



Mapping the potential habitat suitability and opportunities of bush encroacher species in Southern Africa: a case study of the SteamBioAfrica project

Javier Bravo-García¹, Juan Camarillo-Naranjo², Francisco J. Blanco-Velázquez¹, Félix González-Peñaloza¹, María Anaya-Romero¹

¹ Evenor-Tech, Avda. República Argentina, 27 B, A6, Seville, Spain

² Department of Physical Geography and Regional Geography Analysis, University of Seville, Seville, Spain

Corresponding author: Javier Bravo-García (j.bravo@evenor-tech.com)

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Abstract

Senegalia mellifera (Benth) Seigler & Ebinger., *Dichrostachys cinerea* (L.) Wight & Arn. and *Terminalia sericea* Burch. Ex DC., are three important bush encroacher species that contribute to the well-known ecological process named “thicketization” in Southern Africa. This issue has persisted for many years, impacting species distribution, plant communities, soil, and fauna dynamics. According to climate change projections, Southern Africa is expected to become drier and warmer in future scenarios, creating favourable conditions for proliferation of bush encroacher species. MaxEnt is a general-purpose machine learning method widely utilized in various ecological and biological scenarios to predict the potential suitable habitat of species. This is achieved by incorporating presence-only occurrence records and bioclimatic, and topographic variables. The analysis was performed in a Geographic Information System based on the current and future suitable areas for the respective Shared Socioeconomic Pathways (SSP) scenarios according to INM-CM5-0, UK-ESM1-0-LL and MPIES-M1-2-HR climate models. This was done to assess the potential effects of climate change on the distribution patterns of bush encroacher species. Model performance was assessed by the area under the curve (AUC) of the receiver operator characteristic (ROC), with 0.836, 0.822 and 0.738 as results to *Terminalia sericea*, *Dichrostachys cinerea* and *Senegalia mellifera* respectively. The current results show that *Senegalia mellifera* presents a habitat suitability of 56% (1,460,353 km²) of the total area, while *Terminalia sericea* and *Dichrostachys cinerea* have suitability over 37.9% (996,168 km²) and 43.9% (1,154,645 km²) of the area, respectively. These findings indicate that precipitation and temperature variables are the most important factors in explaining the spatial distribution of the

bush encroacher species, predicting a future increase between 8–29.4%, 2.8–24%, and 3–24.2% for *Senegalia mellifera*, *Terminalia sericea*, and *Dichrostachys cinerea* respectively. Furthermore, each species has its own set of important variables and different ecological behaviour patterns. These results imply that an improved understanding of the response of woody species to a changing climate is important for managing bush encroachment in savanna ecosystems.

Highlights

- Based on our analysis, *Senegalia mellifera* is currently suitable in 56% of the total area; while 43.9% of the total area is suitable for *Dichrostachys cinerea*, and 37.87% of the total area is currently suitable for *Terminalia sericea*. In the future scenarios, the habitat suitability increases for all three species compared to the current state.
- The unsuitable areas decrease in all the proposed scenarios with respect to the present, predicting a shrub expansion in the future throughout southern Africa. Furthermore, our results imply that *Senegalia mellifera* is the most potentially affected by bush encroachment in future changes, with a larger distribution area in future scenarios. These findings are supported by many studies, which indicate the probable increase of woody cover and loss of grasslands.
- Temperature and precipitation patterns are the main drivers behind the distribution of these bush encroachers, increasing or decreasing the competitiveness of these species according to these variables and their phenotypic plasticity.

- The increase in habitat suitability occurs throughout the case study, but there is a clear trend of shrub expansion towards the south of the case study. The change maps show a pattern of shrub movement towards South Africa and Botswana. This would fit with climate predictions for South Africa, which predict a decrease in rainfall in the east and north of the country, being more suitable for shrub competitive species.

Keywords

Bush encroaching, climate change, *Dichrostachys cinerea*, habitat suitability, MaxEnt, *Senegalia mellifera*, *Terminalia sericea*, thickening

Introduction

“Thicketization”, “bush encroachment” or “woody plant encroachment” are different concepts used to explain the natural phenomenon characterized by an increase in density of woody plant bushes in the different savanna and grassland land uses (Archer et al. 2017; Schreiner-McGraw et al. 2020; Soubry and Guo 2022; Basant et al. 2023). The concept was first introduced by Bews (1917), describing an increase in the density of species of the genus *Acacia* sp., that refers to the one now classified as *Vachellia* sp. Or *Senegalia* sp. (O'Connor et al. 2014). This phenomenon has emerged as one of the most important problems of the rangelands. This impact will increase in the future, affecting the species distribution and altering the interactions between plant communities, soil, and fauna dynamics (Van Wilgen et al. 2022; Weber-Grullon et al. 2022).

Referring to the impact on rangelands and its effects on species distribution and plant-soil-fauna interactions, it aligns with the modern two-layer theory of savanna ecology (Kulmatiski and Beard 2013). According to this theory, savannas are characterized by a distinct vertical structure consisting of an upper layer dominated by trees and a lower layer dominated by grasses and herbaceous plants. If the herbaceous layer is over exploited, it loses its competitive edge and becomes unable to efficiently utilize water and nutrients, increasing the infiltration rate into the subsoil, favouring the growth of shrubs and trees, enabling them to assume the dominance (De Klerk 2004; Kulmatiski and Beard 2013). In this context, the encroachment of certain plant species or the disruption of natural disturbance regimes can lead to changes in the composition and structure of both the upper and lower layers of the savanna ecosystem (De Klerk 2004; Kulmatiski and Beard 2013). However, this theory is still inconclusive and recent literature suggests that it may be an oversimplification of the root system patterns among savanna plants overlooking the issue of plasticity in root development and

response to environmental conditions (Kulmatiski and Beard 2013; Nakanyala and Hipondoka 2020).

It will pose a challenge to identify a singular factor as the exclusive reason for the disruptions linked to bush encroachment, particularly considering the spatial correlation of all influencing environmental variables (Kgosikoma and Mogotsi et al. 2013; Archer et al. 2017). The explanations of the main causal factors of this dynamic include changes in fire regimes, livestock grazing, loss of browsing herbivores, intensive harvesting of woody plants for fuel, pressure, nutrient availability and climate change (Kgosikoma and Mogotsi 2013; O'Connor et al. 2014; Turpie et al. 2019). The uncontrolled proliferation of woody plants in arid and semi-arid grasslands suggests the importance of broad-scale factors, such as climate change and increases in atmospheric CO₂. These southern Africa regions that are affected by the bush encroachment coincide with high-risk areas due to rising temperatures in the forthcoming decades (Beck et al. 2018; Engelbrecht 2019).

However, many studies have shown that the spread of bushes in semi-arid areas can also have substantially effects (Archer et al. 2017; Cai et al. 2020; Li et al. 2023b). Depending on the species, the soil under shrubs is often characterised by a higher organic substrate, seeds and nutrients than the soils without patches with shrub vegetation, following the ‘fertile island’ effect (Eldridge and Ding 2020). Furthermore, there is growing evidence that soil under shrubs and with controlled grazing was found to be more stable and had higher soil nutrient content, creating more favourable conditions for further vegetation development (Stafford et al. 2017; Cai et al. 2023). These favourable conditions for the development of biodiversity, raw materials, improved soil quality, etc., may coin the ecosystem service term (IPBES 2019).

The central issue in the woody plant encroachment is the role of the water and the landscape water balance. Several studies have shown that bush encroachment increases evapotranspiration and may lead to excessive water use contributing to more severe droughts (Grygoruk et al. 2014; IPCC 2021; Schick and Ibsch 2021). On the other hand, woody vegetation can improve ecosystem services with good management plans (Soliveres and Eldridge 2014; Stafford et al. 2017). According to the literature, soil carbon, microbial activity, nitrogen storage and above-ground net primary productivity were significantly higher under the trees/shrubs layer compared to herbaceous layer (Montané et al. 2010; Li et al. 2016; Turpie et al. 2019). Despite the above positive points shown above, the overgrowth of some shrub species such as *Senegalia mellifera*, which produces a very competitive lateral root system, displaces the herbaceous cover, decreasing biodiversity and drastically altering the habitat (O'Connor et al. 2014). This is the reason why it is so important to know the main areas of bush encroachment zones and where these species are distributed. This is important for good rangeland management that maintains a balance between herbaceous and shrub/shrub cover, avoiding the economic and ecosystem services losses (Briske et al. 2017; IPCC 2021).

Ecological Niche Modeling (ENM) has become a fundamental tool for understanding species' ecological requirements and predicting their distribution patterns, particularly in light of current and future environmental changes (Hirzel and Lay 2008; Franklin 2013). This approach allows researchers to identify the environmental conditions suitable for species survival and forecast potential shifts due to climatic factors. Various methodologies have been developed within ENM, each with its unique characteristics and specific applications, including generalized linear models (GLMs), generalized additive models (GAMs), genetic algorithm for rule set production (GARP), random forest models (RF), maximum entropy models (MaxEnt), and artificial neural network (ANN) models have been used to predict the distributions (Stockman et al. 2005; Elith et al. 2006; Chievrini et al. 2023; Munna et al. 2023a). Species distribution modelling has demonstrated its potency in conservation biogeography, serving as a valuable tool for predicting or extending knowledge into geographical areas where information is lacking (Franklin 2013). Nevertheless, an important point that these models do not consider how species interact in their environment in the presence of other species, i.e., biotic interactions (Araújo and Luoto 2007). It has been shown that interspecific interactions, such as competition for resources, predation and symbiosis, change in one way or another the possible distribution of species in their environment (Pearson and Dawson 2003; Abati et al. 2020). A further factor not considered in such models is the evolution and the genetic adaptation of species (Guisan and Zimmermann 2000). The potential for rapid genetic evolution is immense, occurring mainly in insects and plants, expanding their geographical limits of distribution by becoming more dispersive and/or adapting to incessant climate change (Maron 2004; Garnas 2018; Catullo et al. 2019).

Bioclimatic factors in the study area are projected to change in unprecedented ways. Temperatures in Namibia, Botswana and western South Africa are expected to experience significant warming, ranging from 0.2–0.5 °C per decade, leading to an increase in the number of hot days (Beck et al. 2018; Engelbrecht 2019; Gornott 2023). Precipitation is projected to experience overall reductions in mean annual rainfall by mid-century, showing that the semi-arid and arid areas are likely to become drier than more humid areas. Furthermore, in spite of the projected decreases in rainfall, extreme rainfall events are going to increase over most of the central-east coast of South Africa in low-high mitigation scenarios. (Beck et al. 2018; Engelbrecht 2019; IPCC 2019; Gornott 2023).

The encroachment of both native and non-indigenous invasive woody species, exacerbated by the impacts of climate change, is causing significant environmental, social, and economic harm (De Klerk 2004; Archer et al. 2017). The SteamBioAfrica project aims to demonstrate the application of a superheated steam method to convert invasive woody biomass into environmentally friendly solid biofuel and water across Namibia, Botswana and South Africa. By promoting optimal shrub harvesting and land management techniques and establishing a market for the biomass produced, the ini-

tiative seeks to stimulate effective land restoration. This, in turn, will create promising opportunities for households and industries, benefiting both rural and urban environments.

The selection of three specific species—*Terminalia sericea*, *Dichrostachys cinerea*, and *Senegalia mellifera*—is based on their generalist behaviour, invasiveness, and biomass potential in semi-arid areas, aligning closely with the project's objectives (Fig. 3) (Pedroso and Kaltschmitt 2012; Moyo et al. 2015; Ofentse et al. 2022; Neethling 2023). *Terminalia sericea*, known as “silver cluster-leaf,” thrives along mid-slope seep-lines, forming dense clusters and yielding substantial biomass (Moyo et al. 2015). Widely used as fuelwood and for medicinal purposes in southern Africa, it is a key focus of the initiative (Moyo et al. 2015). *Dichrostachys cinerea*, or “sickle bush,” possesses attributes suitable for clean energy generation and medicinal uses due to its rapid growth, high biomass density, and low burning emissions (Pedroso and Kaltschmitt 2012; Ofentse et al. 2022). *Senegalia mellifera*, commonly known as ‘black thorn’, is the most problematic species causing significant economic losses due to the bush thickening (Neethling 2023). With diverse uses as an energy resource, medicinal plant, and livestock feed, it is another crucial target for the project (Neethling 2023).

The study aims to elucidate the likely distribution of these three species, developing habitat suitability maps based on climate change scenarios proposed by the IPCC in 2021 following an accepted and well-known methodology (Fig. 1). This will increase knowledge about the behaviour patterns of these three invasive shrub species according to the proposed variables. Thus, soil management plans will be strengthened, adapted and improved, in addition to identify the main areas where the species can grow easily, providing additional knowledge for the exploitation of the resources. For instance, transforming the biomass of highly bush encroached areas into clean biofuel and condensate containing water and biochemicals with economic potential during the SteamBioAfrica project. Furthermore, we will use the model's results to verify and compare the state of bush encroachment in southern Africa with existing literature, as well as its future outlook.

Methods

Study site

Our case study (Fig. 2) unfolds in Southern Africa, a region characterized by its unparalleled ecological diversity (Cowling and Hilton-Taylor 1994). Encompassing an expansive area of over 2.5 million km², this part of the continent boasts landscapes that span the spectrum. From the arid deserts of Namibia to the subtropical and humid regions along the South African coast.

Namibia has a total area of 825,418 km² and is the driest country in southern Africa, mainly in the southwest, and slightly wetter in the northeast region bordering Botswana, with over 600 mm of rainfall per year (Harris et al. 2020).

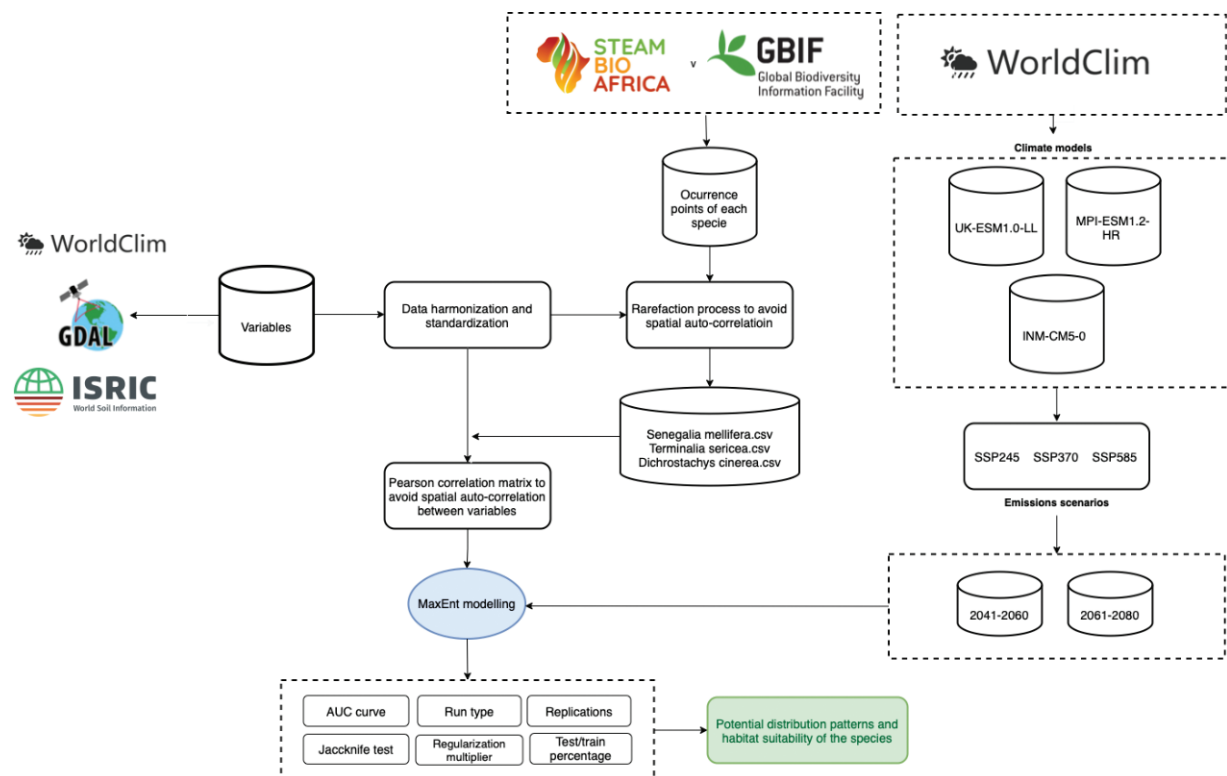


Figure 1. Schematic methodology representation.

It has an average altitude of 700 m.a.s.l and an average annual temperature ranging from 16 °C, more common in the southwest region, to 26 °C. Soils of the arenosol type predominate throughout the eastern half of the country, developed on quartz-rich aeolian sediments, followed in abundance by leptosols, distributed in the western half of the country (Jones et al. 2013; Atlas of Namibia 2022).

Botswana covers an area of over 600,370 km², with an average elevation of over 1100 m.a.s.l. (Harris et al. 2020). Approximately 80% of the country is covered by the Kalahari Desert, one of the world's largest bodies of sand. Rainfall varies from 250 mm in the extreme southwest to 650 mm in the NE, with a warm semi-arid climate predominating over most of Botswana except in the southern part. Arenosols soil predominated over much of Botswana, along with alluvial or colluvial soils (Jones et al. 2013; The Botswana National Atlas).

Finally, South Africa is the largest and most rugged country with 1.22 million km² and an average elevation of

1200 m.a.s.l. (Harris et al. 2020). The range of rainfall is very wide, being 100 mm in the southwest and over 1500 in the southeast, with an average of 465 mm. With an average annual temperature of 17.5 °C, the temperatures are also very variable, ranging from 15–36 °C in summer and -2–26 °C in winter. The variety of climates is greater than in the previous countries, with more humid climates such as the subtropical climate on the southeast coast of the country. In addition, there is also a wide variety of soils than in the other two countries, with leptosols predominating somewhat more prevalent in the south, but also lixisols, vertisols, gypsisols, etc (Jones et al. 2013; Cole et al. 2017; Harris et al. 2020).

The arid tropical climate of the Namib Desert and Kalahari Desert covers large parts of Namibia, Botswana, and certain parts of South Africa (Gornott et al. 2023). A tropical humid to sub-humid climate covers the northern part of Botswana and Namibia, increasing the humidity towards the coastal regions of South Africa, where a sub-humid climate prevails (Gornott et al. 2023).

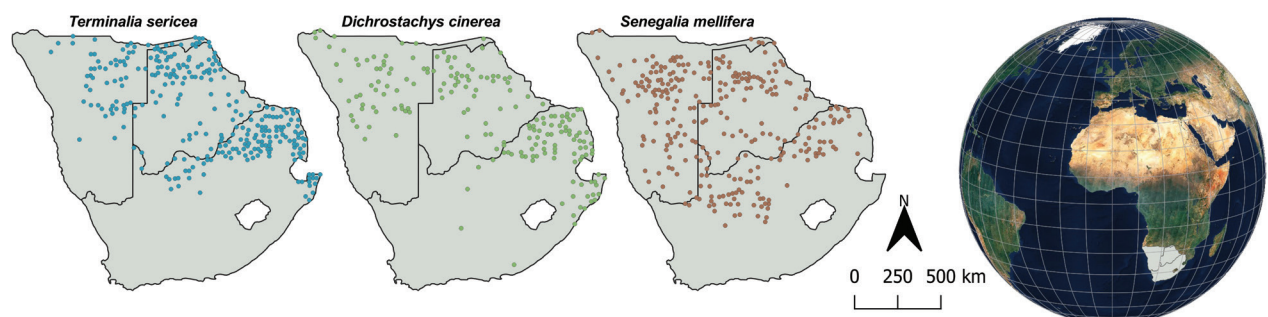


Figure 2. Rarefied occurrence points used in MaxEnt modelling to predict suitable habitat for (A) *Terminalia sericea* (B) *Dichrostachys cinerea* and (C) *Senegalia mellifera*.

Natural distribution data

The presence of species *Senegalia mellifera*, *Terminalia sericea*, and *Dichrostachys cinerea* predominantly occur in savanna ecosystems characterized by seasonal variability in precipitation and temperatures. These species are typically found in areas with annual precipitation ranging from 400 to 1000 mm and mean annual temperatures between 18 °C and 32 °C, depending on the species (Orwa et al. 2009; Guajardo et al. 2010). *Senegalia mellifera*, for instance, is commonly associated with well-drained sandy soils and prefers regions with 400 to 900 mm of rainfall per year (Guajardo et al. 2010). Similarly, *Terminalia sericea* thrives in areas with precipitation levels between 500 and 1000 mm annually, favoring sandy, well-drained soils and temperatures from 20 °C to 30 °C (Orwa et al. 2009). *Dichrostachys cinerea* is known for its adaptability to poorer, compacted soils, often occurring in areas with 300 to 700 mm of rainfall and temperatures between 20 °C and 32 °C (Orwa et al. 2009).

Distribution data for *Senegalia mellifera*, *Dichrostachys cinerea* and *Terminalia sericea* were obtained from literature and the Global Biodiversity Information Facility (GBIF), which compiles a lot of historical and current information on species for each country (Fig. 2). In many cases, this data is biased, fixing mainly large point clouds around urban centers. Therefore, the original layer of points

indicating the distribution of the species is rarefied to avoid the tendency to accumulate many points of occurrence in the same area, preventing models overfit due to spatial autocorrelation and sampling bias. The data was spatially rarefied at approx. 10 km using Python in Visual Studio Code.

For instance, in the case of *Terminalia sericea*, there are a total of 1,017 occurrence points (120 in Namibia, 328 in Botswana, and 569 in South Africa). *Senegalia mellifera* has a total of 755 occurrence points (285 in South Africa, 280 in Botswana, and 190 in Namibia) and *Dichrostachys cinerea* has a total of 1,336 occurrence points (893 in South Africa, 320 in Botswana, and 123 in Namibia). After the rarefaction process for *Terminalia sericea*, *Senegalia mellifera*, and *Dichrostachys cinerea*, they were modeled with 286, 281, and 186 occurrence points respectively.

Environmental data

During the development of the ENMs for these species, the selection of environmental variables was grounded in an extensive review of the existing literature and empirical data on the factors influencing species occurrence (Orwa et al. 2009; Guajardo et al. 2010; Abati et al. 2020; Nakanyala et al. 2020; Shikangalah et al. 2021; Neethling et al. 2023). Precipitation and temperature variables were prioritized as they have been identified as critical determinants

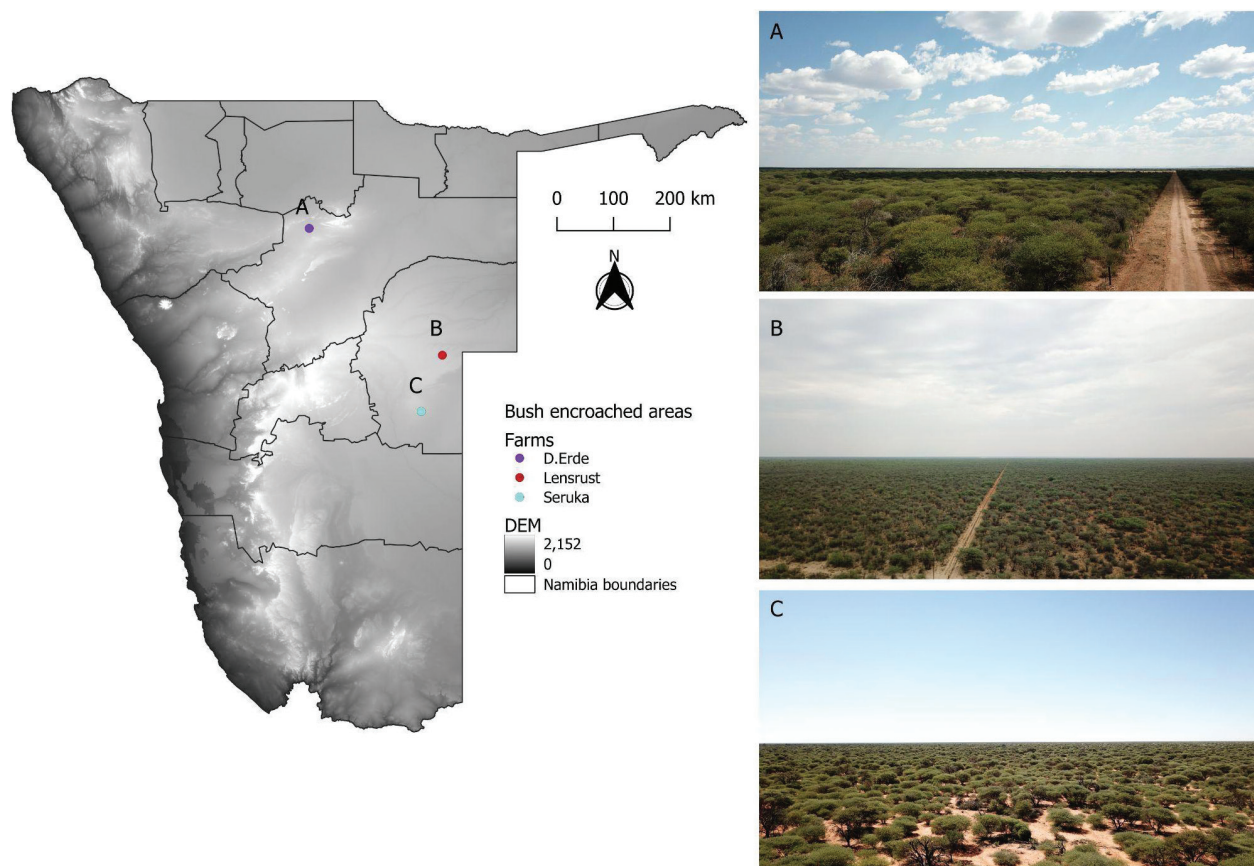


Figure 3. Different encroached farms of Namibia; (A) *Dichrostachys cinerea* and *Terminalia prunoides* encroached zone at Farm Deutsche Erde (Colin Lindeque, Carbon Capital, 8th May 2019), (B) *Terminalia sericea* encroached zone in Farm Lensrust (Colin Lindeque, Carbon Capital, 19 November 2018) and (C) *Senegalia mellifera* encroached zone in Farm Seruka (Colin Lindeque, Carbon Capital, 24th April 2019).

of spatial distribution in these species, directly influencing their growth, survival, and competitive interactions in savanna ecosystems. (Orwa et al. 2009; Nakanyala et al. 2020; Shikangalah et al. 2021).

Three types of variables: edaphic (pH, CEC, coarse fragments, clay, silt, sand and bulk density), physical (slope, elevation, roughness and aspect) and bioclimatic (19 bioclimatic variables) were selected based on research and literature on the habitat of woody encroachers (Table 1). There were 30 variables in total, but not all of them were implemented in the models because the high complexity of the iterations did not reflect reality; in this case, a parsimonious model was followed with a small set of variables for each model (Merow et al. 2013).

The elevation was obtained from WorldClim, a database of high spatial resolution global weather and climate data. This variable was excluded from the modelling due to the controversial use in future projections owing to correlations of elevation with temperature and precipitation (Austin 2007; Hof et al. 2012). Through the elevation layer, it was possible to calculate the other topographic variables in the QGIS environment. The 19 bioclimatic variables were obtained from the WorldClim website (Fick and

Hijmans 2017). The remaining variables were acquired using the SoilGrid download platform. Subsequently, all 30 environmental variable raster data were resampled using QGIS 3.22 to ensure consistent characteristics, range boundaries, and a unified projection coordinate system, specifically EPSG 4326 - WGS84. Finally, the resampled raster data were converted to ASCII format, as required by MaxEnt software (Phillips et al. 2004). Edaphic and physical variables are considered “constant” over time, therefore, the only variables that change in the future scenarios are the bioclimatic ones.

Future projections were made using the shared socio-economic pathways (SSPs) for greenhouse gas concentrations, specifically SSP245-585 across two-time horizons: 2041–2060 and 2061–2180. We utilized WorldClim 1-km resolution climate data from three global Earth System Models (ESMs) from the sixth phase of the Coupled Model Intercomparison Project (CMIP6) that obtained better results than CMIP5 models (Bouramdane 2022; Mmame and Ngongondo 2024): the Max Planck Institute for Meteorology Earth System Model (MPI-ESM1.2-HR), the Hadley Climate Center Earth System Model (UK-ESM1.0-LL) and the Institute Model for Numerical Mathematics (INM-CM5-0).

Table 1. Variables selected for testing in the MaxEnt model. We used environmental variables (clay, sand, silt, coarse fragments, bulk density, pH, cation exchange capacity, elevation, slope, roughness and aspect) and bioclimatic variables from WorldClim (bio1–bio19).

Bioclimatic variables	Code	Resolution	Source
Annual Mean Temperature	BIO1	30 s (~ 1 km)	WorldClim
Mean Diurnal Range	BIO2	30 s (~ 1 km)	WorldClim
Isothermality (BIO2/BIO7)*100	BIO3	30 s (~ 1 km)	WorldClim
Temperature seasonality	BIO4	30 s (~ 1 km)	WorldClim
Max Temperature of the Warmest month	BIO5	30 s (~ 1 km)	WorldClim
Min Temperature of Coldest Month	BIO6	30 s (~ 1 km)	WorldClim
Temperature Annual Range	BIO7	30 s (~ 1 km)	WorldClim
Mean Temperature of Wettest Quarter	BIO8	30 s (~ 1 km)	WorldClim
Mean Temperature of Driest Quarter	BIO9	30 s (~ 1 km)	WorldClim
Mean Temperature of Warmest Quarter	BIO10	30 s (~ 1 km)	WorldClim
Mean Temperature of Coldest Quarter	BIO11	30 s (~ 1 km)	WorldClim
Annual Precipitation	BIO12	30 s (~ 1 km)	WorldClim
Precipitation of Driest Month	BIO13	30 s (~ 1 km)	WorldClim
Precipitation of Wettest Month	BIO14	30 s (~ 1 km)	WorldClim
Precipitation Seasonality	BIO15	30 s (~ 1 km)	WorldClim
Precipitation of Wettest Quarter	BIO16	30 s (~ 1 km)	WorldClim
Precipitation of Driest Quarter	BIO17	30 s (~ 1 km)	WorldClim
Precipitation of Warmest Quarter	BIO18	30 s (~ 1 km)	WorldClim
Precipitation of Coldest Quarter	BIO19	30 s (~ 1 km)	WorldClim
Environmental variables	Code	Resolution	Source
Clay content	clay	250 m	SoilsGrid
Sand	sand	250 m	SoilsGrid
Silt	silt	250 m	SoilsGrid
Coarse fragments	coarsefrg	250 m	SoilsGrid
Bulk density	bd	250 m	SoilsGrid
pH	pH	250 m	SoilsGrid
Cation Exchange Capacity	CEC	250 m	SoilsGrid
Elevation	DEM	30 s (~ 1 km)	WorldClim
Slope	slope	30 s (~ 1 km)	Own source
Roughness	roughness	30 s (~ 1 km)	Own source
Aspect	aspect	30 s (~ 1 km)	Own source

There are four primary Shared Socio-economic Pathways (SSPs) as outlined by Meinshausen et al. (2022). Among them, SSP275-585, which represents medium-high emissions, was chosen due to its alignment with the current global climate change mitigation efforts. This selection reflects the existing policies and clean energy initiatives (IPCC 2021) as well as ongoing disputes over global carbon emission reductions. Notably, some economically advanced nations have shown reluctance in ratifying the Kyoto Protocol (Hovi et al. 2010), further supporting the relevance of SSP3-7.0 in today's context.

The UK-ESM1.0-LL, MPI-ESM1.2-HR and INM-CM5-0 models were chosen for this study because, as noted by Volodin et al. (2019), Gutjahr et al. (2019), and Tang et al. (2019), they have structurally separate ocean and atmosphere model components. In terms of climate sensitivity, MPI-ESM1.2-HR and INM-CM5-0 are low climate-sensitive models, while UK-ESM1.0-LL is a high climate-sensitive model (Gutjahr et al. 2019; Tang et al. 2019; Volodin et al. 2019). Furthermore, these models were well correlated in the southern Africa region (Nooni et al. 2023; Mmame and Ngongondo 2024).

Modelling approach

MaxEnt 3.4.4 software was used to create the species distribution models (SDM), which requires environmental variables, presence data and the selection of the various features to find the distribution which has maximum entropy (Elith et al. 2011; Radosavljevic and Anderson. 2014; Phillips et al. 2017).

In the feature selection, the data were split into two groups; 25% of the distribution points were randomly chosen as the test data set and the remaining 75% of the distribution were used as a training data set. The maximum number of iterations of the model was set to 5000 and the number of repetitions was set to 10. In this way, the model was iterated 10 each time using a different test and training subset. The method employed for repetition was "bootstrapping", aimed at enhancing result variability and subsequently utilizing the average output, giving the possibility to set the training and test configuration to the models (Phillips et al. 2006; Shekede et al. 2016). Cloglog was selected as output format.

The contribution of the different variables was calculated marking the jackknife test analysis in the software (Shekede et al. 2018; Yan et al. 2020). The regularization multiplier was set to 2 to avoid overfitting of the results (Yan et al. 2020; Ahmadi et al. 2022). We have selected hinge (H), product (P), quadratic (Q), linear (L) and threshold (T) feature classes as best combination accepted by the expert community in niche modeling (Elith et al. 2006; Slater and Michael 2012; Mengfei et al. 2022).

High correlation and collinearity between variables can easily lead to the overfitting of the model, thus affecting the accuracy of the resulting predictions, so Pearson correlation matrix through Python was done, compared with

jackknife test (leave-one-out strategy) in MaxEnt (Pearson et al. 2007; Ashraf et al. 2016; Li et al. 2023b; Cárdenas et al. 2023). In order to eliminate multicollinearity effects in the parameters of the SDM, the variables with $r \geq 0.8$ or $r \leq -0.8$ were excluded (Cao et al. 2016; Ashraf et al. 2016; Li et al. 2023b; Cárdenas et al. 2023).

Model performance was assessed by the area under curve (AUC) of the receiver operator characteristic (Elith et al. 2006; Li et al. 2023b; Cárdenas et al. 2023; Munna et al. 2023b). Models with more than 0.7 AUC are considered satisfactory for our study. It is generally thought that $AUC < 0.7$ indicates low accuracy of the model, so prediction results can be adopted when AUC is between 0.7–1, meaning that the prediction results are very accurate, which can be used for subsequent analysis (Alvarado-Serrano and Knowles 2014; Pascoe et al. 2019; Cárdenas et al. 2023).

Finally, the species distribution and habitat suitability map were produced by averaging the 10 replicate runs. Moreover, the habitat suitability thresholds from the model were reclassified using the "10th percentile training minimum presence" (T) of each species model (Vale et al. 2013; Radosavljevic and Anderson 2014). *Terminalia sericea* obtained a T = 0.38, *Senegalia mellifera* a T = 0.49 and *Dichrostachys cinerea* obtained a T = 0.36. In this way, we considered unsuitable areas where the pixel showed probability values under this threshold (T) for each specie. Values between T - 0.60 are considered as "low suitability", 0.60–0.80 as "moderate suitability" and > 0.80 as "highly suitable" (Ashraf et al. 2016; Ngarega 2021).

Results

A total of 57 distribution maps were acquired, with three generated under current conditions and 54 under conditions of climate change. The AUC values spanned from 0.738 to 0.836, denoting their classification performance as favourable ($0.8 < AUC < 0.9$). Specifically, *Terminalia sericea* with a mean AUC of 0.836, *Senegalia mellifera* with 0.738 and *Dichrostachys cinerea* with 0.822.

The outputs from the model were reclassified according to the common threshold established. The next tables show the area of the habitat suitability in km² and % for each climate model, climate scenario and in the different periods.

Habitat suitability for *Terminalia sericea* is mainly associated with annual precipitation (bio12; 55.2%) and annual mean temperature (bio1; 31.2%) (Table 2). It is mainly concentrated in the north-central, north-western, and east-central areas, with the species virtually absent from southern Namibia and north-western South Africa, and its habitat suitability restricted to the northern and eastern limits of the study area (Fig. 4). *Terminalia sericea* improves its habitat suitability compared to the current situation in all scenarios and time periods, with a maximum area gain of 24% in 2061–2080 for the UK-ESM1.0-LL climate model in the SSP585 scenario. The lowest area gains of 3% is in 2041–2080 for the MPI-ESM1.2-HR climate model for the SSP245 scenario (Table 7). Additionally, the catego-

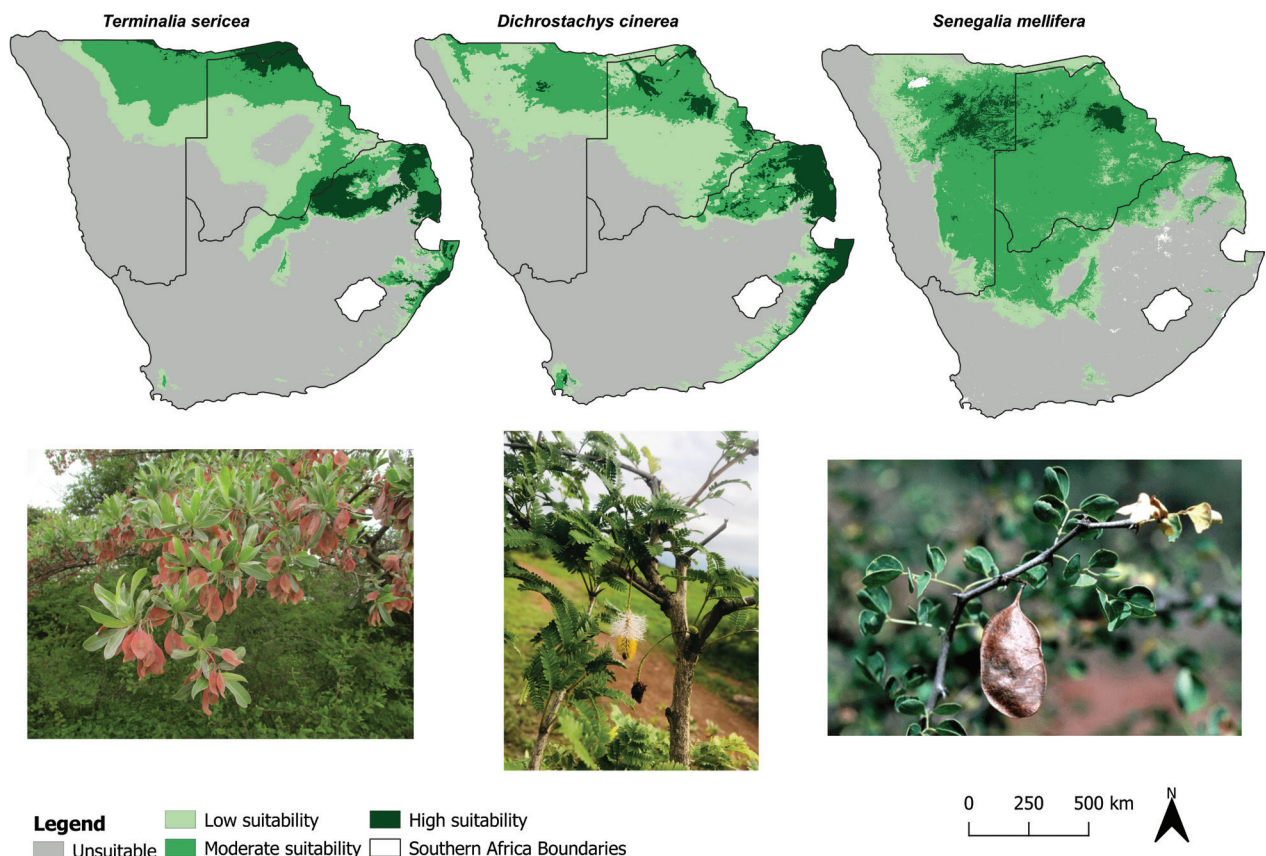


Figure 4. Habitat suitability in the current scenario. This map illustrates variations in habitat suitability for the species, featuring distinct colors to delineate areas deemed unsuitable or suitable for the species. The color spectrum is utilized to convey different levels of suitability: areas in dark green represent the highest suitability, while light green signifies low suitability. Unsuitable areas for the species are depicted in grey.

ries of high suitability register their maxima in the SSP585 emission scenarios, with the UK-ESM1.0-LL climate model recording the highest value in the period 2061–2080, with up to 32.4% high suitability for the species. On the other hand, the INM-CM5-0 climate model shows lower values, reaching up to 23% for the same period and emission scenario, followed by the MPI-ESM1.2-HR with 25.5% under the same conditions (Table 4).

Prediction of habitat suitability for *Senegalia mellifera* was widespread and mainly associated with mean temperature of wettest quarter (bio8; 50.9%), annual mean temperature (bio1; 27.4%) and annual mean precipitation (bio12; 11.1%) (Table 2). The distribution of this species is the most habitat-adapted, occurring over much of central southern Africa, and is absent from the entire west coast of Namibia and the wetter areas of southern South Africa (Fig. 4). *Senegalia mellifera* improves its habitat suitability in all scenarios, with a maximum increase of 29.4% in 2061–2080 for UK-ESM1.0-LL climate model in the SSP585 scenario as happened with *Terminalia sericea*. The lowest gain is registered in the 2041–2060 period, with the INM-CM5-0 climate model, to the SSP245 scenario, with only an 8% of increase in distribution (Table 7).

Additionally, the categories of high suitability register their maxima in the SSP585 emission scenarios, with the UK-ESM1.0-LL climate model recording the highest value

in the period 2061–2080, with up to 58.6% high suitability for the species. On the other hand, the INM-CM5-0 climate model shows lower values, reaching up to 34.9% for the same period and emission scenario, followed by the MPI-ESM1.2-HR with 45.7% under the same conditions (Table 5).

For *Dichrostachys cinerea*, the most related variables are precipitation in the driest month (bio13; 41.3%), mean temperature in the coldest quartile (bio11; 21.8%) and seasonality of temperatures (bio4; 18.9%) (Table 2). The distribution of *Dichrostachys cinerea* has the greatest increase in suitability with respect to the unsuitable areas in the current scenario. Distribution includes southwest of Botswana and northwest of South Africa, with high habitat suitability in the northern half of Namibia and Botswana and northeast of South Africa (Fig. 4). *Dichrostachys cinerea* improves its habitat suitability according to model variables with a maximum area gain of 24.2% during 2061–2080 period, for UK-ESM1.0-LL climate model in the SSP585 scenario as the other species. The lowest gain corresponds to the MPI-ESM1.2-HR climate model, in the SSP245 scenario during the 2041–2060 period, with only 3% of increase of suitable areas (Table 7).

Furthermore, high suitability categories reach their peaks in the SSP585 emission scenarios, with the UK-ESM1.0-LL climate model registering the highest value for the 2061–2080 period, showing up to 47.6% high suitability

Table 2. Mean model outputs from MaxEnt models to predict habitat suitability in southern Africa for three bush encroacher species.

Variables	Code	<i>Terminalia sericea</i>		<i>Dichrostachys cinerea</i>		<i>Senegalia mellifera</i>	
		Percent contribution	Permutation importance	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Annual Mean Temperature	BIO1	31.1	38.2	6.2	15.2	27.4	31.3
Mean Diurnal Range	BIO2	na	na	na	na	na	na
Isothermality (BIO2/BIO7)*100	BIO3	na	na	na	na	na	na
Temperature seasonality	BIO4	2.6	5.9	18.9	12.4	6.6	10.9
Max Temperature of the Warmest month	BIO5	na	na	na	na	na	na
Min Temperature of Coldest Month	BIO6	9.6	3.5	na	na	na	na
Temperature Annual Range	BIO7	1.4	2.9	11.9	30.7	na	na
Mean Temperature of Wettest Quarter	BIO8	na	na	na	na	50.9	16.7
Mean Temperature of Driest Quarter	BIO9	na	na	na	na	na	na
Mean Temperature of Warmest Quarter	BIO10	na	na	na	na	na	na
Mean Temperature of Coldest Quarter	BIO11	na	na	21.8	11.3	na	na
Annual Precipitation	BIO12	55.2	49.5	na	na	11.1	24.6
Precipitation of Driest Month	BIO13	na	na	41.3	30.3	na	na
Precipitation of Wettest Month	BIO14	na	na	na	na	na	na
Precipitation Seasonality	BIO15	na	na	na	na	na	na
Precipitation of Wettest Quarter	BIO16	na	na	na	na	na	na
Precipitation of Driest Quarter	BIO17	na	na	na	na	na	na
Precipitation of Warmest Quarter	BIO18	na	na	na	na	na	na
Precipitation of Coldest Quarter	BIO19	na	na	na	na	na	na
Clay content	clay	na	na	na	na	na	na
Sand	sand	na	na	na	na	na	na
Silt	silt	na	na	na	na	na	na
Coarse fragments	coarsfrg	na	na	na	na	3.9	16.5
Bulk density	bd	na	na	na	na	na	na
pH	pH	na	na	na	na	na	na
Cation Exchange Capacity	CEC	na	na	na	na	na	na
Elevation	DEM	na	na	na	na	na	na
Slope	slope	na	na	na	na	na	na
Roughness	roughness	na	na	na	na	na	na
Aspect	aspect	na	na	na	na	na	na

Table 3. Habitat suitability of the species under current climate scenario.

Habitat suitability	<i>Senegalia mellifera</i>		<i>Terminalia sericea</i>		<i>Dichrostachys cinerea</i>	
Category	Area (km ²)	(%)	Area (km ²)	(%)	Area (km ²)	(%)
Unsuitable	1147234.4	44.0	1634000.7	62.1	1475523.4	56.1
Suitable	1460353.8	56.0	996168.2	37.9	1154645.5	43.9
Low suitability	347455.6	13.3	418297.5	15.9	588943.6	22.4
Moderate suitability	1033229.6	39.6	430823.1	16.4	428755.0	16.3
High suitability	79668.6	3.1	147047.6	5.6	136946.9	5.2

for the species. Conversely, the INM-CM5-0 climate model records lower values, with a maximum of 29.7% for the same period and emission scenario, followed by the MPI-ESM1.2-HR at 36.53% under the same conditions (Table 6).

Discussion

This study predicted habitat suitability for the species *Senegalia mellifera*, *Dichrostachys cinerea*, and *Terminalia sericea* in the southern African region. Distribution predictions were carried out under three different climate models (INM-CM5-0, UK-ESM1.0-LL and MPI-ESM1.2-HR), three emission scenarios (SSP245, SSP370 and SSP585) for the periods 2041–2060 and 2061–2080, highlighting changes relative from the current state. We used the Max-Ent methodology to predict areas at higher or lower risk

of bush encroachment and to identify the key drivers influencing the distribution of these species. This approach provides valuable insights to support future tasks related to climate change and its underlying drivers that affect the distribution patterns of plant species. All models outperformed chance, achieving AUC values greater than 0.736 in all cases, with the *Terminalia sericea* model (mean AUC = 0.836) achieving the highest value.

In general terms, all three species show a pattern of increasing habitability in previously uninhabited areas according to climate scenarios and time periods. Habitability rises as the expected concentration of greenhouse gasses increases for each scenario. The SSP245 scenario (medium pathway of future greenhouse gas emissions) assumes that climate protection measures are being taken, while registering the lowest increase in habitat suitability among the climate change scenarios. Conversely, the

Table 4. *Terminalia sericea* change between scenarios. The model was built under three CMIP6 climate models (MPI-ESM1.2-HR, UK-ESM1.0-LL and INM-CM5-0) and two periods of time (2041–2060 and 2061–2080).

Time period	Habitat suitability	Senegalia mellifera climate models and emission scenarios											
		INM-CM5-0				UK-ESM1.0-LL				MPI-ESM1.2-HR			
		SSP245 (km²)	%	SSP370 (km²)	%	SSP245 (km²)	%	SSP370 (km²)	%	SSP245 (km²)	%	SSP370 (km²)	%
2041–2060	Unsuitable	928580.2	35.6	873144.8	33.5	849512.2	32.6	632117.3	24.2	539693.2	20.7	515546.7	19.8
	Suitable	1679008.0	64.4	1734443.4	66.5	1758076.0	67.4	1975470.9	75.8	2067895.0	79.3	2092041.5	80.2
	Low suitability	246713.3	9.5	236136.6	9.1	255231.1	9.8	211587.6	8.1	204602.3	7.8	199003.1	7.6
	Moderate suitability	974404.1	37.4	951222.0	36.5	913350.2	35.0	754758.4	28.9	641830.2	24.6	616790.5	23.7
2061–2080	High suitability	457890.7	17.6	547084.9	21.0	589494.7	22.6	1009124.9	38.7	1221462.6	46.8	1276247.8	48.9
	Unsuitable	869185.7	33.3	742393.7	28.5	683928.8	26.2	510980.9	19.6	416545.9	16.0	381876.1	14.6
	Suitable	1738402.5	66.7	1865194.5	71.5	1923659.4	73.8	2096607.3	80.4	2191042.3	84.0	2225712.1	85.4
	Low suitability	243989.6	9.4	218026.5	8.4	220400.4	8.5	191733.0	7.4	180873.7	6.9	167256.0	6.4
	Moderate suitability	980264.0	37.6	844356.6	32.4	792590.7	30.4	621628.0	23.8	579928.0	22.2	530999.6	20.4
	High suitability	514148.9	19.7	802811.4	30.8	910668.3	34.9	1283246.3	49.2	1430240.5	54.8	1527456.5	58.6

Table 5. *Senegalia mellifera* change between scenarios. The model was built under three CMIP6 climate models (MPI-ESM1.2-HR, UK-ESM1.0-LL and INM-CM5-0) and two periods of time (2041–2060 and 2061–2080).

Time period	Habitat suitability	Terminalia sericea climate models and emission scenarios											
		INM-CM5-0				UK-ESM1.0-LL				MPI-ESM1.2-HR			
		SSP245 (km²)	%	SSP370 (km²)	%	SSP245 (km²)	%	SSP370 (km²)	%	SSP245 (km²)	%	SSP370 (km²)	%
2041–2060	Unsuitable	1322301.6	50.3	1311514.4	49.9	1222655.3	46.5	1112278.2	42.3	1071213.7	40.7	1064833.6	40.5
	Suitable	1307867.3	49.7	1318654.5	50.1	1407513.6	53.5	1517890.6	57.7	1558955.2	59.3	1565335.3	59.5
	Low suitability	434230.3	16.5	380103.7	14.5	206358.5	7.8	494565.9	18.8	464141.5	17.6	463103.6	17.6
	Moderate suitability	440573.2	16.8	464829.6	17.7	509748.7	19.4	453154.6	17.2	456716.5	17.4	450509.8	17.1
2061–2080	High suitability	433063.8	16.5	473721.3	18.0	691406.5	26.3	570170.2	21.7	638097.2	24.3	651721.9	24.8
	Unsuitable	1325043.9	50.4	1229514.5	46.7	1189522.7	45.2	1051173.3	40.0	1043700.3	39.7	1001239.4	38.1
	Suitable	1305125.0	49.6	1345490.6	51.2	1440646.2	54.8	1578995.6	60.0	1586468.6	60.3	1628929.4	61.9
	Low suitability	323162.8	12.3	323162.8	12.3	413203.8	15.7	458821.0	17.4	462040.1	17.6	412148.8	15.7
	Moderate suitability	446716.4	17.0	459912.3	17.5	422069.2	16.0	456385.2	17.4	431728.7	16.4	364602.8	13.9
	High suitability	535245.8	20.4	562415.5	21.4	605373.3	23.0	663789.4	25.2	692699.8	26.3	852177.9	32.4

Table 6. *Dicrostachys cinerea* change between scenarios. The model was built under three CMIP6 climate models (MPI-ESM1.2-HR, UK-ESM1.0-LL and INM-CM5-0) and two periods of time (2041–2060 and 2061–2080).

Time period	Habitat suitability	Dichrostachys cinerea climate models and emission scenarios																	
		INM-CM5-0				UK-ESM1.0-LL				MPI-ESM1.2-HR									
		SSP245 (km ²)	%	SSP370 (km ²)	%	SSP585 (km ²)	%	SSP245 (km ²)	%	SSP370 (km ²)	%	SSP585 (km ²)	%	SSP370 (km ²)	%	SSP585 (km ²)	%		
2041–2060	Unsuitable	1358133.2	51.6	1294573.8	49.2	1166255.5	44.3	1119215.6	42.6	1043170.1	39.7	1042242.9	39.6	1397773.6	53.1	1240426.3	47.2	1272302.0	48.3733948
	Suitable	1272035.7	48.4	1335595.1	50.8	1463913.4	55.7	1510953.3	57.4	1586998.8	60.3	1587926.0	60.4	1232395.3	46.9	1389742.5	52.8	1357866.9	51.6266052
	Low suitability	459844.2	17.5	379808.8	14.4	349981.1	13.3	352005.1	13.4	320151.9	12.2	322766.5	12.3	437220.2	16.6	416900.4	15.9	408706.1	15.5391564
	Moderate suitability	437526.7	16.6	401174.3	15.3	331330.8	12.6	379313.4	14.4	324476.3	12.3	346149.1	13.2	314569.1	12.0	327187.6	12.4	322029.7	12.2436878
2061–2080	High suitability	374664.8	14.2	554612.0	21.1	782601.5	29.8	779634.7	29.6	942370.5	35.8	919010.4	34.9	480606.0	18.3	645654.5	24.5	627131.2	23.8437609
	Unsuitable	1306886.6	49.7	1207524.4	45.9	1199494.9	45.6	995404.2	37.8	932851.1	35.5	839478.1	31.9	1246120.7	47.4	1127882.9	42.9	898520.3	34.1620781
	Suitable	1323282.3	50.3	1422644.5	54.1	1430674.0	54.4	1634764.6	62.2	1697317.8	64.5	1790690.8	68.1	1384048.2	52.6	1502286.0	57.1	1731648.5	65.8379219
	Low suitability	364018.4	13.8	301512.5	11.5	303053.5	11.5	310556.7	11.8	286373.0	10.9	251913.0	9.6	380750.7	14.5	311232.4	11.8	348467.2	13.2488521
	Moderate suitability	369174.0	14.0	343872.7	13.1	345311.6	13.1	351739.7	13.4	296800.4	11.3	287946.6	10.9	342163.0	13.0	315575.3	12.0	422426.8	16.0608225
	High suitability	590089.9	22.4	777259.3	29.6	782308.9	29.7	972468.3	37.0	1114144.4	42.4	1250831.2	47.6	661134.5	25.1	875478.4	33.3	960754.6	36.5282473

Table 7. Summary tables of percentage change between current and climate change scenarios in the two periods of time.

Time period	<i>Senegalia mellifera</i> area percentage change								
	INM-CM5-0			UK-ESM1.0-LL			MPI-ESM1.2-HR		
	SSP245 (%)	SSP370 (%)	SSP585 (%)	SSP245 (%)	SSP370 (%)	SSP585 (%)	SSP245 (%)	SSP370 (%)	SSP585 (%)
(2041–2060)	8.0	10.5	11.4	19.8	23.3	24.2	11.1	13.0	14.5
(2061–2080)	10.7	15.5	17.8	24.4	28.0	29.4	14.5	18.2	21.5
Time period	<i>Terminalia sericea</i> area percentage change								
	INM-CM5-0			UK-ESM1.0-LL			MPI-ESM1.2-HR		
	SSP245 (%)	SSP370 (%)	SSP585 (%)	SSP245 (%)	SSP370 (%)	SSP585 (%)	SSP245 (%)	SSP370 (%)	SSP585 (%)
(2041–2060)	11.9	12.2	15.6	19.8	21.4	21.6	2.8	11.4	10.5
(2061–2080)	11.7	15.4	16.9	22.1	22.4	24.0	11.0	15.3	23.2
Time period	<i>Dichrostachys cinerea</i> area percentage change								
	INM-CM5-0			UK-ESM1.0-LL			MPI-ESM1.2-HR		
	SSP245 (%)	SSP370 (%)	SSP585 (%)	SSP245 (%)	SSP370 (%)	SSP585 (%)	SSP245 (%)	SSP370 (%)	SSP585 (%)
(2041–2060)	4.5	6.2	11.8	13.5	16.4	16.5	3.0	8.9	7.7
(2061–2080)	6.4	10.2	10.5	18.3	20.6	24.2	8.7	13.2	21.9

SSP585 scenario (less optimistic), which involves drastic emissions increase, correlates with the highest expansion in habitat suitability for all three species.

The results confirm that variables related to rainfall and temperature are the most important for modeling the distribution of these bush encroacher species. *Dichrostachys cinerea* and *Terminalia sericea* showed similar changes in distribution between the current and climate change scenarios, with the species expanding their range limits mainly in South Africa and Botswana. Meanwhile, *Terminalia sericea* it does not have a big spread in Namibia, but it increases in its habitat suitability. However, *Dichrostachys cinerea* increases the distribution along the north of the case study, increasing the habitat suitability in the future scenarios. In the other hand, *Senegalia mellifera* does not respond in the exact same way. The model results record an unsuitable area of 14.6% in the SSP585 scenario (2061–2080), which in comparison to the other species (*Terminalia sericea*: 38.1%; *Dichrostachys cinerea*: 31.9%) indicates that it will be the most generalist and widespread of the three species in scenarios with drastic emissions.

The results in the percentage change between the current scenario and future scenarios also support the idea that *Senegalia mellifera* will cover the most area, with a maximum increase in suitable distribution area of up to 29.4%, obtaining a maximum suitability of 85.4% of the total area. This is followed by *Dichrostachys cinerea*, with a 24.2% of maximum increase in habitat suitability, with a maximum suitability of 68.1% of the total area. Lastly, *Terminalia sericea* shows a 24% of maximum increase, with a suitability of 61.9% of the total area. All these results indicate that the UK-ESM1.0-LL climate model and the SSP585 emission scenario for the period 2061–2080 register the highest bush encroachment. The increase in habitat suitability for the species is highest in this climate model compared to INM-CM5-0 and MPI-ESM1.2-HR, which show lower average habitat suitability.

The figure that summarises changes in habitat suitability according to the proposed scenarios shows differences and similarities in the distribution patterns of the three species (Figs 5–7). For both *Terminalia sericea* and

Dichrostachys cinerea, an increase in habitat suitability is observed in the northern part of the study area, which becomes more pronounced in the UK-ESM1.0-LL and INM-CM5-0 models, also indicating an increase in suitability across South Africa from east to west. The main difference between these two species lies in their potential distribution in Botswana, where *Dichrostachys cinerea* experiences a significant increase flowing from the north to the southeast, particularly in the scenarios of the UK-ESM1.0-LL model. *Terminalia sericea*, on the other hand, maintains low suitability, which seems to increase over time and with higher emission scenarios. In the case of *Senegalia mellifera*, Fig. 5 shows that habitat suitability is quite high, covering a large part of the study area, with high suitability increasing under higher emission scenarios. The UK-ESM1.0-LL and MPI-ESM1.2-HR models show the most significant changes in habitat suitability for this species, with a large portion of Botswana becoming highly suitable in both models.

According to the model outputs, these findings imply that *Senegalia mellifera* is the most potentially bush encroacher for the near future changes, with a larger distribution area and better habitat suitability in most of the scenarios.

This statement does not rule out or ignore the invasive potential of the remaining species due to the climate changes.

These results are similar to findings reported in other studies concerning various species. Based on studies involving growth rings and stem diameter (Shikangalah et al. 2021; Shikangalah et al. 2022), the relationships of *Dichrostachys cinerea* with wetter areas and the distinct adaptation strategy of *Senegalia mellifera* to drier regions have already been described. This species is known for its tolerance to a wider range of environmental conditions, particularly in terms of water availability and temperature extremes (Guajardo et al. 2010; Shikangalah et al. 2021; Shikangalah et al. 2022). This flexibility allows it to expand into new areas more readily under changing climate conditions, leading to a higher predicted increase in suitable habitat compared to *Terminalia sericea* and *Dichrostachys cinerea*. These other two species may have more special-

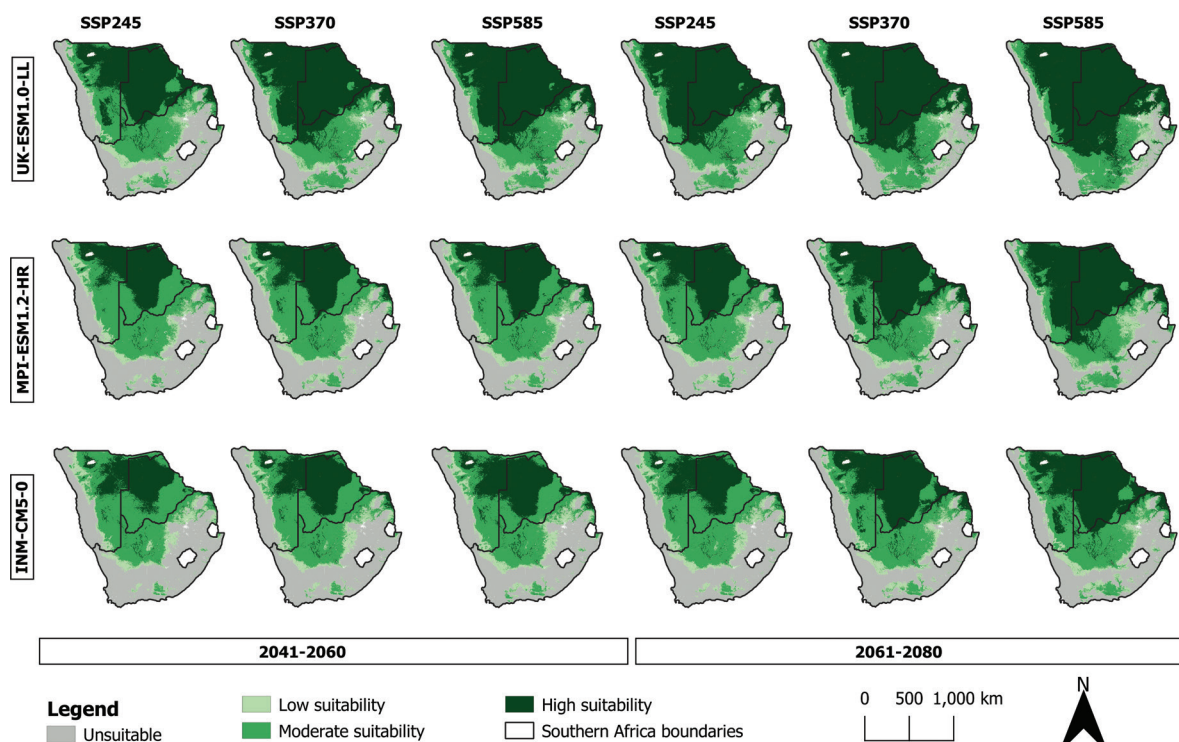


Figure 5. Habitat suitability area per scenario *Senegalia mellifera*. This map illustrates variations in habitat suitability for *Senegalia mellifera*, featuring distinct colors to delineate areas deemed unsuitable or suitable for the species. The color spectrum is utilized to convey different levels of suitability: areas in dark green represent the highest suitability, while light green signifies low suitability. Unsuitable areas for the species are depicted in grey. The map serves as a visual guide to understand how the suitability of habitat changes across different scenarios and climate models for *Senegalia mellifera*.

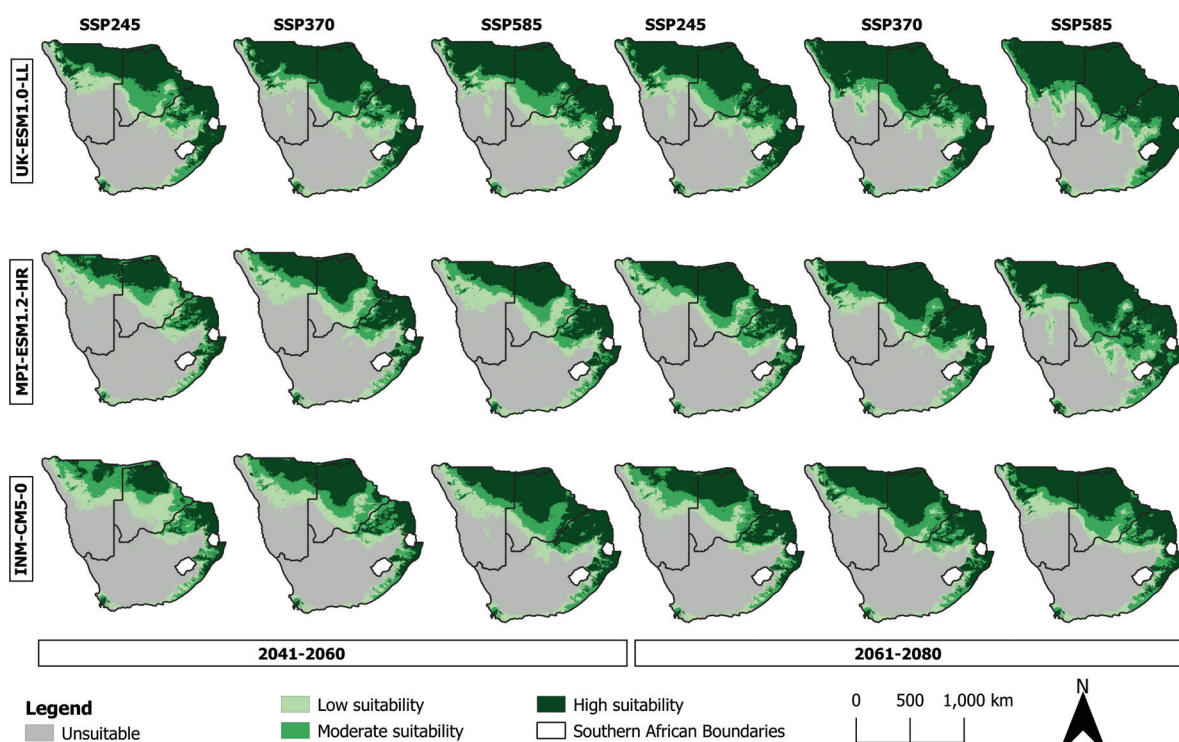


Figure 6. Habitat suitability area per scenario *Terminalia sericea*. This map illustrates variations in habitat suitability for *Terminalia sericea* featuring distinct colors to delineate areas deemed unsuitable or suitable for the species. The color spectrum is utilized to convey different levels of suitability: areas in dark green represent the highest suitability, while light green signifies low suitability. Unsuitable areas for the species are depicted in grey. The map serves as a visual guide to understand how the suitability of habitat changes across different scenarios and climate models for *Terminalia sericea*.

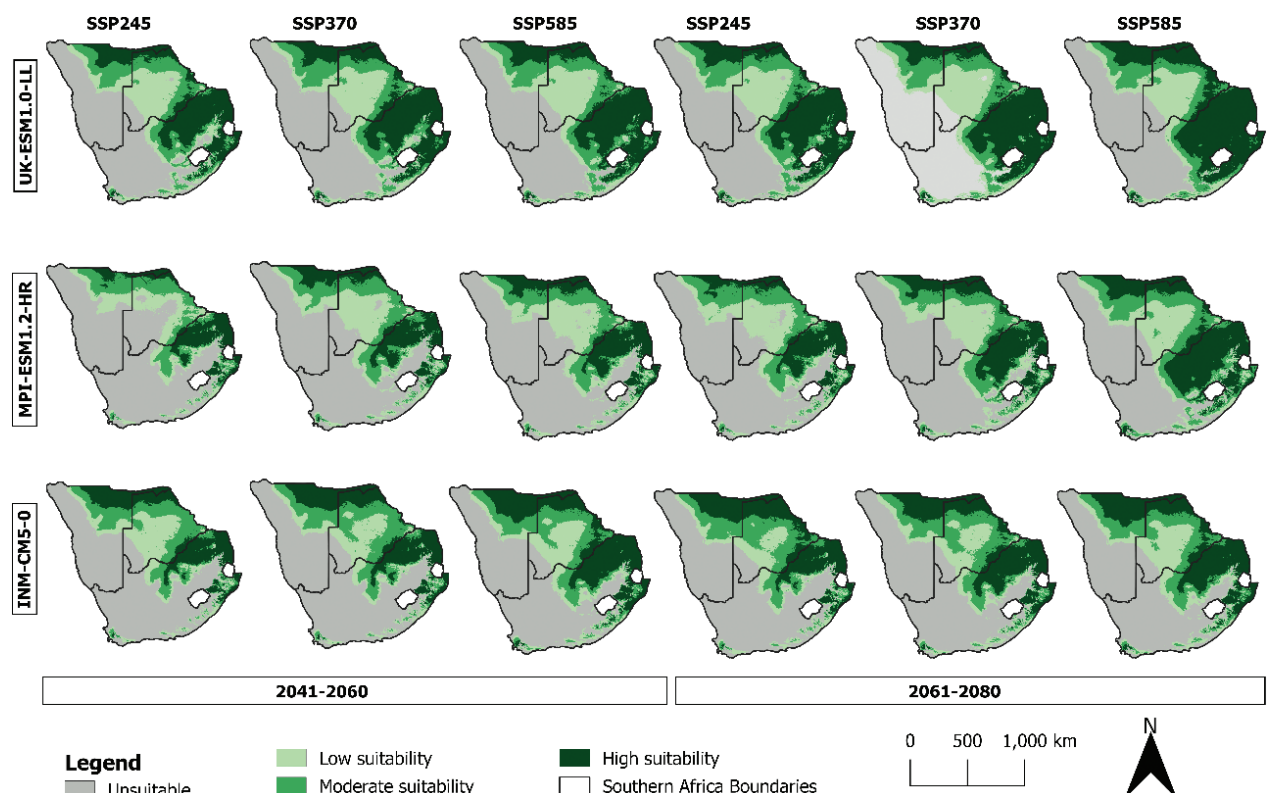


Figure 7. Habitat suitability area per scenario *Dichrostachys cinerea*. This map illustrates variations in habitat suitability for *Dichrostachys cinerea*, featuring distinct colors to delineate areas deemed unsuitable or suitable for the species. The color spectrum is utilized to convey different levels of suitability: areas in dark green represent the highest suitability, while light green signifies low suitability. Unsuitable areas for the species are depicted in grey. The map serves as a visual guide to understand how the suitability of habitat changes across different scenarios and climate models for *Dichrostachys cinerea*.

ized ecological niches, with narrower ranges of tolerance for key climatic factors.

These findings support our model outputs and underscore the importance of the variables considered. In the current distribution scenarios, the model outputs generate distribution maps highly resemblant to the existing maps describing species presence boundaries (De Klerk 2004; Turpie et al. 2019; Marggraff and Venter 2020).

According to present and future Köppen-Geiger climate classification maps by Beck et al. (2018), southern Africa will experience an increase in arid and semi-arid climate areas, especially in South Africa, relating to our species distribution results. Changes in African savanna rangelands were already predicted years ago. Authors such as Midgley et al. (2005) and Tietjen et al. (2009) already expected a decrease in herbaceous vegetation cover and an increase in shrub cover in drylands in Africa caused by the CO_2 levels, rainfall, and temperature changes. According to the most recent studies, an annual increase in shrub covers of up to 0.27% yr⁻¹ confirming global greening trends in Africa (Venter et al. 2018; Saha et al. 2015) a significant increase in vegetation optical depth (VOD) mainly in southern Africa, West and Central Africa was found (Wei et al. 2019) strengthening the idea of the continuous increase in bush encroaching, supporting our future findings in these species. All these studies conclude that the bioclimatic variables in our study are related to the increase in shrub cover throughout this region

of Africa, in addition to other hardly measurable factors as far as overgrazing or fire suppression.

Certainly, socio-ecological processes and biotic interactions pose a significant challenge to quantification and modelling in scientific research. Numerous intricate interactions between species and their environments elude precise measurement, and even models exhibiting impeccable AUC values and statistical metrics cannot ensure absolute perfection. Furthermore, the broad geographical scope of our estimates introduces inherent uncertainty into the assessment of climatic and physical suitability.

Species distribution models have emerged as invaluable tools for implementing conservation strategies or conducting studies on the impacts of climate change, particularly in expansive regions characterized by notable physical and bioclimatic gradients. However, these models predominantly rely on interpolation methods and lack a robust foundation in ecological process theory. Thus, there remains substantial room for improvement, with the development and implementation of novel methodologies being imperative for enhancing our understanding of biotic interactions.

Additionally, it is crucial for biogeographers and ecologists to recognize that the pattern of species association in joint species distribution models is influenced not only by actual biotic interactions but also by shared habitat preferences, mutual migration history, phylogenetic background, and collective responses to absent environmental drivers

(Dormann et al. 2018). Addressing the dearth of this type of data presents a formidable challenge, but it promises to greatly enhance species modeling and deepen our ecological understanding of them.

Conclusion

The objectives of this study were to investigate the potential impacts of climate change on the spatial distribution of these three bush encroachers, important woody species in southern African rangelands, and compare these findings with the existing literature. This study used INM-CM5-0, UK-ESM1.0-LL and MPI-ESM1.2-HR climate models, three emission scenarios (SSP245, SSP370 and SSP585) for the periods 2041–2060 and 2061–2080, combined with georeferenced species occurrence data. The results of the study indicate that the bioclimatic habitat of these species is expected to change significantly in response to climate change in the southern African savannas. Thus, supporting other studies that suggest the greening trends in southern Africa due to woody plant cover change. The main patterns of expansion are related to expected changes in temperature and precipitation over the century. According to the results shown above, *Terminalia sericea*, *Dichrostachys cinerea* and *Senegalia mellifera* improve their habitat suitability in almost all scenarios and time periods compared to the current one. Current results showed in Table 3 indicate that *Senegalia mellifera* exhibits the highest percentage of suitable area at 56%, though it has a smaller area of high suitability, at 3.1%. Closely following is *Dichrostachys cinerea*, with 43.9% suitable area and 5.2% highly suitable area. *Terminalia sericea* is not far behind, with 37.9% suitability and the highest percentage of highly suitable area at 5.6%.

Senegalia mellifera has the biggest increase in the area of high habitat suitability, with a 29.4% increase in the 2061–2080 time period for SSP585 scenario compared to the current scenario, making it the species with the best conditions for establishment throughout southern Africa in the future. *Dichrostachys cinerea* follows with a 24.2% and 24% for *Terminalia sericea*. In summary, *Senegalia mellifera* emerges as the most stable species covering the largest area across all scenarios. Conversely, *Dichrostachys cinerea* and *Terminalia sericea* exhibit a similar distribution pattern, with *Senegalia mellifera* being the most favoured species in future scenarios.

Finally, to contribute to the improvement of savanna rangelands management, we encourage developing new studies to enable innovative management and adaptation plans in line with ongoing climate change in the southern Africa regions. Finally, we recommend conducting validation studies at local scales, analyzing shrub regeneration and its growth in areas that were found to be highly suitable in future scenarios. This should be supported by localized studies measuring the differences between dense and sparse coverages in relation to the ecosystem. This would be very useful for future soil management plans and would support many issues addressed in the Africa 2063 agenda.

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Author contributions

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Data accessibility statement

The data used in this article are openly accessible through the following link on the Zenodo repository: [<https://zenodo.org/records/13735837>]. This ensures transparency and allows for further analysis or replication of the study by other researchers.

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