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Future climatically stable habitat of a vulnerable medicinal tree, *Warburgia salutaris* (Pepper-bark tree), overlaps with some protected areas in southern Africa

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ABSTRACT

Climate change will affect the distribution of medicinal plant species in sub-Saharan Africa, with potential negative consequences to especially rural and poor communities that depend on them for traditional medicines. The aim of the study was to determine future climatically stable habitat of *Warburgia salutaris*, a commonly used vulnerable medicinal plant species. An ensemble species distribution model (SDM) was built from eight algorithms and used to estimate the current and future distributions of the species. Six environmental variables and 146 occurrence records were used to calibrate individual SDMs before combining them into the ensemble SDM. The ensemble SDM was projected to 2041–2060 and 2081–2100 under two shared socioeconomic pathways (SSPs), namely SSP2-4.5 and SSP5-8.5. The projections were made under three general circulation models (GCMs), which were CanESM5, IPSL-CM6A-LR and MIROC6. Results show that the current suitable habitat of the species occurs in South Africa, Eswatini, Malawi, Mozambique and Zimbabwe. Under both time periods and SSPs, the suitable habitat of the species will markedly contract, especially under SSP5-8.5 in 2081–2100 (CanESM5 = -79%, IPSL-CM6A-LR = -87%, MIROC6 = -71%). Climate refuges that overlap with the future suitable habitat of *W. salutaris* were identified in protected areas (PAs), such as Malalotja Nature Reserve (Eswatini), Itala Nature Reserve (South Africa), and Nyanga National Park (Zimbabwe). The climate refuges in PAs may be priority areas to introduce the species.

Keywords: Climate change, Conservation, Protected area, Traditional medicine, *Warburgia salutaris*.

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SIGNIFICANCE STATEMENT

We used ensemble modeling in the R package ‘biomod2’ to estimate distribution of the current suitable habitat of *W. salutaris*, a medicinally important and vulnerable tree species, and to predict shifts in the distribution in future. We used eight algorithms to build an ensemble model for the species. Our work is original and is not under consideration elsewhere. To our knowledge, this is the first study to use ensemble modeling to predict the impacts of climate change on the species across its entire natural range. Our study shows that the size of the suitable habitat of *W. salutaris* will contract under climate change. The contraction is likely to impact people who rely on the species for traditional medicine. Our results also show that there are climate refuges in protected areas (PAs) within the natural range of the species. The climate refuges in PAs may serve as conservation areas of the species.

INTRODUCTION

Warburgia salutaris (Bertol. f.) Chiov. (pepper-bark tree, Canellaceae) is an ethnomedicinally important tree to especially rural dwellers of southern Africa (Meddows-Taylor and Ramadwa 2025). It is naturally distributed in Swaziland, Lesotho, Malawi, Mozambique, South Africa and Zimbabwe (Maroyi 2013; Senkoro et al. 2020; Glennon et al. 2023). Habitat degradation and overharvesting have resulted in population declines of *W. salutaris* throughout its native range (Senkoro et al. 2019). The species is overharvested mainly because of its use as traditional medicine for a variety of ailments (Hollmann and Van der Schijff 1996; Rabe and van Staden 2000; Leonard and Viljoen 2015; Maroyi 2013). Leaf, bark and root extracts have been shown to have pharmacological effects, such as anti-inflammatory, antioxidant, antimycobacterial, antimalarial, and antifungal activities (Glennon et al. 2023, Khumalo et al. 2024). Several bioactive compounds from bark (Khumalo et al. 2019; Abdelfattah et al. 2022) and leaf (Steenkamp et al. 2013; Mashamba et al. 2022) have already been reported, and biomedical studies on the pharmacological efficacy of the compounds are ongoing (Meddows-Taylor and Ramadwa 2025). Adult individuals are severely debarked, which causes tree mortality and ultimately local population extinction (Dludlu et al. 2017). As a result, *W. salutaris* is classified as vulnerable on the IUCN Red List (IUCN 2024). Nationally, the species is classified as endangered in South Africa (van den Bosch et al. 2023) and Malawi (Msekandiana and Mlangeni 2002), critically endangered in Swaziland (Dlamini and Dlamini 2002), and vulnerable in Mozambique (Izidine and Bandeira 2002). In Zimbabwe, the status is more extreme as the species is classified as extinct in the wild (Maroyi 2008), signaling that plans for reintroduction of *W. salutaris* in the country are necessary.

Local ecological knowledge and cultural practices have historically been used to ameliorate some of the threats faced by *W. salutaris* in its native range (Senkoro et al. 2019). The cultural practices include rotational harvesting that allows regeneration, selective harvesting of only mature individuals (Terer et al. 2012; Senkoro et al. 2019), regulating harvesting time according to critical life phases of the species (Schmidt and Ticktin 2012), and controlled debarking that allows bark regeneration and avoids tree mortality (Ssenku et al. 2022). However, recently, the traditional conservation practices of *W. salutaris* are failing to curb overharvesting of especially the bark (Maroyi 2013). Human population growth, the comparatively high cost of modern pharmaceuticals, and the strengthening belief that traditional medicines have fewer side effects than modern drugs are some factors that have led to unsustainable harvesting of medicinally important indigenous tree species, such as *W. salutaris* (Ssenku et al. 2022). To regenerate populations of *W. salutaris*, reintroductions into the wild (Maroyi 2011), distribution of seedlings to traditional healers for regeneration (van den Bosch et al. 2023) and establishment of domesticated populations (Maroyi 2013) have been explored. Introductions, however, should be informed by maps showing where the species is likely to successfully thrive. Introduction in climatically stable protected areas (PAs) has also been suggested as a viable alternative for the conservation of *W. salutaris* since the PAs may provide a higher chance of successful growth under climate change (Hannweg et al. 2016).

In addition to habitat fragmentation and overharvesting, climate change has been identified as a severe threat to medicinal plant species, particularly in sub-Saharan Africa (Jinga et al. 2020; Lyam et al. 2022; Esser and Weldemariam 2023). Mean temperature in sub-Saharan Africa has increased by 0.7°C during the 20th century, and it is forecasted to increase by 0.2°C – 0.5°C per decade in the 21st century (Hulme et al. 2001). While mean temperature is forecasted to increase across the African continent, precipitation will likely show regional variability, with a decrease in southern Africa (Almazroui et al. 2020; Dosio et al. 2021). Temperature and precipitation changes are likely to be major causes of plant biodiversity loss, especially in sub-Saharan Africa (Midgley and Bond 2015; Sintayehu 2018). Range contraction of several African medicinal plant species has already been forecasted under climate change, including *Pterocarpus angolensis* (De Cauwer et al. 2014), *Uapaca kirkiana* (Jinga et al. 2020), *Senegalia senegal* (Lyam et al. 2022), *Afzelia africana* (Balima et al. 2022) and *Boswellia* spp. (Esser and Weldemariam 2023). The forecasted future disappearance of the suitable habitat of medicinal plant species in Africa is especially disastrous to approximately 80% of the population that relies on traditional plant medicines (Ampomah et al. 2023). It is important, therefore, to investigate the impact of climate change on medicinal plant species in southern Africa, such as *W. salutaris*, and to suggest conservation options for long term viability and persistence of populations. The impact of climate change on *W. salutaris* has been investigated at the local level in Mozambique using a single modeling algorithm and fewer occurrence records (Senkoro et al. 2024). This study investigates the impact of climate change over the entire natural range of the species which is not constrained by political boundaries in southern Africa. This study also uses ensemble modeling with more occurrence records, making the results more robust and broad-based for conservation planning across the natural range.

The impact of climate change on the distribution and abundance of species is now commonly investigated by species distribution models (SDMs). SDMs correlate environmental variables to species occurrence records to predict the potential geographic distribution of the species (Sillero et al. 2021). SDMs are also used to forecast changes in the distribution of species under climate change (Santini et al. 2021). The proliferation of online public data portals hosting species occurrence records as well as potential environmental variables have increased the use of SDMs (Zurell et al. 2020). The premise in SDMs is that species are in pseudoequilibrium with the environment (Guisan and Thuiller 2005; Araujo and Guisan 2006; Sinclair et al. 2010). Thus, correlating occurrence records and environmental variables should predict suitable habitat of the species (Sinclair et al. 2010). However, the pseudoequilibrium assumption can be problematic, especially for species under severe pressure due to dispersal limitation and demographic stochasticity (Soley-Gaurdia et al. 2024). Other notable shortcomings of SDMs include failure to simulate dispersal and competition (Sinclair et al. 2010; Moonlight et al. 2020). Regardless of these limitations, SDMs have been successfully applied in conservation planning (Regos et al. 2021), identification of niches under climate change (Estrada et al. 2018), and delineating boundaries of PAs (Carvalho et al. 2011), among several fields. For long-term viability after introductions and or reintroductions of imperiled species, such as *W. salutaris*, SDMs may be used to identify target areas that will remain climatically stable.

The aim of the study was to determine the current geographic distribution and impact of future climate change on *W. salutaris*. Distribution maps are especially important to locate areas where the species may be introduced and to direct botanical explorations and plant surveys. Using an ensemble SDM, we first sought to (i) determine the current suitable habitat of *W. salutaris*, then (ii) project how the suitable habitat of *W. salutaris* changes under different climate change scenarios in 2041–2060 and 2081–2100, and finally (iii) we used the projections to identify climate refuges in national parks and other PAs that are priority targets for conservation and reintroduction efforts. Climate refuges in PAs are usually protected from illegal harvesting (Nutall et al. 2022), and, thus, they are ideal areas to introduce and or reintroduce species at risk from climate change, overharvesting and other anthropogenic threats.

MATERIAL AND METHODS

Occurrence records and environmental variables

Occurrence records were obtained from the Global Biodiversity Information Facility online data portal (www.gbif.org) (GBIF 2024). Automatic filters on the GBIF portal were used to screen occurrence records with potential errors, such as those with out of range coordinates, swapped coordinates, and invalid precision and accuracy coordinates. The advantage of including GBIF occurrence records is that they have a comprehensive coverage since some of them are collected by citizen science tools (Dyderski et al. 2018). Citizen science tools are especially valuable in sampling areas not covered by forest inventories and too large for reliable sampling by researchers. Occurrence records were also obtained from the RAINBIO online data portal (`https://gdauby.github.io/rainbio/download_page.html`) (Dauby et al. 2016). The RAINBIO database is a compilation of 13 datasets of georeferenced occurrence records of African vascular plant species located south of the Sahel. The Tropicos (`http://www.tropicos.org`) online data portal (Missouri Botanical Garden, St. Louis, MO, USA) was also a source of occurrence records. Additional occurrence records were obtained from Senkoro et al. (2020) and Dludlu et al. (2017). All occurrence records falling out of the known south-east African range of *W. salutaris* were removed. Occurrence records collected before 1970 were also discarded to suit the temporal range of bioclimatic variables.

After removing duplicate occurrences in Microsoft Excel using conditional formatting to highlight repeated coordinates, a total of 146 occurrence records were obtained. To have a relatively even distribution, the occurrence records were resampled in R (R Core Team 2024) using the ‘spThin’ version 0.2.0 R-package (Aiello-Lammens et al. 2015). SDMs built with occurrence records showing uneven sampling will fit a biased environmental signal that causes inflated model performances (Hijmans 2012). A minimum distance of 10 km between occurrence records was used in resampling to obtain a relatively uniform distribution and to ensure that at most one record per pixel was retained for use in SDMs (Figure 1).

Bioclimatic variables (Booth et al. 2014) and elevation obtained from the Worldclim version 2.1 online public data portal (www.worldclim.org) (Fick and Hijmans 2017) were used as environmental variables. Bioclimatic variables describe quarterly or yearly variations in temperature and precipitation and are more influential in determining plant distributions than monthly climate variables (Bede-Fazekas and Somodi 2020). Bioclimatic variables are ecologically and phys-

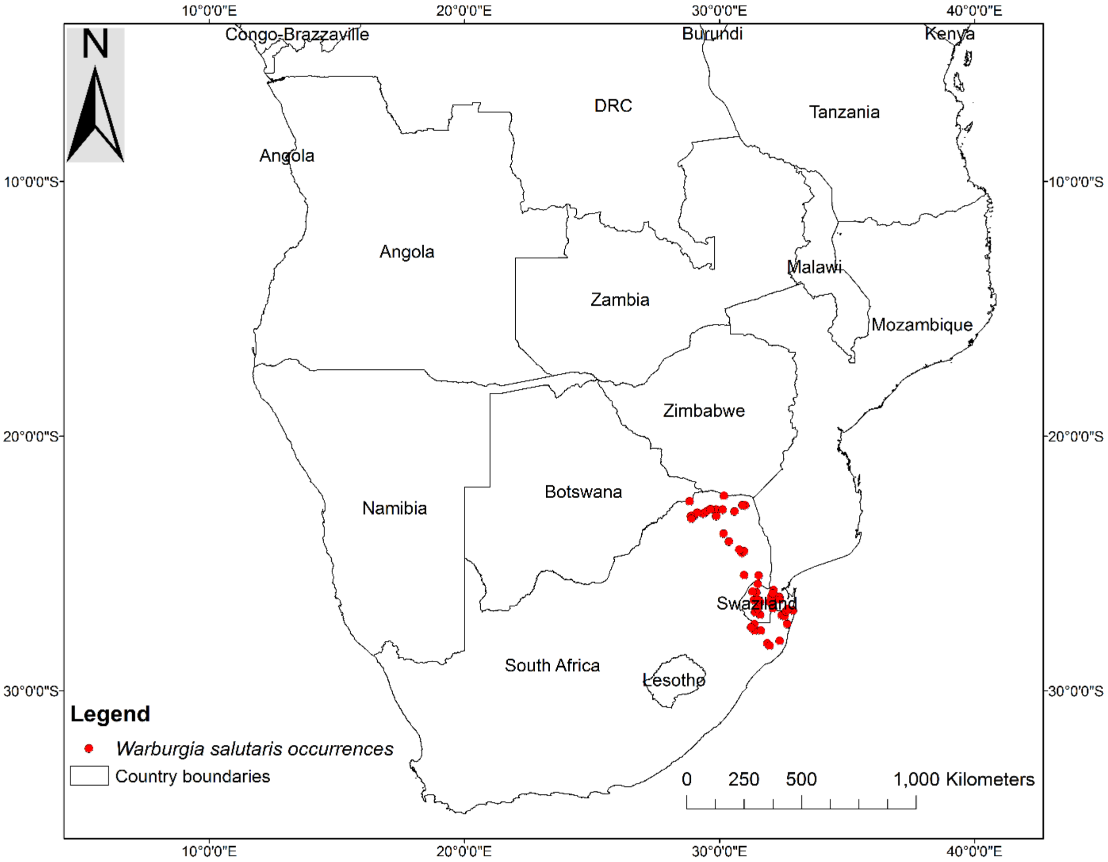

Figure 1. Location of thinned occurrence records of *Warburgia salutaris* (Pepper-bark tree) in southern Africa that were used to calibrate species distribution models.

iologically more relevant to vegetation establishment and growth (Title and Bemmels 2018), and they have been widely used in SDMs to delineate conservation areas (Varela et al. 2022), forecast impact of climate change (Esser and Weldemariam 2023), and to generate distribution maps of species (Hama and Khwarahm 2023), among several applications.

The bioclimatic variables and elevation were selected for calibration of individual SDMs after correlation analysis using the 'usdm' version 2.1-7 R-package (Naimi et al. 2014). Correlated variables, among several drawbacks, increase computation time, decrease model transferability, increase over-fitting, and decrease signal-to-noise ratio (De Cauwer et al. 2014; Jarnevich et al. 2015).Variables with a Spearman's correlation coefficient (r) of less than 0.70 (Dormann et al. 2013; Jarnevich et al. 2015) and a variance inflation factor (VIF) of less than 10 (Steen et al. 2017) were used in individual SDM calibrations. The selected variables, downloaded at a resolution of 2.5 min, were mean diurnal range (BIO2), isothermality (BIO3), mean temperature of wettest quarter (BIO8), precipitation of driest month (BIO14), precipitation of warmest quarter (BIO18), and elevation.

Calibration, evaluation and ensembling of SDMs

An R-based software, 'biomod2' version 4.2-4 (Thuiller 2003; Thuiller et al. 2009, 2023) was used to calibrate and ensemble individual SDMs. Up to 12 individual modeling algorithms can be calibrated simultaneously and ensembled in 'biomod2.' Eight algorithms were used in this study, and these were artificial neural network (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized boosted model (GBM), generalized linear model (GLM), multivariate adaptive regression splines (MARS), random forest (RF) and surface range envelope (SRE). To account for spatial autocorrelation and reduce inflation of model performance due to spatial sorting bias, we implemented spatial block cross-validation. Occurrence records were combined with randomly generated pseudo-absences (n = 10,000) sampled within the study extent (10°S – 38°S latitude and 10°E – 42°E longitude). A relatively large pseudo-absence sample was used to stabilize model parameter estimation and ensure adequate representation of background environmental conditions. Environmental variables were extracted for all presence-pseudo-absence locations, and records containing missing environmental values were removed before modeling. Spatial partitioning was conducted using the "spatialBlock" function in the R-package "blockCV" version 3.2-0 (Valavi et al. 2019). Blocks were generated using a distance threshold of 400 km and partitioned into $k = 10$ folds. The 400 km block size was selected to ensure meaningful geographic separation between training and testing subsets while retaining sufficient sample size within each fold. Ten folds were used to maximize spatial independence across validation runs while maintaining adequate representation of presence and pseudo-absence records per fold. Spatial partitioning provides a more conservative and ecologically realistic estimate of predictive performance compared to random cross-validation, which can inflate evaluation metrics in spatially structured datasets (Roberts et al. 2017; Yates et al. 2023).

Blocks were randomly allocated to folds across 100 iterations to ensure balanced representation of presences and pseudoabsences. Folds containing only a single response class were excluded to prevent model fitting errors. A user-defined cross-validation table was constructed such that, for each run, models were trained on $k - 1$ spatial folds and evaluated on the withheld fold. This spatially explicit cross-validation strategy ensures that training and testing data were geographically separated, thereby providing a more realistic estimate of predictive performance under spatial extrapolation. The SDMs were evaluated using the area under the receiver operating characteristic curve (ROC) and true skill statistics (TSS).

To determine whether spatial structure remained in model residuals, we quantified spatial autocorrelation using Moran's I. Predicted probabilities were extracted for each algorithm and averaged across cross-validation runs to obtain a mean prediction per observation point. Spatial coordinates were projected to a metric coordinate reference system (UTM Zone 35S; EPSG: 32735) prior to distance-based neighbor construction. Moran's I statistic was computed from the models' residuals to test for significant spatial autocorrelation. Statistical significance was assessed using the analytical approximation implemented in the 'moran.test' function in the R-package "spdep' version 1.4-2 (Bivand 2022). This procedure allowed evaluation of whether spatial block cross-validation sufficiently reduced spatial dependence in model residuals. Significant positive Moran's I values would indicate remaining spatial autocorrelation and potential overestimation of model predictive ability.

The cross-validated individual SDMs were combined into an ensemble SDM using a weighted mean approach (Emwmean), retaining only individual models with ROC $\geq$ 0.80. A threshold of ROC $\geq$ 0.80 was applied to ensure that only models demonstrating at least fair discriminatory capacity contributed to the ensemble, thereby enhancing predictive robustness and minimizing the influence of low-performing algorithms (Kafle et al. 2023). Overall ensemble SDM performance has been shown to be highest when individual SDMs are weighted according to their evaluation score compared to other methods (Marmion et al. 2009; Hao et al. 2019). The ensemble SDM was used to determine the current suitable habitat of *W. salutaris* as well as to forecast under climate change. Distribution maps were converted into binary presence/absence maps using a ROC-derived threshold (ROC = 0.901) calculated during ensemble model evaluation in 'biomod2'. The binary maps were used to calculate range size changes under different climate change scenarios.

Identification of future climatically stable areas

The ensemble SDM was projected in southern Africa to 2041–2060 and 2081–2100 under two shared socio-economic pathways (SSPs) and three general circulation models (GCMs). SSPs are successors to representative concentration pathways (RCPs) and they take into consideration population growth, economic advancement, urbanization and technological development in determining future greenhouse gas emissions (Gidden et al. 2019; Riahi et al. 2017). In this study, the middle-of the-road SSP2-4.5 and the pessimistic SSP5-8.5 were used. The two SSPs were used in order to capture the full range of the impact of climate change, from the realistic to the most pessimistic. A map generated under SSP5-8.5 for 2081–2100 was used further to identify climate refuges that corresponded with PAs under climate change. Climate refuges identified under the pessimistic SSP5-8.5 scenario are most likely to be climatically conducive in future even under moderate and optimistic scenarios.

Variability in results of SDMs emanates from GCMs (Goberville et al. 2015). GCMs assess the response of climate to greenhouse gas emissions due to trends in land and energy use (Rogelj et al. 2012). The GCMs vary due to several factors, including use of different spatial resolutions and parameterizations of natural processes (Timbal 2004). To cater for inter-GCM variability, three GCMs were used, and these are the Canadian Earth System Model version 5 (CanESM5) (Swart et al. 2019), the Institut Pierre-Simon Laplace Climate Model version 6A Low Resolution (IPSL-CM6A-LR) (Boucher et al. 2020), and the Model for Interdisciplinary Research on Climate version 6 (MIROC6) (Tatebe et al. 2019). The GCMs were selected due to their predictive accuracy of climatic variables over the African continent (Zebaze et al. 2025) and completeness of data over all SSPs. A single consensus distribution map was produced in ArcGIS software showing presence in all maps generated from the three GCMs for each SSP and time period.

The binary consensus distribution map of *W. salutaris* for 2081–2100 under SSP5-8.5 was overlaid on a map of PAs in southern Africa to identify climate refuges that overlap with or are within the areas under protection. The period 2081–2100 was used to identify climate refuges that will remain stable in the long-term. The map of PAs was obtained from the world database on PAs of the United Nations Environment Program-World Conservation Monitoring Centre (www.protectedplanet.net) (UNEP-WCMC and IUCN 2024). The climate refuges that overlap with the suitable habitat of *W. salutaris* may help conservationists with options on where the species may be introduced and thrive successfully in future.

RESULTS

Model evaluation and current distribution

Mean ROC scores for the individual SDMs ranged from 0.744 to 0.892, while TSS scores ranged from 0.489 to 0.663 (Additional File 1). Averaged across all the SDMs, the scores showed robust performance (ROC = 0.836, TSS = 0.530). The Moran's I value ($I = 0.165$, $P < 0.05$) indicated a weak positive but significant spatial autocorrelation, suggesting that spatial structure in the residuals was minimal and that the spatial blocking strategy sufficiently reduced spatial dependence among folds. The ensemble SDM of the current distribution of *W. salutaris* also showed robust performance (ROC = 0.901, TSS = 0.895). After three permutations, two variables, Elevation and precipitation of warmest quarter (BIO18), showed the highest mean variable importance scores (Additional File 2). The variable importance scores show the contribution of each variable to the predictive power of the ensemble SDM. Response curves showed that the optimum precipitation of warmest quarter (BIO18) for *W. salutaris* is around 600 mm while the optimum mean temperature of the wettest quarter (BIO8) ranges from 20°C to 25°C (Additional File 3). Response curves also showed that suitability of the habitat to *W. salutaris* increases with increasing precipitation of the driest month (BIO14) up to 40 mm, and decreases beyond an altitude of 2,000 m.

The current distribution map shows potential presence of *W. salutaris* in South Africa, Swaziland, Malawi, Mozambique and Zimbabwe (Figure 2). In South Africa, the species was predicted to occur predominantly in the north-eastern provinces of KwaZulu Natal, Mpumalanga and Limpopo. Eswatini, formerly Swaziland, was shown to be largely suitable for *W. salutaris*. The eastern highlands in Zimbabwe and the southern region of Malawi are also priority areas for botanical exploration in search of the species. Mozambique has the largest potential distribution, especially in the provinces of Manica, Maputo and Zambezia. The relatively restricted potential distribution of *W. salutaris* in southern Africa has implications for viability of populations, supply of the species' medicinal products and designing of conservation strategies.

Suitable habitat under climate change

Averaged across three GCMs, the suitable habitat of *W. salutaris* contracted under the two SSPs and time periods. Under SSP2-4.5, the suitable habitat contracted from approximately 647,000 km^2 to 421,000 km^2 (-35%) in 2041—2060, and to 304,000 km^2 (-53%) in 2081–2100. Under SSP5-8.5, the contractions were approximately to 381,000 km^2 (-41%) in 2041—2060, and to 135,000 km^2 (-79%) in 2081–2100. The three GCMs showed similar results of contraction under all the SSPs and time periods (Table 1).

The largest contraction was observed under the pessimistic SSP5-8.5, thus, highlighting the grim consequences of uncontrolled greenhouse gas emission to the occurrence of *W. salutaris*. Under all projections, contraction of the natural range was especially notable in Malawi, Mozambique and Zimbabwe (Figure 3).

There are several PAs that contain or overlap with predicted climate refuges for *W. salutaris* in southern Africa in 2081–2100 (Table 2).The PAs include national parks, nature reserves, forest reserves and state forests. In Eswatini, Malalotja Nature Reserve was identified to contain climate refuges for *W. salutaris*. Most PAs were identified in South Africa and they include Barberton, Coleford, Doreen Clark and Itala Nature Reserves. In Zimbabwe, where *W. salutaris* has been classified as extinct in the wild, the PAs that overlap with climate refuges include Chipinge Safari Area and Nyanga National Park. Some entire PAs are climate refuges, such as Qudeni Forest Reserve in South Africa and Vumba Botanical Garden in Zimbabwe. The larger PAs, such as Addo-Elephant National Park and Maloti Drakensberg Conservation and Development Area in South Africa, partially overlap with climate refuges of *W. salutaris*.

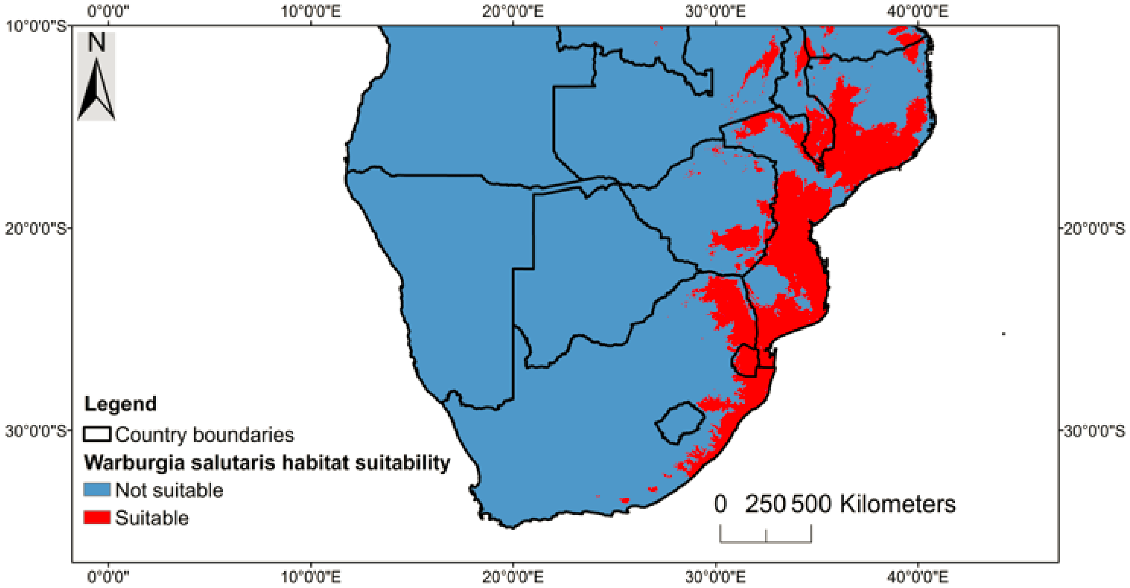

Figure 2. Geographic distribution of the current suitable habitat of *Warburgia salutaris* (Pepper-bark tree) in southern Africa determined by ensemble species distribution modeling.

Table 1. Percentage changes of size of the suitable habitat of *Warburgia salutaris* (Pepper-bark tree) estimated for two time periods by an ensemble species distribution model under three general circulation models (GCM) and two shared socio-economic pathways (SSPs).

	Shared socio-economic pathway (SSP)/ Year (%)			
GCM	**SSP 2-4.5 / 2060**	**SSP 5-8.5 / 2060**	**SSP 2-4.5 / 2100**	**SSP 5-8.5 / 2100**
CanESM5	-39.872	-44.573	-59.701	-78.921
IPSL-CM6A-LR	-29.424	-38.190	-51.869	-87.292
MIROC6	-34.824	-40.502	-46.618	-71.109
Mean change	-34.707	-41.088	-52.729	-79.107

DISCUSSION

The current distribution of *W. salutaris* has often been described as a list of countries where the species has been sampled (e.g., Maroyi et al. 2013; Glennon et al. 2023; van den Bosch et al. 2023) or as occurrence records where samples were collected (e.g., Dludlu et al. 2017; Senkoro et al. 2020). Although useful to some extent, country-level descriptions have the disadvantage of assuming presence even in areas where the species does not occur within the countries (Rathore and Sharma 2023). Similarly, maps of occurrence records only show locations that were accessed by researchers, while those that are inaccessible for sampling due to rough terrain and absence of roads are not represented (Fourcade et al. 2014). The map of the current suitable habitat established in this study represents a first attempt to show the spatial distribution of *W. salutaris* within countries and also in locations beyond the reach of traditional herbalists and researchers. The ensemble SDM map is an additional resource that may be used to determine forest management practices, guide botanical explorations and to suggest areas of introduction or preservation.

Warburgia salutaris is an evergreen species that occupies diverse habitats including coastal and riverine regions, dunes, mundane forests, open woodland, thickets and kloofs (Kotina et al. 2014; Leonard et al. 2023). The suitability of habitat remains high at a wide range of precipitation of driest months. The high habitat suitability under a wide precipitation range infers that the species has some evolutionary traits to respond to water extremes up to some point beyond which suitability declines. The evolutionary traits include stomatal density and thickness of cuticle (Kotina et al. 2014). The leaves have less stomata and thicker cuticle on the adaxial compared to the abaxial leaf surface (Kotina et al. 2014). On the adaxial surface, the cuticle has a mean thickness of 5.0 μm while on the abaxial surface, the mean cuticle thickness is 2.4 μm (Kotina et al. 2014). The thicker cuticle and less stomata on the adaxial surface reduce water loss by evaporative cooling. The ability to reduce water loss likely enables *W. salutaris* to occupy habitats of different water availability levels. However, as temperature of wettest quarter exceeds 25 °C and precipitation of warmest quarter goes below 250 mm, the habitat suitability decreases. This study has shown that although there are some evolutionary traits to respond to water and temperature stress levels, the projected climate change conditions are beyond the tolerance limit of *W. salutaris*, likely rendering the evolutionary traits inadequate for adaptation.

Globally, climate change has been shown to reduce the natural range of medicinal plants. The range contractions are a result of several factors, such as intolerance to climate extremes of the medicinal plants (Applequist et al. 2019) and climate change-accelerated spread of invasive species and exotic pathogens (Pyšek et al. 2020; Guégan et al. 2023). Intolerance to climate extremes has been shown in *Draba litamo* (Rodríguez et al. 2018), *Tylophora hirsuta*, (Khanum et al. 2013), *Rosa arabica* (Abdelaal et al. 2019), *Pterocarpus angolensis* (De Cauwer et al. 2014) and *Boswellia* sp. (Lemenih et al. 2014; Bongers et al. 2019). This study has also demonstrated the intolerance of *W. salutaris* to climate change. Overharvesting and climate change will combine to exacerbate population contraction that will cause inbreeding and loss of genetic variation, making the small populations less resilient to pests and diseases. In addition to disruption of the primary healthcare of economically vulnerable communities, the unavailability of medicinal plants due to climate change in Africa would also be devastating to collectors and vendors who rely on selling traditional medicinal products.

The forecasted higher contraction under SSP5-8.5 shows the dire consequences of unmitigated greenhouse gas emissions and associated climatic disruption. In southern Africa, the predicted long-term increase in mean temperature (Hulme et al. 2001) and decrease in mean annual precipitation (Dosio et al. 2021) due to climate change will likely disrupt establishment and growth, especially of those plants adapted to mesic environments. To mitigate the effects of the forecasted contraction of the natural range in the immediate term, current cultivation efforts by communities living in areas found in this study to be suitable for the species should be encouraged and supported. Once populations of *W. salutaris* are established in climatically suitable habitat, the communities may also be educated on the importance of sustainable harvesting and the practice of other traditional ecological man-

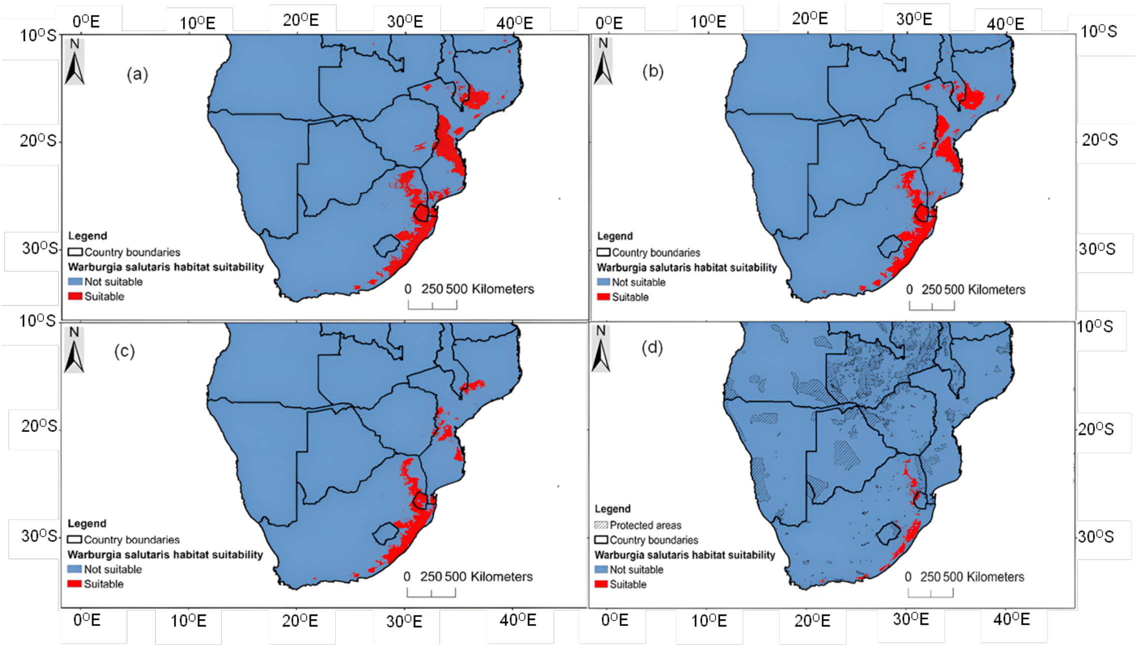

Figure 3. Consensus maps generated from three General Circulation Models of the forecasted distribution of the suitable habitat of *Warburgia salutaris* (Pepper-bark tree) under SSP2-4.5 in 2041–2060 (a), SSP5-8.5 in 2041–2060 (b), SSP2-4.5 in 2081-2100 (c), and SSP5-8.5 in 2081-2100 overlaid with protected areas (d).

Table 2. Protected areas that overlap with or contain predicted climate refuges of *Warburgia salutaris* (Pepper-bark tree) in 2081–2100 in southern Africa.

Country	Name of protected area	Type of protected area
Eswatini	Malatotja	Nature Reserve
South Africa	Addo-Elephant	National Park
	Barberton	Nature Reserve
	Coleford	Nature Reserve
	Doreen Clark	Nature Reserve
	Entumeni	Nature Reserve
	Golden Gate Highlands	National Park
	Karkloof	Nature Reserve
	Maloti Drakensberg	Conservation Area
	Mount Currie	Nature Reserve
	Nkandla	Nature Reserve
	Qudeni	Nature Reserve
Zimbabwe	Chipinge	Safari Area
	Stapleford	State Forest
	Nyanga	National Park
	Erin	State Forest
	Nyangui	State Forest

agement practices.

The establishment of PAs has been hailed as a significant conservation strategy to prevent biodiversity loss (Elsen et al. 2020; Leberger et al. 2020). In recognizing their role in conservation, countries under the Convention on Biological Diversity set a target to extend PAs to cover at least 17% of terrestrial and inland water, and 10% of coastal and marine areas (CBD 2024). PAs often contain large contiguous patches of natural land cover that provide critical habitat for sensitive and threatened species. The contiguous natural land cover helps to maintain intact, functioning ecosystems (Langdon and Lawler 2015). Climate refuges within PAs may potentially support species that migrate into them by providing climatically stable habitat (Hole et al. 2009; Sweet et al. 2019). In southern Africa, the PAs shown to contain climate refuges for *W. salutaris* may play a crucial role in conservation of the vulnerable species.

The climate refuges within PAs identified in this study may be used to establish pilot plots of *W. salutaris*. Establishment of the plots should ideally be a joint activity among government agencies responsible for PAs, university researchers, NGOs, and other interested stakeholders. The pilot plots may be used to track ecological data on development and survival before full-scale introduction. The established populations in the PAs may serve as future sources of seeds or cuttings for afforestation where the species can be harvested. It is, therefore, recommended that the identified climate refuges in PAs be considered as potential areas where *W. salutaris* may be introduced and maintained for long term persistence.

CONCLUSION

The study applied ensemble species distribution modeling to more accurately map the current range of *W. salutaris*, a culturally and medicinally tree species threatened by climate change, habitat loss, and overharvesting. Climate projections indicate a marked contraction of its suitable habitat, highlighting the species' vulnerability to rising temperatures and shifting precipitation patterns. However, the identification of climate refuges within PAs located in the natural range of the species offers a strategic opportunity for conservation planning. By integrating ensemble modeling with spatial conservation priorities, this research offers a strategic framework for safeguarding *W. salutaris* in the face of climate uncertainty. While the ensemble modeling results are robust and provide a valuable foundation for conservation planning, future studies would benefit from incorporating biotic interactions, such as competition and dispersal dynamics. These additions in modeling would enhance ecological realism and improve predictive accuracy, especially under rapidly changing environmental conditions.

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DATA AVAILABILITY

Occurrence records of *Warburgia salutaris* are publicly available at https://doi.org/10.15468/dl.f935qg, `https://gdauby.github.io/rainbio/download_page.html`, and `http://www.tropicos.org`. Ocurrence records are also available from Senkoro et al. (2020) and Dludlu et al. (2017). Environmental variables are publicly available at `www.worldclim.org`. The global map of protected areas is available at `http://protectedplanet.net`. The R code for model calibration, validation, ensembling and projection is available from the authors upon request.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

CONTRIBUTION STATEMENT

Conceived of the presented idea: PJ, TM Carried out the experiment: PJ
Carried out the data analysis: PJ
Wrote the first draft of the manuscript: PJ
Review and final write of the manuscript: PJ, TM
Supervision: PJ, TM

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Additional Files

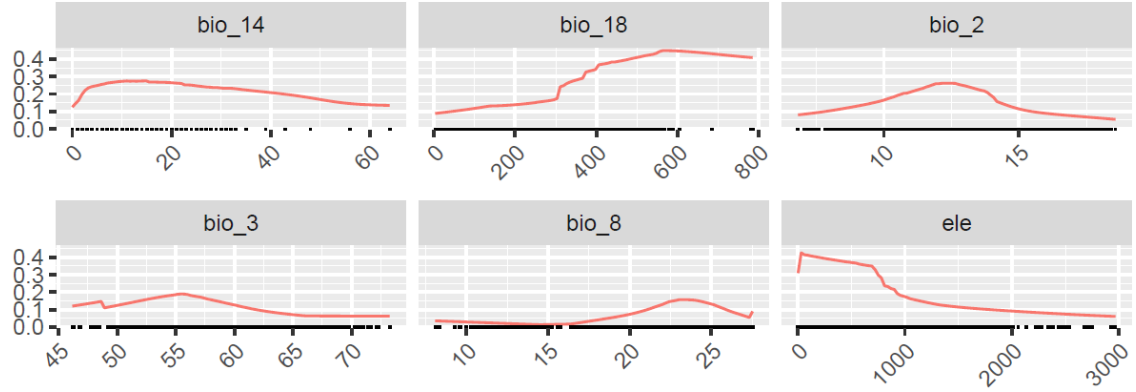
Add File 1. Mean evaluation scores of SDMs combined into an ensemble SDM used to predict the suitable habitat of Warburgia salutaris in southern Africa.

Algorithm	**Validation TSS**	**Validation ROC**
ANN	0.642	0.831
CTA	0.489	0.744
FDA	0.535	0.789
GBM	0.626	0.877
GLM	0.663	0.875
MARS	0.654	0.867
RF	0.009	0.892
SRE	0.624	0.812

Add File 2. Importance scores of variables used in an ensemble species distribution model to determine the current suitable habitat of Warburgia salutaris (Pepper-bark tree) in southern Africa.

Variable	**Permutation Score**			**Mean Score**
	1	2	3	
BIO2	0.122	0.118	0.127	0.122
BIO3	0.032	0.033	0.030	0.032
BIO8	0.085	0.083	0.085	0.084
BIO14	0.120	0.121	0.121	0.121
BIO18	0.155	0.152	0.153	0.153
Elevation	0.187	0.180	0.189	0.185

BIO2 = Mean diurnal range, BIO3 = Isothermality, BIO8 = Mean temperature of wettest quarter, BIO14 = Precipitation of driest month, BIO18 = Precipitation of warmest quarter



Add File 3. Response curves for variables used in an ensemble species distribution model to determine the current and future suitable habitat of Warburgia salutaris (Pepper-bark tree).

Bio_2 = Mean diurnal range, Bio_3 = Isothermality, Bio_8 = Mean temperature of wettest quarter, Bio$_1$4 = $Precipitationofdriestmonth, Bio\_18 = Precipitationofwarmestquarter, ele = Elevation$