B., Mwadalu, R., Omondi, S., Kivuti, M., Wairagu, N., Oduor, T., & Gachie, P. (2022). Influence of soil nutrients, tree age, and sandalwood provenances on sandalwood oil yield and quality. *International Journal of Forestry Research*, *2022*, 1–11. https://doi.org/10.1155/2022/1577979

GBIF (Global Biodiversity Information Facility). (2023). GBIF Occurrence Download https://doi.org/10.15468/dl.9ajz7j. Accessed on 23 June 2023

Groner, V. P., Nicholas, O., Mabhaudhi, T., Slotow, R., Akçakaya, H. R., Mace, G. M., & Pearson, R. G. (2022). Climate change, land cover change, and overharvesting threaten a widely used medicinal plant in South Africa. *Ecological Applications*, *32*(4).https://doi.org/10.1002/eap.2545

Hengl, T., Miller, M. A. E., Križan, J., Shepherd, K. D., Sila, A., Kilibarda, M., Antonijević, O., Glušica, L., Dobermann, A., Haefele, S. M., McGrath, S. P., Acquah, G. E., Collinson, J., Parente, L., Sheykhmousa, M., Saito, K., Johnson, J.-M., Chamberlin, J., Silatsa, F. B. T., … Crouch, J. (2021). African soil properties and nutrients mapped at 30 m spatial resolution using two-scale ensemble machine learning. *Scientific Reports*, *11*(1). https://doi.org/10.1038/s41598-021-85639-y

Janitza, S., Strobl, C., & Boulesteix, A. L. (2013). An AUC-based permutation variable importance measure for random forests. *BMC Bioinformatics*, *14*(1), 1–11. https://doi.org/10.1186/1471-2105-14-119

Jefferson, T. A., Becker, E. A., & Huang, S. L. (2023). Influences of natural and anthropogenic habitat variables on indo-Pacific humpback dolphins Sousa chinensis in Hong Kong. *Endangered Species Research*, *51*, 143–160. https://doi.org/10.3354/esr01249

Kamondo, B. M., Kariuki, J. G., Nyamongo, D. O., Giathi, G., Wafula, A. W., & Muturi, G. (2021). Effect of temperature and storage duration on viability of east African sandalwood. *East African Agricultural and Forestry Journal*, 10–17.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 1–20. https://doi.org/10.1038/sdata.2017.122

Kefford, B. J., Ghalambor, C. K., Dewenter, B., Poff, N. L., Hughes, J., Reich, J., & Thompson, R. (2022). Acute, diel, and annual temperature variability and the thermal biology of ectotherms. *Global Change Biology*, *28*(23), 6872–6888. https://doi.org/10.1111/gcb.16453

Khan, S., Ikram, M., & Faisal, M. (2021). *Commercial, cosmetic, and medicinal importance of sandal (Santalum album): Avaluable forest resource* (pp. 129–144). Non-Timber Forest Products: Food, Healthcare, and Industrial Applications. https://doi.org/10.1007/978-3-030-73077-2_6

Khayota, B., Mwamodenyi, J., Ojuang, F. B., Kyalo, S., Gachie, P., Lusweti, A. M., Saitabau, H., Nyingi, J. K., Kamau, J., Kagunyu, L., Nduta, M., & Kipkoech, S. (2021). Cites Tree Species Programme. Conservation and Sustainable Management of Osyris lanceolata, for Economic Development in East Africa. Output 3.1: Conducting Forest Inventories, management measures, production with a view of establishing Harvesting Quota: F. https://cites-tsp.org/sites/default/files/project_files/2023-03/CTSP_Kenya_Inventory_Report_final-min.pdf

Lauenroth, W. K., Schlaepfer, D. R., & Bradford, J. B. (2014). Ecohydrology of dry regions: Storage versus pulse soil water dynamics. *Ecosystems*, *17*(8), 1469–1479. https://doi.org/10.1007/s10021-014-9808-y

Maundu, P., & Tengnäs, B. O. (2005). Useful trees and shrubs for Kenya. In *ICRAF technical handbook series edition no.35*. World agroforestry Centre- eastern and Central Africa Regional Programme (ICRAF-ECA).

Morales, M. B., Merencio, Á., & de la Morena, E. L. G. (2023). Evaluation of a potential umbrella species using favourability models: The case of the endangered little bustard (*Tetrax tetrax*) and steppe birds. *Biodiversity and Conservation*, *32*, 3307–3327. https://doi.org/10.1007/s10531-023-02655-2

Mudereri, B. T., Abdel-Rahman, E. M., Dube, T., Landmann, T., Khan, Z., Kimathi, E., Owino, R., & Niassy, S. (2020). Multi-source spatial data-based invasion risk modeling of Striga (Striga asiatica) in Zimbabwe. *GIScience and Remote Sensing*, *57*(4), 553–571. https://doi.org/10.1080/15481603.2020.1744250

Mugula, B. B., Kiboi, S. K., Kanya, J. I., Egeru, A., Okullo, P., Curto, M., & Meimberg, H. (2021). Knowledge gaps in taxonomy, ecology, population distribution drivers, and genetic diversity of African sandalwood (*Osyris lanceolata* Hochst. & Steud.): A scoping review for conservation. *Plants*, *10*(1780), 1–18. https://doi.org/10.3390/plants10091780

Mugula, B. B., Omondi, S. F., Curto, M., Kiboi, S. K., Kanya, J. I., Egeru, A., Okullo, P., & Meimberg, H. (2023). Microsatellites reveal divergence in population genetic diversity, and structure of *Osyris lanceolata* (Santalaceae) in Uganda and Kenya. *BMC Ecology and Evolution*, *23*(1), 73. https://doi.org/10.1186/s12862-023-02182-2

Mukonyi, K. W, Kyalo, S., Lubia, I. K., Leitoro, E., Mutungi, P., Mbaka, R. M., Lusweti, A. M., Kamau, P., & Mutwiri, F. M. (2012). Status and distribution of East African Sandalwood (Osyris lanceolata) in Kenya: A rapid assessment Kenya Wildlife Service Report −2012.

Mwang'ingo, P. L., Teklehaimanot, Z., Hall, J. B., & Zilihona, J. E. (2008). Sex distribution, reproductive biology, and regeneration in the dioecious species Osyris lanceolata (African sandalwood) in Tanzania. *Tanzania Journal of Forestry and Nature Conservation*, *76*(1), 118–133. https://doi.org/10.4314/tjfnc.v76i1.40723

Mwang'ingo, P. L., Teklehaimanot, Z., Hall, J., & Lulandala, L. L. (2003). African sandalwood (*Osyris lanceolata*): Resource assessment and quality variation among populations in Tanzania. *The Southern African Forestry Journal*, *199*(1), 77–88. https://doi.org/10.1080/20702620.2003.10431751

Mwangi, J. G., Haggar, J., Mohammed, S., Santika, T., Umar, K. M., & Kingdom, U. (2023). The ecology, distribution, and anthropogenic threats of multipurpose hemi-parasitic plant *Osyris lanceolata*. *Journal for Nature Conservation*, *76*, 126478. https://doi.org/10.1016/j.jnc.2023.126478

Mwangi, J. G., Njoka, J. T., & Spaling, H. (2021). The cultural beliefs, values, and utilization of East Africa sandalwood Osyris lanceolata (Hochst & Steud.) in and around Chyulu Hills ecosystem, Kenya. *Ethnobotanical Research and Applications*, *22*, 1–18. https://doi.org/10.32859/era.22.12.1-18

NMK (National Museums of Kenya). (2019). Project to the Convention on International Trade in Endangered Species (CITES): "Supporting sustainable management of endangered tree species": Conservation and Sustainable Management of Osyris lanceolata, for Economic Development in East Africa. https://cites-tsp.org/wp-content/uploads/2019/06/KE-TZ-UG-PCA-no-budget_compressed.pdf. Accessed 28 August 2022.

Ochanda, V. K. (2009). Conservation and management of sandalwood trees: (Osyris lanceolata Hochst & Steudel,) in Chyullu Hills Kibwezi District, Kenya. published Msc Theses, Kenyatta University, Kenya.

Omay, P. O., Muthama, N. J., Oludhe, C., Kinama, J. M., Artan, G., & Atheru, Z. (2023). Changes and variability in rainfall onset, cessation, and length of rainy season in the IGAD region of eastern Africa. *Theoretical and Applied Climatology*, *152*(1–2), 871–893. https://doi.org/10.1007/s00704-023-04433-0

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., & Simons, A. (2009). *Osyris lanceolata agroforestry database: A tree reference and selection guide version 4.0. Osyris lanceolata Hochst. & Steud. Ex a.* DC. *Santalaceae*. Available from: Http://www.Worldagroforestry.org/af/treedb/. Last Accessed date 10-20-2011.

Padmanabha, H.S.A. (2003). Information memorandum on investment opportunity of Indian Sandalwood. <http://www.quintis.com>. Accessed 15 February 2021.

Rajan, N. M., & Jayalakshmi, S. (2017). Predictive species habitat distribution modelling of indian sandalwood tree using GIS. *Polish Journal of Environmental Studies*, *26*(4), 1627–1642. https://doi.org/10.15244/pjoes/68887

Rodríguez-Gallego, C., & Navarro, T. (2015). Vegetative and reproductive phenological patterns in coastal dunes in S Spain. *Anales Del Jardin Botanico de Madrid*, *72*(1), 1–17. https://doi.org/10.3989/ajbm.2371

Searcy, C. A., & Shaffer, H. B. (2016). Do ecological niche models accurately identify climatic determinants of species ranges? *American Naturalist*, *187*, 423–435. https://doi.org/10.1086/685387

Sebata, A. (2017). Ecology of Woody plants in African savanna ecosystems. In Y. Zubaida (Eds.),*Plant Ecology - Traditional Approaches to Recent Trends*(pp.25-42). https://doi.org/10.5772/intechopen.69865

Semenya, S. S., & Maroyi, A. (2019). Source, harvesting, conservation status, threats and management of indigenous plant used for respiratory infections and related symptoms in the Limpopo province, South Africa. *Biodiversitas*, *20*(3), 789–811. https://doi.org/10.13057/biodiv/d200325

Strohbach, B. J. (2012). Providing relevant, useful information on Namibian vegetation types. *Agricola*, *22*.

Teixeira Da Silva, J. A., Kher, M. M., Soner, D., & Nataraj, M. (2016). African sandalwood or Nepalese sandalwood: A brief synthesis. *Notulae Scientia Biologicae*, *8*(1), 57–61. https://doi.org/10.15835/nsb.8.1.9714

Thoithi, W., Blamey, R. C., & Reason, C. J. C. (2021). Dry spells, wet days, and their trends across southern Africa during the summer rainy season. *Geophysical Research Letters*, *48*(5), 1–10. https://doi.org/10.1029/2020GL091041

Thomson, L. A. J. (2020). Looking ahead–global sandalwood production and markets in 2040, and implications for Pacific Island producers. *Australian Forestry*, *83*(4), 245–254. https://doi.org/10.1080/00049158.2020.1841441

Thuiller, W., Lafourcade, B., Engler, R., & Araujo, M. B. (2009). BIOMOD – A platform for ensemble forecasting of species distributions. *Ecography*, *32*, 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Těšitel, J., Li, A.-R., Knotková, K., McLellan, R., Pradeepa, C. G., & Bandaranayake, D. M. W. (2021). The bright side of parasitic plants: What are they good for? *Plant Physiology*, *185*(4), 1309–1324. https://doi.org/10.1093/plphys/kiaa069

UNEP-WCMC. (2019). *User manual for the world database on protected areas and world database on other effective area-based conservation measures: 1.6*. UNEP-WCMC. Available at: http://wcmc.io/WDPA_Manual

van Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J., & Raes, N. (2016). Minimum required number of specimen records to develop accurate species distribution models. *Ecography*, *39*(6), 542–552. https://doi.org/10.1111/ecog.01509

Wilson, B. 2018. Osyris lanceolata. The IUCN red list of threatened species 2018: E.T200642A2675362. https://doi.org/10.2305/IUCN.UK.2018-1.RLTS.T200642A2675362.en. Accessed on 01 October 2024

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *73*(1), 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Zaniewski, A. E., Lehmann, A., Overton, J. M. (2002). Predicting species spatial distributions using presence-only data: A case study of native New Zealand ferns. *Ecological Modelling*, *157*, 261–280. https://doi.org/10.1016/S0304-3800(02)00199-0

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Mwangi, J. G., Mohammed, S., Umar, K. M., Haggar, J., & Santika, T. (2025). Towards the sustainability of African sandalwood: Understanding the distribution and environmental requirements. *Plants, People, Planet*, 1–13. https://doi.org/10.1002/ppp3.10630