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The right tree in the right place: predicting and mapping global-scale suitable areas for Marula tree, *Sclerocarya birrea*, (A. Rich.) Horchst, subspecies cultivation, conservation, and use in restoring global drylands

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Abstract

The marula tree, *Sclerocarya birrea* (*S. birrea*) (A. Rich.) Horchst, is native to Africa, used to restore drylands, and introduced outside Africa as a pilot towards commercial cultivation due to its economic potential. However, there is a global paucity of information regarding where subspecies can survive beyond Africa. We aimed to predict and quantify global-scale suitable areas for *S. birrea* and its subspecies beyond their native ranges under the current environmental conditions and future warming climates. The areas were predicted by using MaxEnt algorithm using occurrence data from Africa and, climatic and topographical environmental variables and, the Max Planck Institute for Meteorology and Hadley Climate Center's global Earth Systems Models under shared socio-economic pathways (SSPs) greenhouse gas concentrations, SSP3-7.0, for the year 2050 and 2080. The results show that the models' predictive power was robust, with the Receiver Operating Characteristic's Area under the Curve (AUCs) ranging from 0.90-0.98. Currently, suitable areas exist in all continents except Europe and Antarctica and, occupy 3,751,057 km^2 to 24,632,452 km^2 of Earth's terrestrial area scattered in 54 to 107 countries predominantly in global biomes with climatic conditions ranging from desert tropical to temperate humid. Under future climates, the areas will retract by 64-100%, shifting to high latitudes and being limited to global biomes with tropical desert-to-desert temperate, Mediterranean warm conditions, and some regions of Eastern Europe will become suitable areas. Suitable areas for *S. birrea* and its subspecies exist beyond Africa, and they will retract and migrate to high latitudes under future warming climates.

Highlights

- The marula tree, *Sclerocarya birrea*, is a drought-tolerant multipurpose fruit tree native to Africa, with potential for global drylands restoration and rehabilitation and commercial cultivation beyond Africa, but facing declining population and poor understanding of where its subspecies can establish and strive beyond their native ranges under the current and future warming climates.
- Ecological niche modeling approach was applied to model and predict global-scale suitable areas where *S. birrea* subspecies can be conserved, cultivated, and used to restore and rehabilitate global drylands.
- The currently suitable areas for *S. birrea* subspecies will be affected differently by climate change, and subsp. *caffra* will be affected the most, followed by subsp. *multifoliata* and subsp. *birrea*, and only subspecies *birrea* and *multifoliata* will thrive under future warming climates.

Keywords: climate change, ecological niche models, GIS, machine learning, MaxEnt, restoration, species distribution modelling

Introduction

Drylands cover about 41% of the earth's terrestrial surface (Mortimore 2009, White and Nackoney 2003), which is equivalent to 54 million km^2 (Arraiza et al. 2014) and continued to expand rapidly over the last sixty years (Feng and Fu 2013). Drylands harbor over a third of the global biodiversity hotspots, with the potential for global carbon stock in the soil and vegetation estimated at 30% (Hanan et al. 2021). Over 2.5 billion people, or more than 30% of the world's population, live in drylands and rely on them for their livelihoods (Mortimore 2009, Reynolds et al. 2007). As a result, the main obstacle to sustainable development is the increase of drylands, which directly contributes to desertification (Reynolds et al. 2007). Dryland restoration is recognized globally as key to future sustainable development (James et al. 2013) with significant resources invested (Cao et al. 2011, Merritt et al. 2011, James et al. 2013). However, dryland ecosystems have a poor restoration success rate. Failures in dryland restoration are frequently caused by a lack of knowledge of the ecology and biology of species as well as a failure to take into account climate variability (Cortina et al. 2011). As drylands restoration is a long-term intervention, knowledge about species' capacity to adapt to changing climates is of urgent importance (Cortina et al. 2011). One potential species suitable for drylands restoration and rehabilitation is the Marula tree, *Sclerocarya birrea* (*S. birrea*) (A. Rich.) Horchst, a drought-tolerant, ecologically and socio-economically important fruit tree that stands out in the African landscape (Hall et al. 2002).

Native to Africa, *S. birrea* can be found in dry and semi-arid regions in over 29 African countries. Three subspecies of *S. birrea* are subsp. *birrea* (A. Rich. Horchst), subsp. *caffra* (Sond.) Kokwaro, and subsp. *multifoliata* (Engl.) Kokwaro (Hall et al. 2002, Jinga et al. 2021). Tanzania is regarded as a global center of genetic diversity because it harbors all three subspecies (Hall et al. 2002, Kadu et al. 2006). The multiple uses of *S. birrea* set it apart as an important tree in African drylands (Jinga et al. 2021). *Sclerocarya birrea* is among the native tree species used in a large-scale tree planting program, the Great Green Wall (GGW), to address the impacts of climate change, reverse desertification, and restore degraded drylands in Sahel region countries (Diallo et al. 2017). Moreover, *S. birrea* is a multipurpose fruit tree that is of ecological (Cook and Henley 2019, Gadd 2002), nutritional (Machani et al., 2007), medicinal (Hall et al. 2002), winery (Leakey et al. 2005), and cosmetic industry (Leakey et al. 2005, Mariod and Abdelwahab 2012) importance. Thus, *S. birrea* has attracted attention worldwide for domestication and commercialization due to its economic potential (Wynberg et al. 2002). Currently, *S. birrea* is part of the ICRAF/World Agroforestry Centre's African Orphan Crops Consortium program, which uses genomic research to develop tree varieties with high yields, nutritional qualities, and climate-adaptability (Hendre et al. 2019). Moreover, *Sclerocarya birrea* has been introduced outside Africa for decades now, including in Israel and China (Nerd and Yosef 1993, Hall et al. 2002, Hillman et al. 2008, Li et al. 2015) as a move toward commercial cultivation. However, its potential global-scale suitability maps have not yet been fully developed to provide guidance on where to cultivate and use it in restoring and rehabilitating drylands in and beyond its native range.

Macroecological techniques that generate quantitative projections of species abundance and distribution, over large areas, and continents level, can be used to predict the broad-scale effects of climate change on the spatial distribution of species (Kerr et al. 2007). Ecological niche models (ENMs) are correlative techniques that have been used extensively to predict potentially suitable habitats in various spatial and temporal ranges (Jiang et al. 2021, Kulhanek et al. 2011) by creating and projecting ecological niche models onto a region to create a map depicting the potential distribution of that species (Mothes et al. 2019, Ren et al. 2020). There are a variety of ENMs (Beaumont et al. 2005, Byeon et al. 2018), but maximum entropy (MaxEnt) is one that is widely used to predict species distributions (Ren et al. 2020). The MaxEnt has been successful in modeling and mapping plant species' ecological niches at the continental level, including *S. birrea* and its subspecies on the African continent (Jinga et al. 2021), and other plant species at the continental and global scale (Paź-Dyderska et al. 2021, Wang and Wan 2021) and, infectious diseases including coronavirus disease (COVID-19) (Coro and Bove 2022). Thus, the approach can be adopted for mapping and predicting suitable areas for *S. birrea* and its subspecies at a global scale.

In this study, we aimed to (i) predict and quantify global-scale suitable areas for *S. birrea* and its subspecies under the current environmental conditions, and (ii) predict and quantify global-scale suitable areas under future warming climates. The information will be useful in guiding local, regional, and continental-scale field inventories, cultivation, conservation, and use of *S. birrea* subspecies in restoring and rehabilitating global drylands in and beyond Africa.

Materials & Methods

Input Data for Ecological Niche Models

Occurrence Data

The study used *S. birrea* and its subspecies occurrence data from Africa (Figure 1). Field surveys and secondary sources were used to get subspecies occurrence data. Field surveys were conducted in Tanzania and documented 242 records for the subsp. *multifoliata* in the village of Malinzanga in the Iringa Rural district, 77 records for the subsp. *caffra* in the village of Kiegea B in the Morogoro Municipality, and 108 records for the subsp. *birrea* in Holili and Bonchugu villages in the Rombo and Serengeti districts, respectively. Additional subspecies occurrence data were obtained from the RAINBIO (Dauby et al. 2016) and the Global Biodiversity Information Facility (https://doi.org/10.15468/dl.fg5bx6) databases, yielding 1165 occurrence data, of which 750, 277, and 138 were for the subsp. *caffra*, *multifoliata*, and *birrea*, respectively.

At the species level, 2490 occurrence records for *S. birrea* were obtained from the GBIF and RAINBIO databases, which were then combined with subspecies occurrence records to give 2917 occurrence records. To avoid model over-fit due to spatial auto-correlation among occurrence data (Boria et al. 2014, Hijmans 2012), the spatial-rarefication function in the SDMToolbox software version 2.4 (Brown 2014) was used to trim the original occurrence data of *S. birrea* and its subspecies at a 1-km distance, and retain 2003, 433, 29, and 23 occurrences for *S. birrea*, subsp. *caffra*, subsp. *birrea*, and subsp. *multifoliata*, respectively (Figure 1).

Environmental variables

The study used climatic and topographical variables (Table S1). Topography and climate are considered to have a significant impact on natural species distribution at large spatial scales (Pa-Dyderska et al. 2021, Pearson and Dawson 2003, Jinga et al. 2021, Magory-Cohen et al. 2019, Stein 2015), and aridity due to leeward shadow effect (Huang et al. 2017). For the current climate (1981-2010), we obtained 19 bioclimatic variables at a 30-arc second (~1 km) spatial resolution dataset version 2.1 from Climatologies at high-resolution for the earth's land surface areas (CHELSA) database, https://chelsa-climate.org/ (Karger et al. 2017). We opted to use CHELSA data over the Worldclim data because CHELSA substantially differs from WorldClim over the mountain regions, especially for rainfall-based indicators because the basic algorithm incorporates further orographic predictors (Karger et al. 2017, Noce et al. 2020). In addition, Worldclim data overestimate precipitation and, hence, does not accurately predict species range (Karger et al. 2017). Thus, using climate data from this data source could compromise the validity of our study findings. Potential evapotranspiration and topographical environmental variables at a 1-km resolution were obtained from the Environmental Rasters for Ecological Modeling (ENVIREM) data portal- https://envirem.github.io (Title and Bemmels 2018) (Table S1).

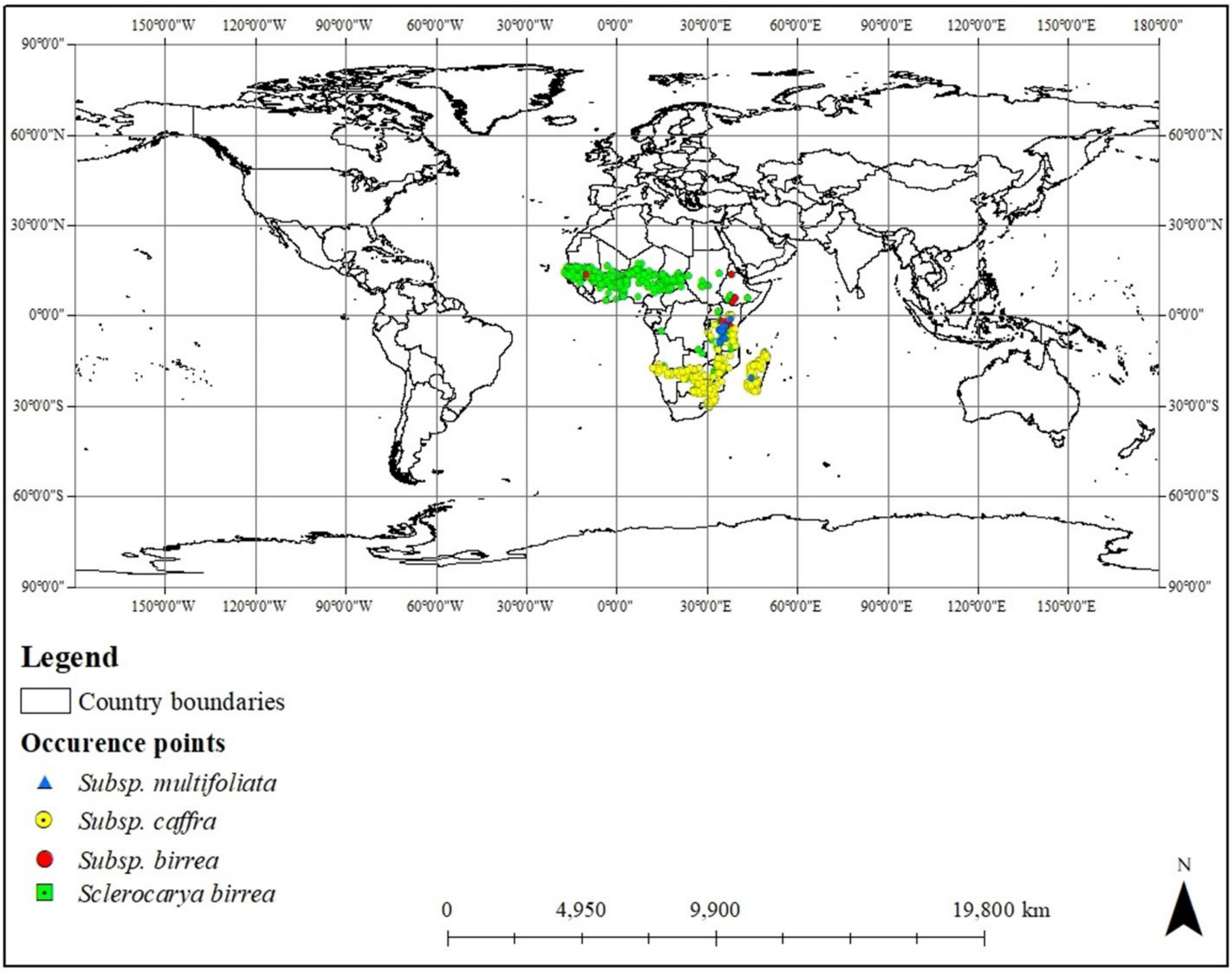

Figure 1. A global map showing the distribution of spatially-rarefied occurrence data for *S. birrea* (green) and subsp. *birrea* (red), subsp. *caffra* (yellow) and subsp. *multifoliata* (blue) in Africa.

Future predictions were made under the shared socio-economic pathways (SSPs) greenhouse gas concentrations, SSP3-7.0 in two-time horizons; 2050 (2041-2070) and 2080 (2071-2100). We used 1-km resolution CHELSA's climate data from two global Earth System Models of the Sixth phase of the Coupled Model Inter-comparison Project 6 (CMIP6): The Max Planck Institute for Meteorology Earth System Model (MPI-ESM1.2-HR) and the Hadley Climate Center Earth System Model (UK-ESM1.0-LL). There are four main shared socio-economic pathways (SSPs) (Liao et al. 2022). We chose SSP3-7.0, which represents medium-high emissions, over other SSPs because it is more realistic based on ongoing global climate change mitigation policies, for example, REDD+ (Angelsen et al. 2018, Kambiré et al. 2016) and clean energy (IPCC 2011) and, global carbon emissions reduction disagreements including the reluctance of some economically advanced countries to ratify the Kyoto Protocol (Hovi et al. 2012, Lassa 2006). In contrast to other global earth system models, the UK-ESM1.0-LL and MPI-ESM1.2-HR models were chosen for this study because, according to Lange (2021), their ocean and atmosphere model components are structurally separate and their process representation is fair (MPI-ESM1- 2-HR) to good (UK-ESM1-0-LL) and, in terms of climate sensitivity, MPI-ESM1-2-HR is a low climate-sensitive earth system model and UK-ESM1-0-LL is a high climate-sensitive earth system model. Other global earth system models, like the Geophysical Fluid Dynamics Laboratory Earth System Model (GFDLESM 4.1), were disregarded for this study due to their bias, which included underrepresenting semi-arid and desert regions in Western North America, Central Europe, South America, Southern Africa, and Central Asia (Dunne et al. 2020). The cross-correlation among environmental variables was checked for *S. birrea* and its subspecies by using SDMToolbox software version 2.4 (Brown 2014), and only one variable from any pair of variables with Pearson's correlation coefficient (r) value ≤ 0.7 was retained (Dormann et al. 2013, Jinga et al. 2021), based on their influence in defining suitable areas for each subspecies during preliminary models development, and the biological relevance of that variable in influencing *S. birrea* and its subspecies ecology, see Hall et al. (2002).

Modelling and mapping

MaxEnt machine learning software version 3.4.1 (Phillips et al. 2006) was used to simulate and map the suitable areas, as MaxEnt performs better with small sample sizes than other modeling techniques (Jiang et al. 2021, Ren et al. 2020, Heidari 2019, Phillips and Dudik 2008). The ENMs of subsp. *birrea* subsp. *multifoliata* were fitted by using a cross-validation option, 10000 background data, maximum iterations of 5000, minimum training presence with 10 replicates, and a regularization multiplier of 2.0. For *S. birrea* and subsp. *caffra*, ENMs were fitted by using 10000 background data, maximum iterations of 5000, 10 percentiles training presence, a regularization multiplier of 2.0, and 75% and 25% of occurrence data were used for model training and validation respectively. Other ENM settings were as per Phillips et al. (2006). The Jackknife test was used to determine the contribution of environmental factors to the ENMs of *S. birrea* and its subspecies. The predictive power of *S. birrea* and subspecies ENMs was assessed by using the Receiver Operating Characteristics (ROC)'s Area under the Curve (AUC) threshold. Our ENMs'AUCs were classified using the Thuiller et al. (2008) AUCs classification criterion as excellent (>= 0.90), good (0.8-0.9), acceptable (0.7-0.80), bad (0.6-0.70), and invalid (0.5-0.60). Suitability maps were projected onto the Behrmann Equal Area Cylindrical projection system (Kennedy and Kopp 2000, Murali et al. 2021, Roll et al. 2017, Yildirim and Kaya 2008). At a broad spatial scale, this projection system minimally distorts the areas around the poles (Kennedy and Kopp 2000, Yildirim and Kaya 2008). Suitability maps were classified into four suitability classes for the current environmental conditions: not suitable (0-0.23), moderately suitable (0.23-0.50), suitable (0.50-0.75), and highly suitable (0.75-1.00), and two suitability classes for future climates: not suitable (0-0.23) and suitable (0.23-1.00), and the areas were quantified by using ArcGIS 10.8. The value of unsuitable class was conservatively selected in reference to Liao et al. (2022), Jinga et al. (2021), Creley et al. (2019), and Kogo et al. (2019).

Results

The performance of models and the contribution of environmental variables to the global-scale ecological niche models of S. birrea and its subspecies

The predictive power of our models was excellent with training and test areas under the curves (AUCs) of 0.90, 0.90, and 0.96, 0.96 for *S. birrea* and subsp. *caffra* respectively, and mean AUC of 0.96 and, 0.98 for subsp. *birrea* and subsp. *multifoliata* respectively (Figure S1). The ENMs results show that potential evapotranspiration of the coldest quarter, annual mean temperature, and precipitation seasonality are environmental variables that contributed the most to the ENM of *S. birrea* (Table S2a), and continentality, potential evapotranspiration of the coldest quarter and climatic moisture index contributed the most to the ENM of subsp. *birrea* (Table S2b). Moreover, isothermality, potential evapotranspiration of the wettest quarter, and potential evapotranspiration seasonality contributed the most to the ENM of subsp. *caffra* (Table S2c) and, temperature seasonality, precipitation of the driest quarter, and potential evapotranspiration seasonality contributed the most to the ENM of subsp. *multifoliata* (Table S2d).

The global-scale suitable areas for S. birrea and its subspecies under the current and future warming climates

Under the current environmental conditions and, though there are variations among *S. birrea* and its subspecies, ENMs results reveal global-scale suitable areas for *S. birrea* and its subspecies to exist in global biomes in all continents except Europe and Antarctica, mostly in regions with tropical and subtropical climates (Figure 2a-d, Figure S3). ENMs results further show that suitable are for all three *S. birrea* subspecies to coexist in various parts of the world including South America (Figures 2b–d), and in Australia for subspecies *birrea* and *caffra* (Figures 2b–c). Suitable areas for *S. birrea* are predicted to exist in 102 countries mostly in tropical semi-arid, desert tropical, and temperate semi-arid global biomes in Africa, South America, North and Central America, Australia, and Asia continent (Figure 2a, Figure S3). *S. birrea* covers an estimated total area of 24,632,452 km^2 of the earth's land area (Table 1). However, MPI-ESM1.2-HR and UK-ESM1.0-LL models predict the currently suitable area for *S. birrea* to retract by more than 98% by the end of 2050 and 2080 (Table 1, Figure 3a-d). Future climates will result in the shifting of suitable areas for *S. birrea* to high latitudes north of the equator and be limited to desert temperate and probably boreal semi-arid global biomes (Figure 3a-d, Figure S3).

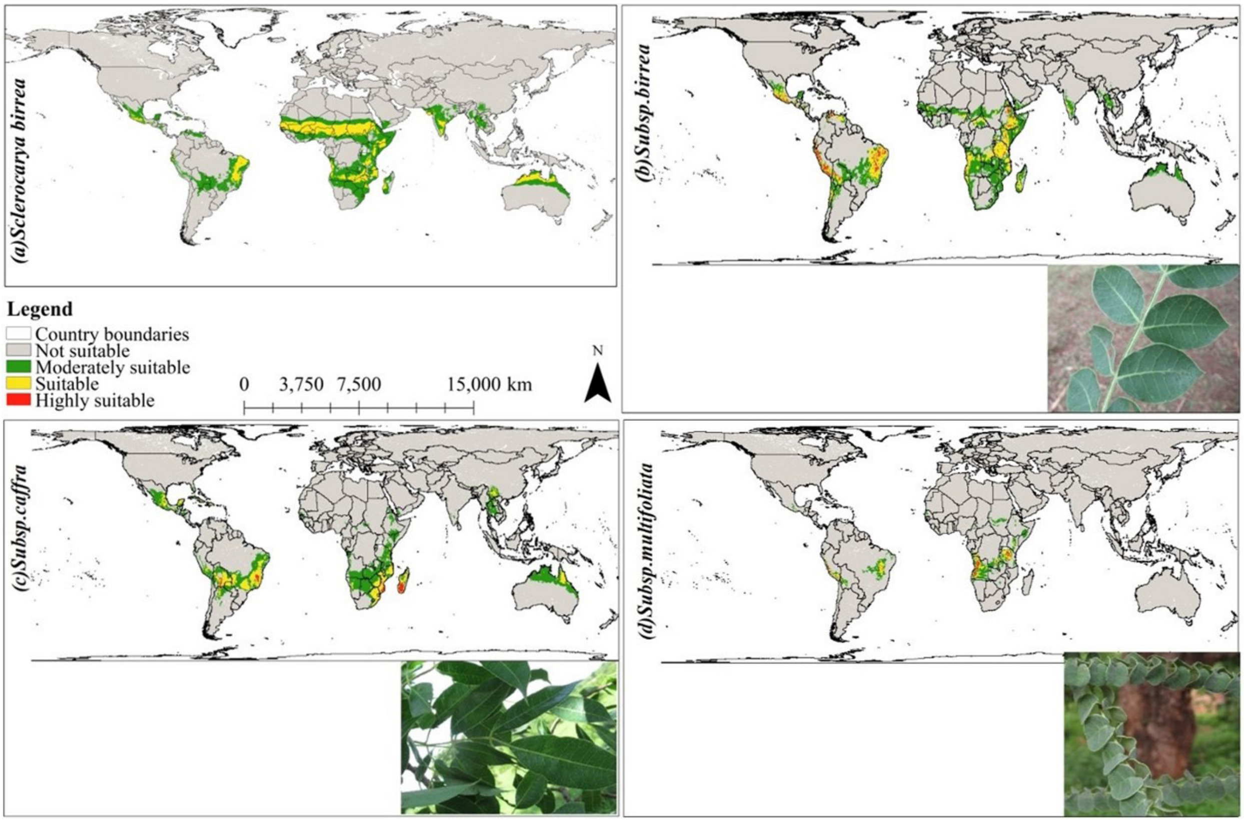

Figure 2. Global-scale suitable areas for (a) *Sclerocarya birrea* (b), subsp. *birrea* (c), subsp. *caffra* and (d) subsp. *multifoliata* under the current environmental conditions.

Table 1. Predicted global-scale suitable areas for *S. birrea*, subsp. *birrea*, subsp. *caffra* and subsp. *multifoliata* under the Current and Future Climates. Note: The area under the current and future climates is in 100,000 km^2, Δ denotes the change in area size, "+" implies positive change and "-" implies a negative change; "MPI-ESM1.2-HR" is Max Planck Institute for Meteorology Earth System Model version 1.2 and "UK-ESM1.0-LL" is United Kingdom's Hadley Climate Center Earth System Model version 1.0.

	Suitability Class	Area (km^2) under the current climate	MPI-ESM1.2-HR						UK-ESM1.0-LL					
			2050			2080			2050			2080		
			Predicted	Δ(+/-)	Δ(%)	Predicted	Δ(+/-)	Δ(%)	Predicted	Δ(+/-)	Δ(%)	Predicted	Δ(+/-)	Δ(%)
S. birrea	Not suitable	1,037.14	1,347.13	+310	+30	1,346.42	+309	+30	1,346.50	+309	+30	1,347.84	+311	+30
	Suitable	246.32	1.31	-245	-99	2.96	-243	-99	1.95	-244	99	1.54	-245	-99
Subsp. *birrea*	Not suitable	1,163.64	1,279.49	+116	+10	1,287.14	+124	+11	1,292.42	+129	+11	1,296.35	+133	+11
	Suitable	177.66	68.95	-109	-61	62.24	-115	-65	56.03	-122	68	53.03	-125	-70
Subsp. *caffra*	Not suitable	1,138.47	1,348.44	+210	+18	1,349.38	+211	+19	1,348.44	+210	+18	1,349.38	+211	+19
	Suitable	145.00	0.00	-145	-100	0.00	-145	-100	0.00	-145	100	0.00	-145	-100
Subsp. *multifoliata*	Not suitable	1,246.00	1,348.44	+102	+8	1,349.38	+103	+8	1,348.41	+102	+8	1,349.3	+103	+8
	Suitable	37.51	0.00	-38	-100	0.00	-38	-99.9	0.00	-38	100	0.00	-38	-100

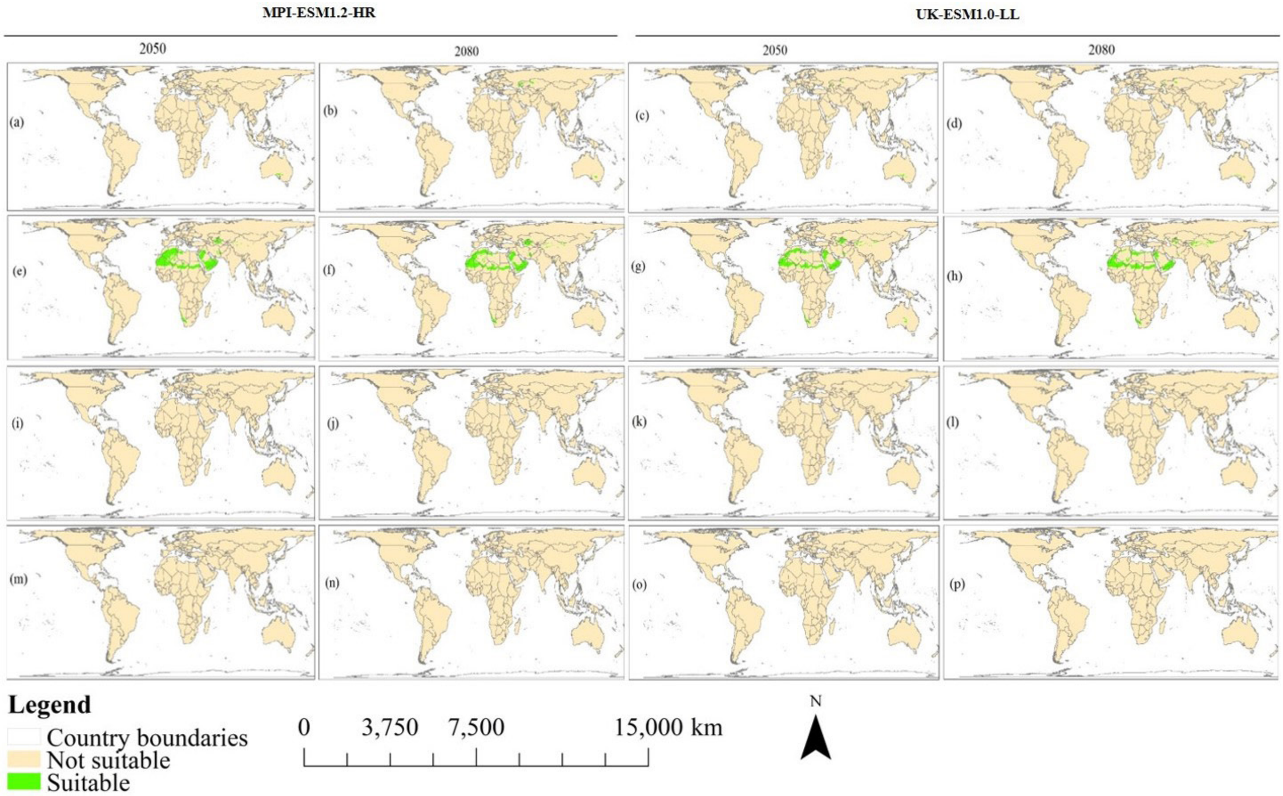

Figure 3. Global-scale suitable areas for *S. birrea* (a)-(d), subsp. *birrea* (e)-(h), subsp. *caffra* (i)-(l) and subsp. *multifoliata* (m)-(p) under future climates predicted by using MPI-ESM1.2-HR and UK-ESM1.0-LL Earth System models. Note: "MPI-ESM1.2-HR" is Max Planck Institute for Meteorology Earth System Model version 1.2 and "UK-ESM1.0-LL" is United Kingdom's Hadley Climate Center Earth System Model version 1.0.

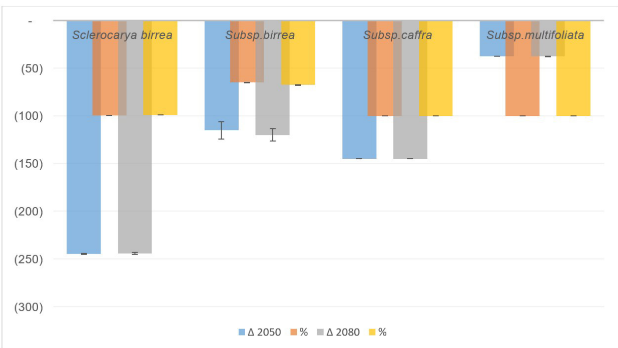

Figure 4. Global-scale mean area change (100,000 km^2) for *Sclerocarya birrea* and subsp. *birrea*, subsp. *caffra* and subsp. *multifoliata* under future climates. Note: "Δ" implies a change in area size, and brackets in x-axis values imply a negative value. Respectively, bars with blue and orange colors show the mean area and percentage change for the year 2050, and bars with grey and yellow colors show the mean area and percentage change respectively, for the year 2080.

The ENM model results for subsp. *birrea* indicates suitable areas for this subspecies to be harbored in 101 countries, predominantly in tropical semi-arid and desert tropical biomes that are patchily distributed across Africa, South America, North and Central America, Asia, and Australia continent (Figure 2b, Figure S3). The estimated total suitable area for subsp. *birrea* is 17,765,991 km^2, and under future climates, the MPI-ESM1.2-HR and UK-ESM1.0-LL models predict this subspecies to lose more than 64% of its current suitable area by the end of 2050 and 2080 (Figure 3e-h, Table 1, Figure 4). Similarly, the currently suitable area for subsp. *birrea* will be shifting to high latitudes north of the equator under future climates, and mostly be confined in the global biomes with Mediterranean warm, tropical deserts, and boreal semi-arid climatic conditions (Figure 3e-h, Figure S3).

The subsp. *caffra* ENM model results show that suitable areas for this subspecies to be found in tropical semi-arid, temperate semi-arid, temperate humid, tropical humid, and desert tropical global biomes harbored in 107 countries worldwide, spanning across Africa, South America, Asia, Australia, and North and Central America continent (Figure 2c, Figure S3). This subspecies occupies an estimated area of 14,499,813 km^2 of earth's landmass that the MPI-ESM1.2-HR and UK-ESM1.0-LL models predict to vanish under future climates in 2050 and 2080 (Figure 3i-l, Table 1). Moreover, subsp. *multifoliata* have a limited geographic range, occurring in 54 countries scattered across Africa, South America, Asia, North America, and Central America, mostly in tropical semi-arid and desert tropical global biomes (Figure 2d, Figure S3).

This subspecies occupies an estimated area of 3,751,057 km^2 of earth's terrestrial area that the MPI-ESM1.2-HR model predicts to be unsuitable by 2050, and slightly recover in 2080 and be limited in tropical semi-arid and desert tropical conditions in South America (Figure 3n, Table 1). However, the UK-ESM1.0-LL model predicts the currently suitable area to vanish by the end of 2050 and 2080 (Figure 3o-p).

Discussion

The predictive power of our ENMs was robust with AUCs ranging from 0.90 to 0.98 (Figure S2). Our findings that the global-scale ENMs of *S. birrea* and its subspecies are most influenced by environmental factors (Table S2a-d) are generally consistent with Hall et al. (2002) and Jinga et al. (2021). With increasing continentality, less precipitation and, on average, drier condition is expected (Hasler et al. 2015). For instance, the distance between the Sahara and central Asia from major moisture sources contributes to the arid climates of these regions (Huang et al. 2017). Soil moisture is a key element influencing hydrological processes, regional microclimate, plant growth, and recovery, which is a key indicator of surface hydrological processes (Wei et al. 2022). Moreover, many ecosystems in tropical and subtropical latitudes experience water stress, which is in turn regulated by the temporal fluctuations of soil moisture (Rodriguez 2003).

Our ENMs results show *S. birrea* and its subspecies can adapt in many dryland areas globally (Figure 2a-d) but with variable sizes among subspecies (Table 1). This implies that *S. birrea* and its subspecies can be introduced for conservation and commercial cultivation, and used to restore and rehabilitate global drylands detailed by White and Nackoney (2003), Laity (2009), and Cartereau et al. (2022). The *S. bierra* and its subspecies can be used to mitigate desertification in some parts of the Sahel region, Kalahari Desert and Sahara Desert in Africa; Chihuanhuan Desert, Sonoran Desert and Mexican Plateau in North America; parts of Atacama Desert, Cerredo and Caatinga in South America; Arabian Desert and Gobi Desert in Asia, and dry sub-humid and arid areas in Australia (White and Nackoney 2003, Laity 2009). Furthermore, the predicted global-scale suitable areas offer an opportunity for ex-situ conservation through the establishment of field genebanks to enhance the conservation of *S. birrea* and its subspecies beyond their native ranges, considering that *S. birrea* seeds are semi-recalcitrant (Machani et al. 2007). Biodiversity across the world is currently threatened by the invasion of native ecosystems by exotic plant species (Lake and Leishman 2004). However, the likelihood of *S. birrea* becoming an invasive species beyond its native range is minimal, though, given that its population is currently declining and is projected to do so under future warming climates. Considering the characteristics of invasive species described by Lake and Leishman (2004) and Baker et al. (1974), the *S. birrea* is unlikely to be invasive. However, assessment of the potential for *S. birrea* subspecies to become invasive is beyond the purview of this study and requires further research before introducing them for commercial cultivation and conservation purposes and using them to rehabilitate global drylands outside of their native ranges.

The currently suitable areas for *S. birrea* and its subspecies are predicted to contract under future warming climates (Table 1, Figure 3a-p). This is in line with Dirzo et al. (2014) findings, that biodiversity shifts and decreases, and biotic community reorganization are mostly influenced by global environmental change. Our results that the currently suitable area for *S. birrea* to retract by the end of 2050 and 2080, and relocate to desert temperate and boreal semi-arid regions (Figure 4, Figure S3) are consistent with other studies. Huang et al. (2017) and Parmesan (2006) pointed out that tropical species often migrate into areas with temperate climates in response to warming trends at lower latitudes, similar to our findings. The general declining trend for suitable areas for subsp. *birrea* (Figure 4) and vanishing of suitable area for subsp. *caffra* (Figure 3i-l) under future climates by the end of 2050 and 2080, and subsp. *multifoliata* by 2050 is similar to the findings by Aitken et al. (2008). There are three likely outcomes for forest tree populations as a result of climate change: they will completely vanish, adapt to new environmental conditions in their current locations, or continue to move naturally to suitable ecological niches (Aitken et al. 2008). In the context of Africa, our findings on the contraction of suitable areas for subsp. *multifoliata* under future climates are generally in line with those reported by Jinga et al. (2021). However, our findings for *S. birrea* and subspecies *birrea* and *caffra* deviate from those reported by Jinga et al. (2021). This difference is probably due to variations in environmental variables selected and used as predictors (Guisan and Zimmermann 2000, Pearson et al. 2007) and the climate models used (Heubes et al. 2013, Lange 2021). The choice of climate data is another possible source of nonconformity. Jinga et al. (2021) used climate data from Worldclim, which is probably not suitable for dryland species like *S. birrea* and its subspecies, in light of the concern raised by Karger et al. (2017) and Ocón et al. (2021) regarding the use of climate data from this climate data source. Furthermore, Jinga et al. (2021) used a spatial auto-correlation of 5-km distance and low-resolution 2.5′(~4.5 km) climate data. This contrasts with the climate data, resolution, and the spatial auto-correlation used in our study. Accuracy in predicting habitat suitability is impacted by the use of low-resolution environmental data. According to Ross et al. (2015), low-resolution environmental data may obscure fine-scale topographic features, leading to an overestimation of the spatial extent of the habitat (Rengstorf et al. 2013, Ross et al. 2015). According to Hijmans et al. (2005), the spatial resolution of the climatic data for a given study is determined by the intended use of the findings and the climate data that are readily available. However, to capture environmental variability, which may be partially lost at low resolutions, climate data with a fine (1 km^2) spatial resolution are needed for many applications (Hijmans et al. 2005).

Moreover, species models require finer climate data in order to simulate the impacts of climate change (Navarro-Racines et al. 2020). This is especially important in tropical regions, especially in Africa where landscapes have large spatial variations, especially in orography, climate especially precipitation, and soils, which change over short distances (Navarro-Racines et al. 2020, Platts et al. 2015).

Sclerocarya birrea, and thus its subspecies, is a drylands tree species, and our findings on the decline of suitable areas under future climates are consistent with Cartereau et al. (2023) that, even under the most favorable conditions, between 44-88% of warm drylands tree species will experience climate aridification with a high risk of decline. Even at the regional scale, the majority of warm drylands tree species are predicted to experience climate aridification in the future at a rate ranging from 21-90% (Cartereau et al. 2023). In general, severe drought was highlighted as a major threat to populations of *S. birrea* in various studies on the subsp. *birrea* and *caffra* in Western Africa, according to Hall et al. (2002). The subsp. *birrea* population in the Senegal Ferlo had 15.6% mortality and 11–15% loss of standing subsp. *birrea* trees in Faira, Niger, during the drought that affected western Africa from 1979 to 1982. Additionally, during the 1983–1985 drought in Senegal, more subsp. *birrea* trees died more than any other species of woody plants (Hall et al. 2002).

The *S. birrea*, however, is a mesophytic plant species, making it well adapted to soils with little water availability and low fertility (Hall et al. 2002, Rivera et al. 2017). This suggests that *S. birrea* can endure prolonged seasonal dry spells and extremely dry conditions (Hall et al. 2002). Seghieri et al. (1995) dubbed the *S. birrea* tree an "arido-active" plant species, referring to its capacity to maintain metabolic activity during the dry season (Hall et al. 2002). Though it will be impacted by future climates, our study suggests that subsp. *birrea* to be more adaptive to future warming climates. According to Hall et al. (2002), subsp. *birrea* can survive and form populations in dry conditions. The subsp. *birrea* is a dry savanna species, semi-sclerophyllous with mesic and marginally xerophytic characteristics (Hall et al. 2002), meaning that it can adaptably strive under both xeric and mesic environmental conditions. According to the Thornthwaite climate index categories, the subsp. *birrea* is more usually related to sub-humid, semi-arid, and arid environments. The mesic characteristics of the *subsp. birrea* supports our study findings that suitable areas for this subspecies will change and become more confined, including in the Sahel region in West African countries where climate change is predicted to result in an increase in rainfall (Heubes et al. 2011, Heubes et al. 2013, Platts et al. 2015). The subsp. *caffra* and *multifoliata* are mostly associated with sub-humid and semi-arid conditions (Hall et al. 2002), suggesting that they will likely be severely impacted by future warming climates. Plants with increased drought resistance often have xeromorphic structures including, small or strongly lobulated leaves (Rivera et al. 2017, Simioni et al. 2018). The leaflet size varies among *S. birrea* subspecies (Figures 2b-d). According to Hall et al. (2002) and the leaves samples collected during field surveys as shown in Figures 2b-d, subsp. *multifoliata* has the smallest leaflets, followed by subsp. *birrea* and subsp. *caffra*. This suggests that subsps. *birrea* and *multifoliata* are probably more drought-tolerant, and they will withstand future warming climates than subsp. *caffra*.

Major climatic variations in temperature and precipitation will continue to have an impact on the ecology of natural systems across the world, according to Cowles et al. (2018) and Madsen et al. (2021). However, the *S. birrea*, subsp. *birrea*, and subsp. *multifoliata* will thrive in future warming climates even though their current suitable areas are predicted to contract under future climates. However, species-specific changes in plant distribution will occur in response to future climates (Hufnagel and Garamvölgyi 2014). Species react differently to climate change because they have different physiological tolerances, life-history strategies, chances of population extinctions and colonization, and dispersal capacities (Eeley et al. 1999, Parmesan and Yohe 2003, Chuine and Beaubien 2001). As a result of plasticity and genetic adaptability, various tree species and populations may exhibit varying capacities to adjust to climatic change (Rehfeldt et al. 2002). Even among species that are prone to identical climatic trends, there is a considerable degree of individual variation in the strength of climate response, which is likely explained by these individualized characteristics (Parmesan and Yohe 2003).

Global climate models (GCMs) are currently one of the best tools available for researching climate change (Parsons 2020). However, due to internal variability, model uncertainty, and scenario uncertainty, see Wu et al. (2022), quantitative climate projections from GCMs are highly uncertain (Tebaldi et al. 2020, Wu et al. 2021). As a result, it is challenging to accurately predict future climate change and determine how these predictions would affect other fields (Wu et al. 2022), a situation which complicates accurate inference including how future climate change will affect plant species and ecosystems (Balima et al. 2022). Thus, the results of the current study on the suitable areas for *S. birrea* and its subspecies under the current environmental conditions can be used to guide the cultivation, conservation, and use of the subspecies to restore and rehabilitate drylands around the world. However, due to uncertainties in climate projections by GCMs, suitable areas for *S. birrea* and its subspecies under future warming climates should be continuously monitored through re-modelling them as improved climatic data and GCMs become available.

Conclusion

The global-scale suitable areas for *S. birrea* and its subspecies were modelled by using ENMs developed in MaxEnt machine learning by using climatic and topographical and potential evapotranspiration variables. Potential evapotranspiration of the coldest quarter, annual mean temperature, and precipitation seasonality contributed the most to the ENM of *S. birrea*; continentality, potential evapotranspiration of the coldest quarter, and climatic moisture index to the ENM of subsp. *birrea*. Moreover, isothermality, potential evapotranspiration of the wettest quarter, and potential evapotranspiration seasonality contributed the most to the ENM of subsp. *caffra*, and temperature seasonality, precipitation of the driest quarter, and potential evapotranspiration seasonality to the ENM of subsp. *multifoliata*. Suitable areas for *S. birrea* and its subspecies exist beyond their current known native ranges, in Africa, North America and Central America, South America, Asia, and Australia. Future climates will result in the vanishing of areas currently suitable for subsp. *caffra* and, global range shifts for *S. birrea* and subsp. *birrea*. The subsp. *birrea* will strive under future warming climates, followed by subsp. *multifoliata*. Moreover, under future climates, suitable areas for *S. birrea* will be more confined to desert temperate biomes mostly in Africa and some parts of Eastern Europe, and desert tropical and desert temperate biomes will be suitable for subsp. *birrea*. Suitable areas for subsp. *multifoliata* will be confined in tropical semi-arid-desert temperate biomes in South America. Africa is the continent with the most suitable areas for *S. birrea* and subsp. *birrea* under the current and future climates. Large-scale patterns of species richness and distribution have been linked to climate (Pa-Dyderska et al. 2021, Ter Steege et al. 2006). Although there are many different habitats and environments in which the vegetation has grown and evolved, microenvironments account for a substantial portion of the biological diversity of tropical flora (Esquivel-Muelbert et al. 2019). Additionally, niche shifts are expected to be more noticeable at lower spatial scales since plant distribution is influenced by small-scale topography and irradiance, soil fertility, moisture, and temperature (Gwitira et al. 2014, John et al. 2007, Liu et al. 2015). In addition, changes in terrain and precipitation patterns influence the functional makeup of tree communities, wherein less rainfall might amplify drought-resistance mechanisms (Blanchard et al. 2019). Therefore, global micro-scale modeling studies that incorporate environmental variables such as topographical and edaphic variables would improve our understanding of suitable areas for *S. birrea* and its subspecies at micro-landscapes around the world. Moreover, suitable areas for *S. birrea* and its subspecies will be altered by future climates to a varying degree. Further research is needed to investigate morphological, anatomical, and physiological trait variations among the subspecies to understand the variations in adaptive capacity to future warming climates. Furthermore, germplasm collection and preservation will guarantee the conservation of subsp. *caffra* and subsp. *multifoliata* which, respectively, their suitable areas are predicted to vanish and nearly vanish under future warming climates.

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Author Contributions

A.H.M., conceptualization, methodology, software, data curation and analysis, interpretation of results, writing the first draft, reviewing and editing of the manuscript, and project administration; P.H., N.A.A and A.D.W., methodology, validation, and interpretation of results; reviewing and editing of the manuscript. All authors endorsed the publication of the manuscript.

Data Availability Statement

The data generated during the current study are available from the corresponding author upon reasonable request.

Supplementary Materials

The following materials are available as part of the online article at https://escholarship.org/uc/fb

Figure S1. Ecological Niche Models' Receiver Operating Characteristic (ROC)'s areas under the curves (AUCs) for (a) *Sclerocarya birrea* (b) subsp. *birrea* (c) subsp. *caffra*, and (d) subsp. *multifoliata*.

Figure S2. Jackknife test results show the contribution of environmental variables that define global-scale suitable areas for (a) *Sclerocarya birrea* (b) subsp. *birrea* (c) subsp. *caffra*, and (d) subsp. *multifoliata*.

Figure S3. The distribution of major biomes of the world (Source: USDA, 1999).

Table S1. List of environmental variables downloaded from CHELSA and ENVIREM databases.

Table S2. List of environmental variables and their contribution to the ENMs of (a) *Sclerocarya birrea* (b) subsp. *birrea* (c) subsp. *caffra*, and (d) subsp. *multifoliata*.

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