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Tracing the range shifts of African tree ferns: Insights from the last glacial maximum and beyond

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ABSTRACT

African tropical forests are experiencing rapid decline as a result of several factors, including increasing population pressure, recurrent wildfires, selective logging practices, land use changes, intensified agricultural activities, and other social and economic issues. Using MaxEnt, paleoclimatic data, and future climate scenarios, the present study seeks to explore the presence of tree ferns in tropical and Saharan Africa during the Last Glacial Maximum, African Holocene Humid Period (AHHP; ca. 14,500–5000 years ago) and to project the effects of climate change on the distribution of tree ferns in Africa under two future climatic scenarios, Representation Concentration Pathways (RCP) 4.5 and 8.5. Our study reveals that despite a significant increase in precipitation during the AHHP, precipitation distribution was variable and insufficient to support the five tree fern species examined in this study. While some tree fern species have experienced range shifts over time, we found that most of them have maintained their presence within refuge areas that probably endured the late Pleistocene extinction event. These refugia provided a haven for some tree ferns, allowing them to persist and survive amidst challenging and varying environmental conditions. This highlights tree ferns' remarkable adaptability in changing climate as well as the critical importance of these refugial areas in safeguarding their populations during climatic upheaval. Our study further demonstrates that different species respond to climate change differently, with some experiencing minimal range contractions of 2.0 %, up to more than 57.0 % range expansion in other species. Preserving refugia not only safeguards tree fern populations but also contributes to conserving overall forest biodiversity and ecosystem functioning. This knowledge is crucial for implementing targeted conservation actions that promote sustainable forest management and can mitigate the threats posed by climate change and anthropogenic activities in African closed wet forests.

1. Introduction

Ferns (Class Polypodiopsida) account for 2–5 % of vascular plant species diversity and play a variety of ecological roles in Earth's ecosystems. Most fern diversity is concentrated in the tropics, subtropics, and south-temperate areas of the world (Barrington, 1993; Korall and Pryer, 2014), especially in mid-altitude cloud forests and oceanic islands. Tree ferns (members of the order Cyatheales, and especially the family Cyatheaceae) contribute to the stability of tropical and temperate forests in maintaining healthy and functioning ecosystems (Abernethy et al., 2016).

Tree ferns are strongly associated with Tropical Cloud Forests (TCF); on a global assessment level, Karger et al. (2021) found that tree ferns have the highest relative association with these forests, with 409 species (~62 % of total diversity) entirely restricted to Tropical Cloud Forests. Tree ferns have been widely exploited for commercial purposes across the globe, leading to a significant decline in populations (Bowd et al., 2018; Karger et al., 2021). For example, the trunk of *Alsophila dregei* (Kunze) R.M. Tryon has been extensively used in the production of various handcrafted items and as a substrate to cultivate orchids and

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other epiphytes (Ranil et al., 2011; Suryana et al., 2018). Exacerbating the issue, many wild populations have been harvested for landscaping, leading to local extinction in some areas (Ndangalasi et al., 2007). To curb this over-harvest, some countries have implemented laws and regulations to protect against further exploitation. In support, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listed one of the tree fern families, Cyatheaceae, for trade monitoring.

In Africa, varied climatic patterns, such as the length and intensity of dry and rainy seasons, contribute to a wide range of ecosystems such as wetlands, grasslands, savannas, mountain ranges, and forests (Pool-Stanvliet and Clüsener-Godt, 2013). Despite the splendor and beauty of these tropical ecosystems, African tropical forests are rapidly declining due to mounting human population pressure, recurring wildfires, selective logging, land use changes, augmented agricultural operations, and other socio-economic issues such as poverty, land use rights, and tenure (Laurance et al., 2017). On a local and global scale, forest fragmentation coupled with climate change are exacerbating biodiversity loss and species extinction (Määttänen et al., 2023; Wudu et al., 2023).

Although several studies have examined the impact of climate change on plant species occurring in Africa (John et al., 2020; Padonou et al., 2015), attention given to African ferns has been insufficient or lacking, except for a few recent studies (e.g., Karichu et al., 2022; Pie et al., 2022). Janssen et al. (2008), for example, provided fundamental insights into the evolution of Madagascan tree ferns, however, their study did not delve into the deeper implications and effects of climate change on continental African fern species. Although there are only a few studies on fern distribution models in Africa, the findings of Karichu et al. (2022) yielded discouraging results as several fern species appear to be on the brink of extinction in Africa; other recent studies have reached similar conclusions for ferns in other parts of the world (e.g., Pie et al., 2022; Watts and Watkins Jr, 2022). In addition, most previous studies in Africa have focused on the pluvial Equatorial region (Karichu et al., 2022; Mkala et al., 2022; Ngarega et al., 2022a, 2022b), neglecting the arid Sahara despite its high ecological relevance. Overlooking this vast region disregards the fact that it was once lush and verdant during the early Holocene period (Shanahan et al., 2015; Williams, 2021).

The African Humid Period (AHP) sometimes referred to as the African Holocene Humid Period (AHHP) (ca. 14,500 to 5000 years ago), was a period of significant climate change in northern and eastern Africa (Bard, 2013) that set the stage for the development of modern ecosystems across the African continent. This period, which occurred between the Last Glacial Maximum (LGM) and Mid-Holocene periods, approximately 22,000 and 5000 years ago respectively, was marked by increased precipitation and higher humidity levels fueled by orbital forcing (Claussen et al., 2017; Wright, 2017) and significantly impacted the African continent's flora and fauna, including ferns. Ferns are extremely sensitive to variations in temperature and precipitation (Della, 2022; Pie et al., 2022) but predicting how they will react to climate change is challenging (Blake-Mahmud et al., 2024; Ranker and Haufler, 2008). When critically examined, historical data can offer insights into species distribution, while recent observations can reveal additional, relatively rapid climate change impacts (Sharpe, 2019). To our knowledge, the past distributions of ferns during the LGM, the AHHP (when the Sahara region was wetter than today), and the consequent impacts of this historical climate change for shaping the modern fern flora, have not been investigated. Given the availability of paleoclimatic data for this time period, employing climatic and niche modeling could provide insights into the historical occurrence and distribution of African tree ferns, allowing for a comparison with present-day conditions and potential behavior of species under future climate scenarios.

Identifying regime shifts in the palaeoecological record presents additional challenges, especially when attempting to establish consistent timescales across multiple ecological indicators (Rull, 2014). However, advancements in modern ecological machine learning techniques, such as maximum entropy (MaxEnt), offer a solution by effectively handling complex interactions and enabling more realistic predictions of species distribution (Guisan and Thuiller, 2005).

Ecological niche modeling and thorough exploration of ferns' existence in continental Africa, particularly North Africa, has been inadequately evaluated, likely due to the presumed unsuitability of the region's dry conditions to support ferns. The current study examines possible scenarios of fern distribution in Africa. Is the current ecological scenario and distribution of tree ferns in agreement with paleoclimatic data records, or is it aberrant considering the current patterns in comparison to data from the previous millennium? Intrigued by this question, we used a species distribution modeling algorithm to reconstruct the potential ranges of tree ferns in Africa at several time points, including during the AHHP and under future climate scenarios for 2050–2070. We used paleoclimatic and occurrence data of five African tree fern species for the following reasons: (i) tree ferns produce minute, light-weight and copious amounts of spores that would be expected to disperse over long distances, (ii) except for one of the species (*Alsophila dregei*, which occurs both in continental Africa and the island of Madagascar), the selected fern species are endemic and widely distributed in continental Africa and may provide valid insights into the historical, current, and future impacts of climate change across the African continent, and (iii) tree ferns can be used as a model to predict biome-specific speciation in response to triggers of climate change since they are suited to and rely on the ecological niches presented by rainforest ecosystems (Janssen et al., 2008).

The objectives of this study were to (i) use paleoclimate data to infer the possible existence of tree ferns in tropical and Saharan Africa during the African Humid Period (AHHP), (ii) compare environmental and geographical drivers of tree fern distributions in North, West, Eastern, Central, and Southern Africa, and (iii) predict the impact of climate change on the future distribution of tree ferns in Africa. On the likely presence or absence of tree ferns in the Sahara region during the AHHP, we formulated the following hypothesis: 1) tree ferns could have existed during the onset of pluvial AHHP but could not survive the increased aridity and abrupt termination of the African Humid Period, and 2) tree ferns may have not successfully established in North Africa or other dry regions, since the onset and termination of the AHHP has been hypothesized to have been short-lived (Dallmeyer et al., 2020).

2. Materials and methods

2.1. Species selection and occurrence localities

The Cyatheaceae family comprises more than 600 species globally (PPG I, 2016). Mainland Africa has a relatively low species richness of the family, with approximately 14 species (Roux, 2003; Roux et al., 2016). The island of Madagascar, in contrast, boasts a significantly higher species richness: 51, with 95 % endemic to the region (Janssen et al., 2008; http://www.worldplants.de/). Species from continental Africa with fewer than 10 occurrences at the time of data collection were excluded from the dataset, and so the current study focused on five species of tree ferns with sufficient data available: *Alsophila camerooniana* (Hook.) R. M. Tryon, *Alsophila dregei* (Kunze) R. M. Tryon, *Alsophila humilis* (Hieron.) Pic. Serm, *Alsophila manniana* (Hook.) R. M. Tryon, and *Alsophila thomsonii* (Baker) R. M. Tryon. These species were chosen using the following process. First, we obtained the occurrence data of all the taxonomic treatments of *Alsophila* in Africa following Korall et al. (2007) and the Pteridophyte Phylogeny Group (PPG I, 2016) classification. All the species formerly recorded as *Cyathea* in Africa were treated as synonyms to the corresponding *Alsophila* species based on Korall et al. (2007) and World Flora Online (https://www.worldfloraonline.org/). *Alsophila camerooniana,* which has been recorded to have about eight infraspecies, was treated uniformly as *A. camerooniana* (Hook.) R. M. Tryon. The geographic localities for *Alsophila* were retrieved from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/), author field notes collected during fieldwork in Kenya in 2022–2023, herbarium specimen data from the East African Herbarium (EA), and Meise Botanic Garden (BR). Next, the species occurrence data were assessed for accuracy of the longitude and latitude data to ensure the species' geographical correctness. Google Earth (https://earth.google.com/web) was utilized to retrieve the relevant longitude and latitude coordinates for specific species that lacked geographical coordinates but had other comprehensive information about the species' locality. Finally, species records that lacked sufficient geographic location descriptions were deleted (Elith et al., 2011). The final species list had 717 localities in total: *A. humilis* (29), *A. thomsonii* (29), *A. camerooniana* (168), *A. dregei* (236), and *A. manniana* (255) (Fig. 1; Table S1).

2.2. Environmental variables

We obtained past climatic variables from WorldClim 1.4 (Hijmans et al., 2005), and the current and future climatic variables from the WorldClim2.1 database (Fick and Hijmans, 2017) through the Coupled Model Intercomparison Project (CMIP5) (Gent et al., 2011). These climate factors include seasonal and annual average precipitation and temperature, as well as other factors. CMIP models have been used extensively due to their biological relevance, but they still have several weaknesses and limitations that can affect their utility in modeling species. We chose CMIP5 for the following reasons; While both CMIP5 and CMIP6 suffer from model biases related to cloud-precipitation processes, CMIP5 appears to perform better in terms of representing the cloud feedback mechanism (Mülmenstädt et al., 2021). This is especially important for Africa's complex climate systems and the large variation in climate across different regions, from deserts to rainforests. Additionally, the CMIP6 models shows significant limitations in accurately simulating both climate change and its natural variability. (Scafetta, 2021, 2023).

Temperature and precipitation variables, Bio1–Bio11 and Bio12–Bio19 (Table S2), respectively, were derived at a spatial resolution of 2.5 arcmin (20.25 km^2) for the Community Climate System Model version 4 (CCSM4) (1970–2000) for the current climate as well as two past (paleo) and two future climate scenarios. For the future climatic scenarios, we included two representative concentration pathways (RCPs) to represent the moderate (RCP 4.5) and high emission (RCP 8.5) scenarios for the 2050s (2041–2060) (van Vuuren et al., 2011). The paleoclimatic layers comprised the Mid Holocene (MH; 6000 years before present) and the last glacial maximum (LGM; 22,000 yr. BP). In addition to the bioclimatic data, elevation data were sourced from the WorldClim2.1 database.

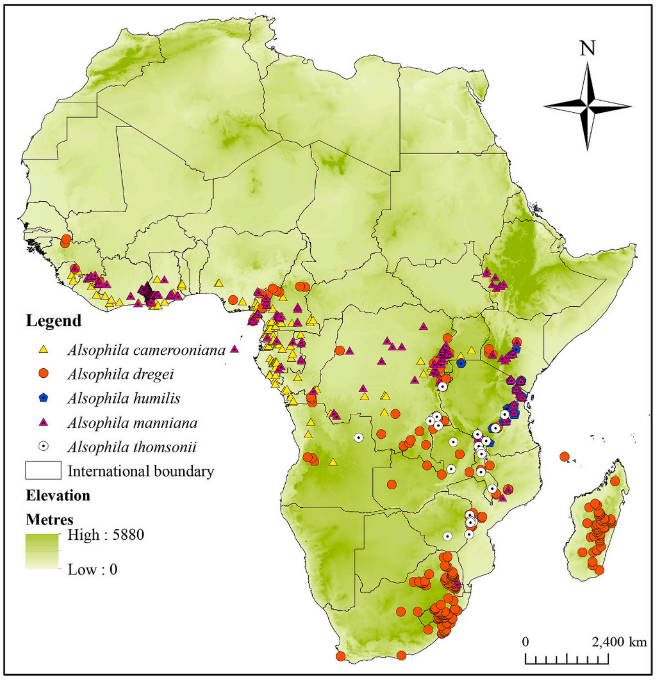

Fig. 1. Map of occurrence points of five *Alsophila* species in Africa, with elevation shown.

A focus on bioclimatic and topography variables when conducting species distribution modeling is quite typical. However, it is important to note that the Aridity Index (AI) also significantly influences these models, and may be important for fern species (Vacchiano and Motta, 2015). Unfortunately, we could not incorporate AI into our modeling due to the unavailability of historical aridity data, as the available Global Aridity Index dataset only covers the period from 1970 to 2000 (Zomer et al., 2022). Since our study spans multiple time periods, including in the ancient past (LGM and Mid-Holocene), the lack of AI data for those times would have led to a non-comparable model if we had included it only for one time period. Instead, we focused on precipitation and temperature, the primary factors influencing the aridity index (AI). The aridity index is determined by the balance between precipitation and evaporation, which is influenced by temperature. By including both precipitation and temperature in our models, we aim to capture the key drivers of aridity. We also made the assumption that elevation would remain constant in our simulations of potential geographic distribution under climate change. For a detailed list of environmental variables, please refer to Table S2.

2.3. Data cleaning

2.3.1. Cleaning and spatial thinning of the occurrence points

Unclear, duplicate, and adjacent records were eliminated from the distribution data in the environment layer raster using the SDMToolbox v.2.5 extension in ArcGIS v.10.8.2 (Brown et al., 2017). To limit sample variance, only a single occurrence record was selected for each square grid cell of 4.5 km on the ground (20.25 km^2), corresponding to the resolution of the bioclimatic variables.

2.3.2. Multicollinearity test of the predictor variables

Collinearity indicates the presence of two or more linear correlated variables that may result in multicollinearity-related bias in the models (Dormann et al., 2013), overfitting of the models, and inflation of the confidence interval (CI) and standard error (SE), thus limiting the determination of each variable to the dependent variable (Dormann et al., 2013). To avoid model multicollinearity, the collinear variables were eliminated with a variance inflation factor value (VIF, Akinwande et al., 2015), using the VIFstep function of the "*usdm*" package in R (Naimi, 2015). Variables with VIF score values of 10 and below were retained for progressive analysis (Elith et al., 2011) (Table S3).

2.4. Model development and evaluation

Species distribution modeling was performed using the maximum entropy technique (MaxEnt 3.4.4) (Phillips and Dudík, 2008). When compared to other modeling algorithms, this prominent correlative modeling methodology performs better (Elith et al., 2011). Furthermore, unlike masked data (presence-absence data), it can perform well with little presence data irrespective of the geographic distribution of a species (Radosavljevic and Anderson, 2014). We randomly separated occurrence points into 75 % training and 25 % testing, to decrease uncertainty due to sampling artifacts. To assess the models' reliability, 10 replications were performed using a subsampling approach, which divides the presence points into random testing and training sets and averages the results. We then set the max of background data to 10,000, and the max number of iterations to 5000 to find the best solution, while the remaining parameters were left at their default settings (Phillips et al., 2006). This approach has proven effective (Syfert et al., 2013) and allowed us to focus on other critical aspects of model development, such as selecting relevant environmental variables and refining presence data. In addition, the tree fern species under study exhibit diverse ecological preferences (Table 1). By leaving some default settings, we ensured that our initial models were built on a broadly applicable framework, reducing the potential for overfitting. This generality is particularly important for species-specific models (Moreno-Amat et al., 2015), and given the varied habitats (e.g., moist forests, grasslands) and elevational ranges (from 200 m to 2600 m) of the tree ferns under this study. To further reduce model uncertainties, we utilized the variable contribution and Jackknife tests within MaxEnt (Supplementary Fig. S1) to evaluate the importance and effects of each environmental variable (Bradie and Leung, 2017). Finally, the maximum training sensitivity plus specificity (MTSS) logistic threshold was used to create suitability maps for the five *Alsophila* species, accomplished in ArcGIS v.10.8.2 (Liu et al., 2016a).

We used the area under the curve (AUC) of the receiver operating characteristic (ROC; Phillips et al., 2006) and the true skill statistics TSS (Allouche et al., 2006) to assess model discriminatory power. The AUC and TSS values vary between 0 and 1 to test the correctness of each model (Table 2). The following criteria were used to assess the accuracy of the resultant models: poor performance (AUC 0.5), fair performance (AUC 0.5–0.7), and excellent performance (AUC $>$ 0.7) (Guisan and Thuiller, 2005; Phillips and Elith, 2010).

2.5. *Environmental habitat suitability and range change*

We utilized the MTSS threshold to change the continuous suitability (range of 0 to 1) of the MaxEnt averaged output available in the American Standard Code Information Interchange (ASCII) format into binary suitability (1/0) in ArcGIS v.10.8.2 (Tables 2 and S4). We then used the Zonal Statistics available in the Spatial Analyst tools in ArcMap to obtain the potential ranges and used the current (baseline) period as a reference for obtaining the changes under past and future conditions. Changes in habitat suitability were then calculated by SDMToolbox (Brown et al., 2017), by comparing the binary outputs of the past and future conditions with reference to the current climate binary maps. To assess changes during different time periods we employed the following protocol: For the AHHP, we subtracted the distribution of all *Alsophila* species in the MH (6000 yr. BP) from their respective LGM (22,000 yr. BP) distributions, which allowed us to comprehend the shifts that occurred between the onset and termination of the AHHP, i.e., over the intervening time interval. As for future range changes, we subtracted the projected species distribution in future scenarios from their present distribution (Fig. 2).

Table 2
Overview of distribution data and SDMs for each studied species.

Species	No of occurrences used in final SDMs	AUC(SD)	TSS	MTSS
Alsophila camerooniana	168	0.961 (0.005)	0.909	0.1027
Alsophila dregei	236	0.952 (0.003)	0.879	0.1663
Alsophila humilis	29	0.980 (0.007)	0.899	0.1884
Alsophila manniana	255	0.947 (0.016)	0.860	0.1760
Alsophila thomsonii	29	0.961 (0.026)	0.922	0.1866

MTSS, Maximum Training Sensitivity plus Specificity logistic threshold.

3. Results

3.1. *Model performance and variable contribution*

The MaxEnt model predicted *Alsophila* habitat suitability based on presence records, climate and elevation data, with an average AUC ranging between 0.947 ± 0.016 and 0.980 ± 0.007 and a TSS above 0.879 (Table 2), indicating strong discriminatory power in predicting *Alsophila* habitats in Africa. Variable contributions varied by species (Table. 3). Annual Mean Temperature (Bio1) had minimal influence on *A. camerooniana* (0.7 %), *A. humilis* (0.6 %), and *A. manniana* (3.1 %), while strongly impacting *A. thomsonii* (17.5 %), and *A. dregei* (39.1 %). The Mean Diurnal Range (Bio2) had minimal influence on *A. dregei* (2.3 %), *A. manniana* (6.8 %), and *A. humilis* (13.1 %), but was substantial for *A. camerooniana* (17.0 %), and *A. thomsonii* (19.9 %). Isothermality (Bio3) and Precipitation Seasonality (Bio15) collectively had $<$10 % impact across all species. Precipitation of the Wettest Month (Bio13) was the lowest contributor for *A. humilis*, *A. manniana*, *A. dregei*, and *A. thomsonii* at (12.4 %, 14.6 %, 23.5 %, 24.3 % respectively), but contributed significantly to *A. camerooniana,* at 42.3 %. Precipitation of the Driest Month (Bio14) had a minimal influence on *A. thomsonii* (1.9 %), but substantial effect on *A. dregei*, *A. camerooniana*, *A. humilis* (20.8 %, 26.6 %, 36.8 % respectively) and highest influence on *A. manniana* at 60 %. Elevation significantly influenced the models across all species, except for *A. camerooniana* and *A. dregei,* where its contribution was $<$10. (Table 3). Overall, Bio13, Bio14, and Elevation had a significant contribution to model predictions.

Table 1
Characteristics and Habitat Preferences of Selected Tree Fern Species.

Species	Elevational Range	Temperature Range	Preferred vegetation Type	Fire Resistance	Other Traits
A. camerooniana [1,2]	1200–1400 m	22–28 °C	Moist forest, often near streams, riverbank in high forest	Undocumented	Erect trunk 2–3 m tall, dark stipe covered with scales, highly variable
A. dregei [1,2,3,4,5, This study]	400–2600 m	20–30 °C	Along streams in open grasslands, swamp edges, riverine forest, forest margin, at the base of cliffs in montane grassland, partially shaded or exposed and less often in dense forest	Highly Pyrophytic (well adapted to tolerate fire)	Caudex stout, erect, simple, to 3 m tall. 450 mm in diameter, densely covered with adventitious roots, not edaphically bound,
A. humilis[1,2,5,This study]	900–2250 m	11.6–30.7 °C	Moist forests, often near streams	Undocumented	Erect trunk, dead fronds often retained, forming an irregular skirt around the trunk, stipe is light brown
A.manniana[1,2,5, This study]	200–2700 m	22–30.7 °C	Gregarious, in forest along streams, also found in deep shade on streambanks in forested ravines	Undocumented	Shade tolerance, black spines on the caudex,
A. thomsonii [1,2]	1200–2250 m	11.6–30.7 °C	Along streams in moist forests, shaded streambanks in evergreen or semi-deciduous forest, swamp forests, and near waterfalls	Undocumented	Caudex slender with no spines, stipe glossy brown, over 2 m tall

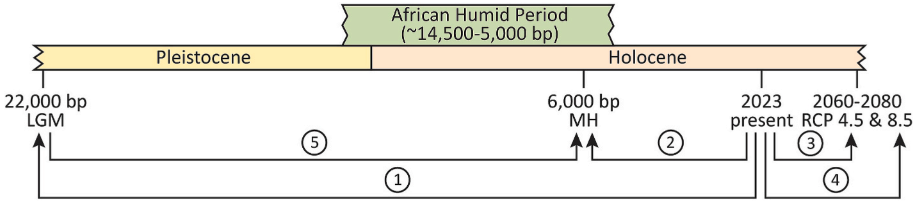

Fig. 2. Timeline considered in this study, from the Last Glacial Maximum (LGM) through the Mid Holocene (MH) to the present (2023), and on to 2050–2070, for which we tested two future emissions scenarios (RCP 4.5 and 8.5). The African Humid Period (AHP) occurred roughly 12,000–5000 years before present (bp). Arrows below the timeline indicate five comparisons we made in order to investigate changes in suitable habitat availability between timepoints: 1, 2, 3, and 4 compare the LGM, MH, RCP4.5 and RCP 8.5 to the present, with the present serving as baseline in all comparisons, while 5 compares the LGM to the MH, with the latter serving as the baseline, to capture habitat change across the AHP.

Table 3
Percent contribution of the selected variables on the studied species.

Species	Bio1	Bio2	Bio3	Bio13	Bio14	Bio15	ELEV
A. camerooniana	0.7	17.0	1.7	42.3	26.6	9.1	2.7
A. dregei	39.1	2.3	6.8	23.5	20.8	0.5	7.0
A. humilis	0.6	13.1	6.6	12.4	36.8	5.4	25.2
A. manniana	3.1	6.2	3.0	14.6	60	2.0	10.6
A. thomsonii	17.5	19.9	8.9	24.3	1.9	2.3	25.3

3.2. Potential distribution of Alsophila under current climate conditions

Based on the binary maps and the MTSS threshold, the current potential distribution area varied from 1,339,214 km^2 (*A. humilis*) to 4,246,808 km^2 (*A. manniana*) (Table 4). In addition, the generated map of potential distribution for the examined species based on present climatic conditions is broadly coherent with the known geographical ranges of these five taxa (Figs. 1 and 4). The current potential distribution was observed to be mostly in the tropical regions including east (e.g., Uganda, Kenya, Ethiopia, Tanzania, Rwanda, and Burundi), west (e.g., Ghana, Benin, Nigeria, Togo), and central Africa (e.g., Cameroon) for most species. However, *A. dregei*, *A. manniana,* and *A. thomsonii* occurred as well in southern African countries (e.g., South Africa, Zimbabwe, Eswatini, Lesotho, Mozambique). While all the species have potentially suitable habitats in Madagascar, only *A. dregei* currently has a shared occurrence between continental Africa and Madagascar (Fig. 3).

Table 4
Current suitable habitat area in Africa for five *Alsophila* species, and the amount of area predicted as lost, gained, or remaining stable, compared to current conditions, under two past climate scenarios (LGM and MH) and two future greenhouse gas emission scenarios (RCP 4.5 and 8.5). Green boxes are those for which the percentage of stable habitat plus habitat gained exceeds 100 % of current area; yellow and orange boxes are scenarios where this totals 90–99 % or less than 90 % of current area, respectively.

Species	Current Area (km^2)		LGM Area (km^2)	% of current area		MH Area (km^2)	% of current area		RCP 4.5 Area (km^2)	% of current area		RCP 8.5 Area (km^2)	% of current area
A. camerooniana	4,065,465	Loss	731,696	-18%	Loss	697,830	-17%	Loss	750,124	-18%	Loss	562,198	-14%
		Gain	275,799	7%	Gain	657,540	16%	Gain	39,893	1%	Gain	160,989	4%
		Stable	3,333,769	82%	Stable	3,367,636	83%	Stable	3,369,232	83%	Stable	3,427,652	84%
		Stable + Gain	3,609,598	89%	Stable + Gain	4,025,176	99%	Stable + Gain	3,409,125	84%	Stable + Gain	3,588,641	88%
A. dregei	2,141,135	Loss	487,739	-23%	Loss	130,893	-6%	Loss	138,919	-6%	Loss	150,573	-7%
		Gain	352,447	16%	Gain	777,514	36%	Gain	364,378	17%	Gain	320,134	15%
		Stable	1,653,396	77%	Stable	2,010,242	94%	Stable	2,008,952	94%	Stable	1,998,782	93%
		Stable + Gain	2,002,917	93%	Stable + Gain	2,787,746	130%	Stable + Gain	2,373,330	111%	Stable + Gain	2,318,916	108%
A. humilis	1,339,214	Loss	349,392	-26%	Loss	425,164	-32%	Loss	216,983	-16%	Loss	100,878	-8%
		Gain	477,540	36%	Gain	265,893	20%	Gain	500,189	37%	Gain	723,189	54%
		Stable	989,823	74%	Stable	914,051	68%	Stable	1,081,198	81%	Stable	1,203,994	90%
		Stable + Gain	1,367,363	110%	Stable + Gain	1,179,944	88%	Stable + Gain	1,581,387	118%	Stable + Gain	1,927,183	144%
A. manniana	4,246,808	Loss	1,659,800	-39%	Loss	421,738	-10%	Loss	102,081	-2%	Loss	430,081	-10%
		Gain	134,046	3%	Gain	1,369,889	32%	Gain	1,112,098	26%	Gain	609,231	14%
		Stable	2,587,008	61%	Stable	3,825,070	90%	Stable	4,036,898	95%	Stable	3,907,987	92%
		Stable + Gain	2,721,054	64%	Stable + Gain	5,194,959	122%	Stable + Gain	5,148,986	121%	Stable + Gain	4,517,218	106%
A. thomsonii	1,805,017	Loss	85,503	-5%	Loss	187,532	-10%	Loss	109,298	-6%	Loss	112,083	-6%
		Gain	1,036,204	57%	Gain	616,277	34%	Gain	306,082	17%	Gain	402,009	22%
		Stable	1,719,514	95%	Stable	1,617,486	90%	Stable	1,720,311	95%	Stable	1,721,027	95%
		Stable + Gain	2,755,718	152%	Stable + Gain	2,233,763	124%	Stable + Gain	2,026,393	112%	Stable + Gain	2,123,036	117%

LGM, Last glacial maxima; MH, Mid Holocene; RCP, Representative concentration pathways.

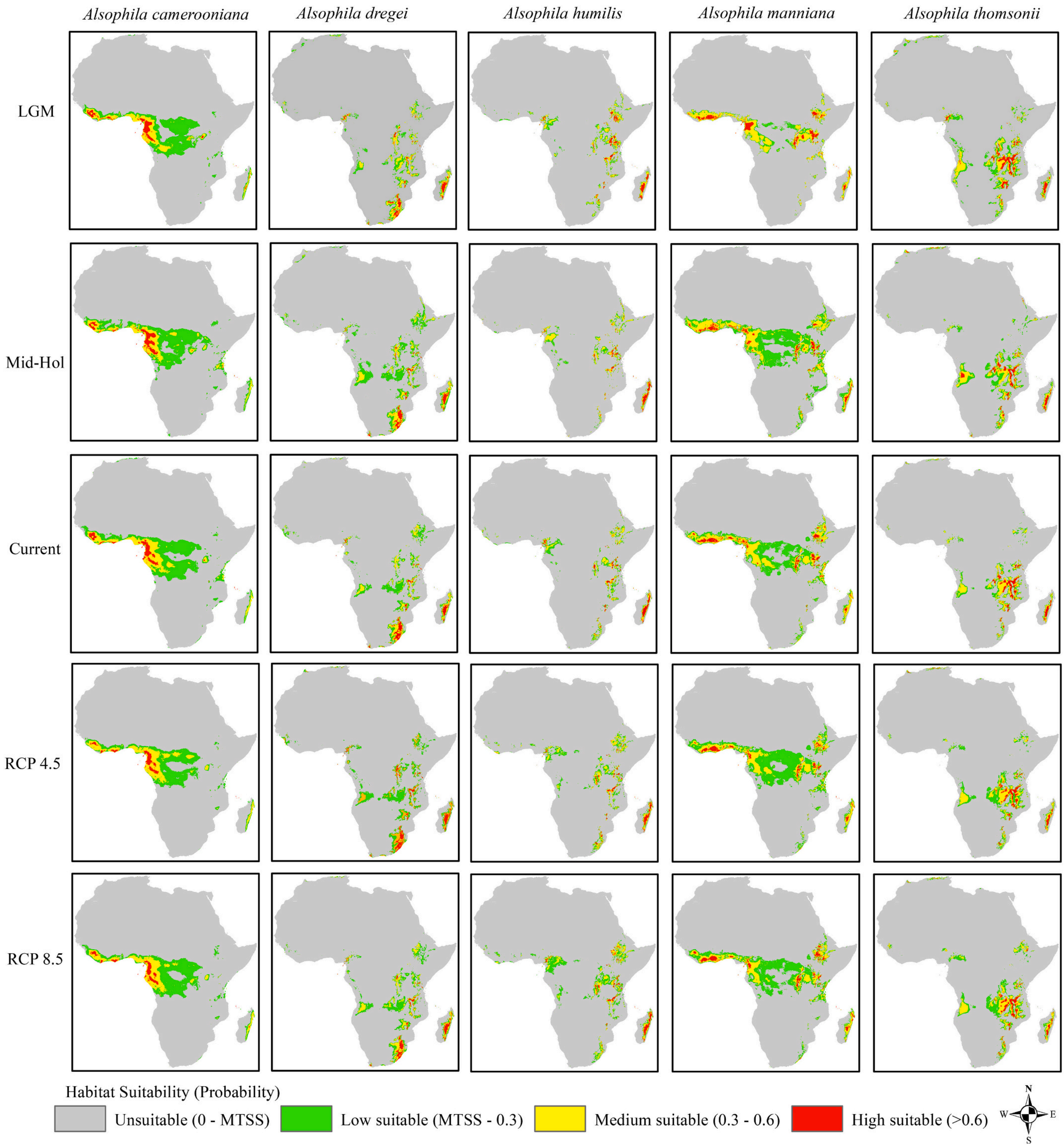

Fig. 3. Estimated habitat suitability in Africa during two past conditions (LGM and MH), current conditions, and under two future (2040–2060) climate scenarios (RCP 4.5 and 8.5) for the five studied *Alsophila* species.

3.3. Changes in suitable habitat area under past and future climate conditions

Our results showed that *Alsophila* species have responded and will respond differently to past and future climate scenarios (Figs. 4 and 5). Four out of five species had an increased suitable range size, compared to the present, in three or four of the past (LGM and MH) and future (RCP 8.5 and RCP 4.5) climate scenarios (Table 4). For example, *A. thomsonii* was predicted to increase its range size (stable plus gained area) to a total of 152 % and 124 % in the LGM and MH, respectively, and is estimated to have a stable plus gained area of 112 % and 117 %, respectively, under the RCP 4.5 and 8.5 scenarios (Table 4).

In comparison with the baseline climate, under the LGM conditions (~22,000 yr. BP) the modeled species were predicted to have had a variety of habitat stability, expansion, and contraction. Area loss ranged from 5 % in *A. thomsonii* to 39 % in *A. manniana*, while gains ranged from 7 % in *A. camerooniana* to 57 % in *A. thomsonii*. Stable habitat was roughly consistent across species, with *A. manniana* recording the lowest

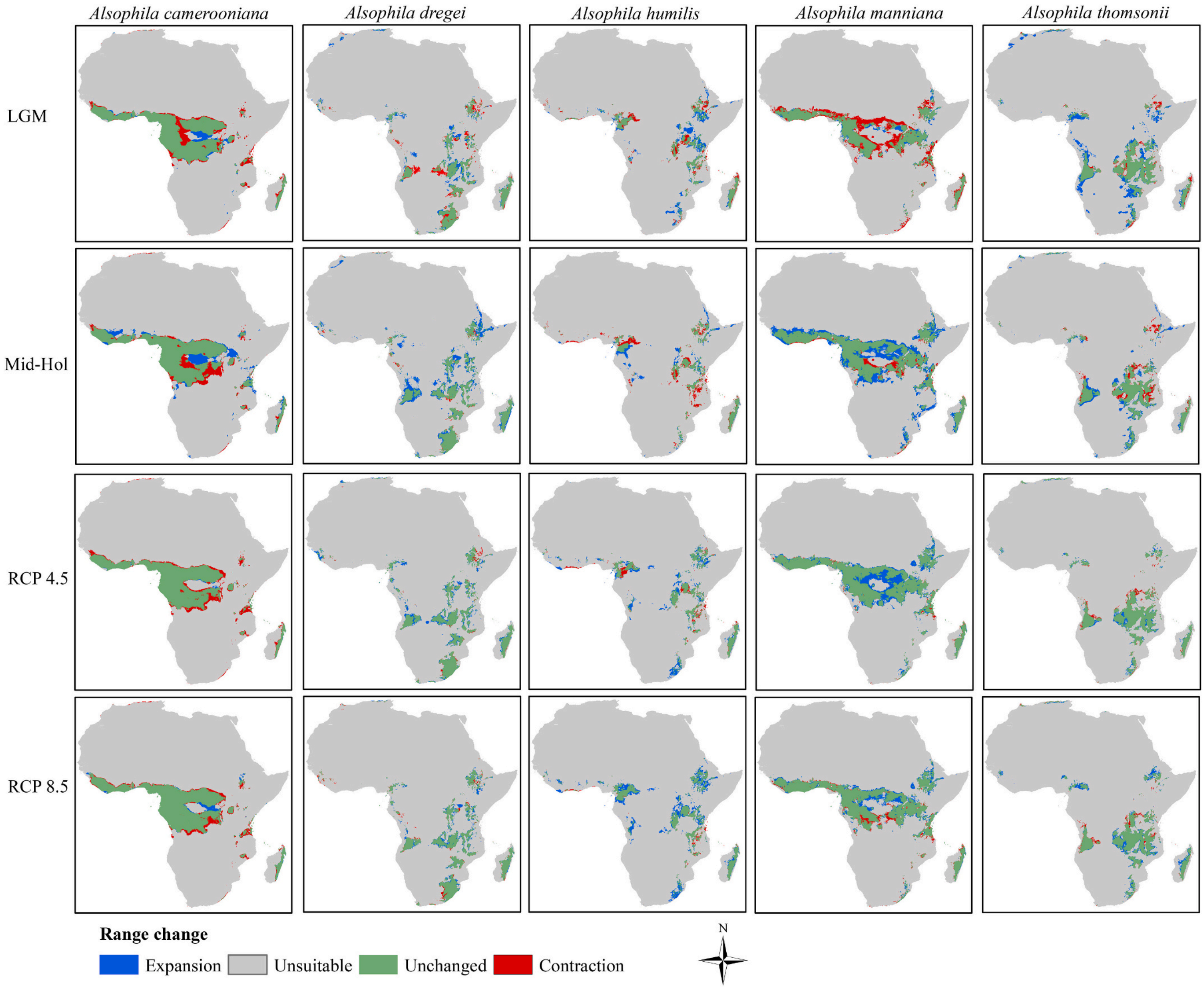

Fig. 4. Predicted changes in distribution areas between current (baseline), compared to two past (LGM and Mid-Holocene) and two future climate scenarios (RCP 4.5 and RCP 8.5).

at 61 %, and *A. thomsonii* the highest at 95 % (Table 4).

When comparing the MH conditions (~6000 yr. BP) to the current conditions as the baseline, the predicted range loss was highest for *A. humilis* at 32 %. *A. camerooniana* followed at 17 %, then both *A. thomsonii* and *A. manniana* at 10 %, and *A. dregei* at 6 % (see Table 4). All species except *A. humilis* recorded stable habitat of more than 80 % of their current distribution (Table 4). Habitat expansion in the MH compared to the present was predicted to range from 16 % for *A. camerooniana* to 36 % for *A. dregei*. In contrast, when assessing the change between the current and MH (~6000 yr. BP) climate conditions (with MH as the baseline period), *A. camerooniana*, *A. dregei*, *A. manniana,* and *A. thomsonii* species were observed to gain suitable ranges on the upper limits of their distributional range, implying a northern shift.

In the context of the future climate scenarios for the 2050s (RCP 4.5 and RCP 8.5), with respect to the current climate, the models for *A. camerooniana* predict a reduction in its potential habitat extent under both scenarios, with overall suitable habitat remaining only 83 % and 84 % of the current suitable area, respectively. Conversely, the other four species exhibited an expansion of their overall suitable habitat, although to a varying degree. *Alsophila thomsonii,* for instance, may experience a moderate increase to 112 % under RCP 4.5 and 117 % under RCP 8.5. In contrast, *A. humilis* was predicted to have a substantial habitat expansion, expanding to a total of 118 % or 144 % of its current suitable habitat under RCP 4.5 and 8.5, respectively (Table 4). These predicted expansions are driven by very limited predicted loss of current habitat, with substantial current range both retained and new range gained. In comparison to the current (baseline) scenario, *A. camerooniana* was observed to have a range shift in the upper and the lower limits of its distributional range, for both future climate conditions (RCP 4.5 and RCP 8.5), also inferring a latitudinal shift.

3.4. *Alsophila range shifts in the African Holocene humid period (AHHP)*

For changes during the AHHP, for which we compared the LGM to the MH, using LGM as the baseline, most species experienced a northward or northwestern expansion as a response to the increased rainfall and expansion of more hospitable habitats, but each species had a unique trend, probably due to local climatic conditions. *Alsophila humilis* gained 52 % of its current range area, followed by *A. thomsonii* with a 38 % expansion, while the remaining three species experienced expansions of 12 % (*A. camerooniana*), 10 % (*A. dregei*), and 3 % (*A. manniana*) of their current area. (Table 5). In terms of contractions of the ranges, *A. manniana* was observed to lose as much as half of its suitable range

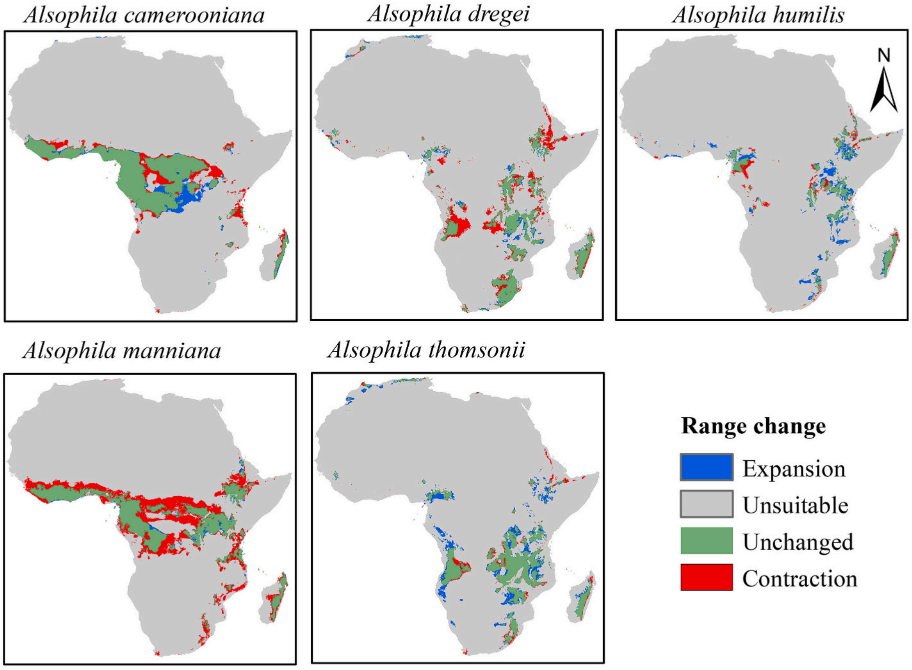

Fig. 5. Changes in predicted suitable habitat for five *Alsophila* species between the Mid-Holocene and the LGM, to illustrate the differences in habitat suitability between the onset and the end of the African Humid period (AHP).

Table 5
Changes in the projected ranges for each of the five *Alsophila* species, for the predicted area with high suitability (> MTSS) under past climatic conditions and comparing the Mid Holocene (MH) to the Last Glacial Maximum (LGM). The range comparison for these two periods is expressed in km^2 and percentages in parentheses represent the area lost, gained, or remaining stable.

	Predictions		Comparisons of MH versus LGM		
	Predicted Area with high suitability (> MTSS) under MH conditions (km^2)	Predicted Area with high suitability (> MTSS) under LGM conditions (km^2)	Stable (km^2) (%)	Expansion (km^2) (%)	Contraction (km^2) (%)
Alsophila camerooniana	3,982,661	3,589,310	3,208,190 (80.5)	489,036 (12.2)	852,651 (21.7)
Alsophila dregei	2,563,141	2,001,516	1,700,192 (66.0)	256,093 (10.0)	998,065 (39.0)
Alsophila humilis	1,215,445	1,470,937	832,893 (69.0)	635,092 (52.0)	306,128 (25.0)
Alsophila manniana	5,011,019	2,689,925	2,499,135 (50.0)	138,903 (3.0)	2,519,882 (50.0)
Alsophila thomsonii	2,241,310	2,752,017	1,920,839 (86.0)	834,240 (38)	306,262 (14.0)

(50.0 %), while *A. dregei* lost 39 %, *A. humilis* 25 %, *A. camerooniana* 22 %, and *A. thomsonii* 14 %. *Alsophila mannianna* and *A. camerooniana*, which occupied a larger range in West Africa in the LGM, were predicted to lose considerably more of their suitable range compared to the rest of the species (Fig. 4). Additionally, *A. humilis* and *A. dregei* are also observed to lose part of their ranges in the west and central African regions over the time period corresponding to the AHHP, as well as in the highlands of Ethiopia (Fig. 5).

4. Discussion

Global climate change significantly alters species distributions globally through rising temperatures and shifting rainfall patterns (Ngarega et al., 2021; Padonou et al., 2015), with variable impacts on different species, as shown in this study. In addition, variations in the intensity and magnitude of extreme events, such as heat waves, drought, and floods (Tramblay et al., 2020), as well as historical climatic conditions (Shanahan et al., 2015), have the potential to influence the establishment and long-term survival of many species. In this study, we incorporate several of these factors to evaluate potential shifts in the ranges of five tree fern species from two time points in the past (22,000 and 6000 yr. BP) to the present and into the future (the 2050s) under two estimated emissions (RCP 4.5 and 8.5) scenarios. The results demonstrate that substantial range shifts have taken place over the last 22,0000 years and that future climate change will likely have significant ecological impacts on vegetation in Africa by altering species' distribution and occurrence. Remarkably, we found that most of the species we studied are predicted to increase their range size under both future climate change scenarios that we tested, in contrast with previous studies on the African continent that have highlighted the potential negative future impacts of climate change for ferns (Karichu et al., 2022).

4.1. Range shifts of African tree ferns in the LGM

The Last Glacial Maximum (LGM) was marked by increased ice sheets, low atmospheric CO$_2$, and cold and dry conditions (Clark et al., 2009; Hamilton and Taylor, 1991) that had a striking impact on continental Africa. In northern (i.e., Saharan) Africa, evidence exists for the presence of widely distributed ancient sand dunes (Lüning and

Vahrenholt, 2019), which almost certainly would not have supported the existence of tree ferns, which require adequate precipitation for establishment. This is evident from our reconstruction maps, as no suitable habitat is projected for any of the five tree fern species in this vast region at that time (Figs. 4 and 5). Similarly, in the Atlantic, ocean upwelling systems linked with eastern boundary currents influenced the coastal climate by cooling the adjacent land areas, such as off the northwest coast of Africa (Cropper et al., 2014), rendering this habitat unsuitable for tree ferns.

Meanwhile, relatively minor cooling was observed closer to the equator across all oceans (Prentice et al., 2000). This could explain the relatively stable distribution of tree ferns in equatorial Africa (Table 4; Figs. 3 and 5). Evidence of refugia that would have supported species survival across the Pleistocene extinction has also been discovered in west Cameroon and southwest Gabon (Maley, 1989, 1991), and our results show that tree ferns would have had substantial suitable habitat across these refuges (Figs. 3, 4, and 5) during the last 22,000 years. This may be partly driven by these regions (Eastern Africa, Cameroon, and Nigeria, and the coastal regions of Liberia, Sierra Leone, and Guinea) receiving higher rainfall (i.e., annual precipitation) than other parts of the continent. Analysis of pollen records retrieved from Lake Bosumtwi in Ghana (west Africa) (Maley and Da, 1983) and Lake Borombi Mbo in Cameroon (Giresse et al., 1994) further reveals that prior to 9500 yr. BP, the region lacked any significant tree cover and pollen levels dropped, signaling a sharp decrease in temperature of 3–4 °C (Maley and Da, 1983). This sharp decline in pollen is attributed to a decline in pollen-producing plants, which could not survive in the harsh, cold conditions caused by the changing climate and the advance of glaciers at the poles. While Maley (1991) asserted that rainforests in Ghana completely disappeared during the Last Glacial Maximum (LGM), our modeling results contradict these claims and suggest that tree ferns could have thrived in this region at that time. It is more likely, therefore, that these rainforests experienced a significant range contraction rather than complete disappearance. This is supported for some species, such as *A. manniana*, for which we predicted a substantial loss of range (~39 %) during the LGM compared to the present (Table 4; Fig. 4). Prentice et al. (2000) also reported a significant tropical forest reduction during the LGM, which is consistent with the results from our study that show substantial changes during the LGM (see Figs. 4 and 5). This habitat loss in the LGM potentially suggests species retreated to more hospitable refugia that experienced less severe glacial conditions compared to the surrounding regions.

The rainforest in central and western Africa certainly diminished during the LGM (Armitage et al., 2015). While the extent of this reduction remains uncertain, our model indicates a southward shift in comparison with the current distribution of *Alsophila* species. This overall trend of reduced forest cover is consistent with other regions of Africa during the LGM. Additionally, Hamilton (1982) proposed the existence of an LGM African rainforest refuge in the east-central region based on biogeographical evidence. These patches still occur today (Figs. 1 and 4). The rich presence of tree fern species in this region cements these claims, e.g., that the East Africa Montane region (EAM) is a biodiversity hotspot for tree fern species and points to the role of ecological isolation in shaping species distribution.

Surprisingly, *A. humilis* and *A. thomsonii* showed a substantial range expansion during the LGM (Table 4). This suggests several possibilities. Despite the expansion of glaciers in the East African Montane region (EAM) during the LGM (Kelly et al., 2014), the preference of *A. humilis* and *A. thomsonii* for higher elevations (Figs. 1 and 2), combined with potentially less severe impacts on temperatures and precipitation in specific microclimates within the region, could have facilitated their range expansion during this period. Additionally, local extinctions (Aldasoro et al., 2004; Janssen et al., 2008; Kornas, 1993; Liu et al., 2016b) in certain regions of West Africa may have contributed. Today, their distribution is primarily restricted to EAM (Watuma et al., 2022) and some parts of the Cape region. These findings highlight the complex interplay between climate, species distribution, and local environmental factors during the LGM.

The Congo region, characterized by its high rainfall, might lead one to expect widespread distribution of tree ferns. However, this was not the case during the Last Glacial Maximum (LGM). Runge (1996) describes the dominant climate in the eastern Congo Basin, specifically in Eastern Zaire, Kivu-Province, and Burundi, between 30,000 and 11,000 yr. BP as savanna-open woodland. This unique climate would have favored the presence of *Alsophila dregei* (also known as the Savannah Tree Fern in the Congo region due to its affinity with woodland savanna and forest margins) (Table 1) (Edwards et al., 2005; Holttum, 1981; Roux, 2003; Roux et al., 2016). Our data support this notion, particularly concerning Bio1 (Annual Mean Temperature), which emerged as an important predictor variable for *A. dregei* compared to the other species. *Alsophila dregei* may have likely evolved adaptations to tolerate low precipitation during the LGM (Table 3), as it experienced a gradual shift from tropical rainforest to grasslands. Consequently, during the LGM, the eastern Congo Basin received around 1000 mm of rainfall annually and experienced a seasonal climate with rainy and dry periods, leading to high erosional activity. Forests were likely restricted to narrow stretches of 'gallery forest' along rivers (Runge, 1996), which might be a last refuge for tree ferns restricted to rainforests. This reflected a significant decrease in rainfall, ranging from approximately 1000–1400 mm less compared to present-day rainfall of 2000–2400 mm. Given that the eastern Congo Basin currently has one of the wettest climates in the area, it is possible that other parts of the Basin experienced even more significant forest loss.

4.2. *Tree ferns in the African Holocene Humid Period (AHHP)*

The African humid period was a time of significant climate change on the African continent, characterized by increased precipitation and high humidity (Dinies et al., 2021). Although there is no consensus about the exact times of the onset and disappearance of the AHHP, several scholars have suggested that it lasted between 14,500 and 5000 yr. BP (Wright, 2017). A major shift towards a drier climate began around 6100 yr. BP and increased around 4500 yr. BP, towards the termination of the African humid period (De Menocal, 2015). Several studies (e.g., Gatto and Zerboni, 2015; Lange, 2007) have presented evidence of the emergence of colossal lakes such as Mega-Chad and the gradual disappearance and drying up of other lakes towards the onset of the Mid-Holocene, confirming a dramatic shift in precipitation across the continent in this period. Although the climate was significantly wetter than it is today during the early Holocene, the AHHP was not uniform and some regions such as East Africa and North Africa experienced intense humid conditions (Clarke et al., 2016), leading to the varied distribution of tree ferns during the Mid-Holocene (Figs. 3, 4 and 5). Despite more humid conditions, there is no evidence for an analogous situation to the Greening of Sahara (a scenario in which the arid Sahara Desert region in North Africa experienced a transformation into a more habitable and green landscape ~14,500–5000 yr. BP) (Fig. 3) due to some possible reasons discussed below.

Tropical African and East African precipitation is dictated by two major convergence zones (Tierney et al., 2011), the east-west oriented intertropical convergence zone (ITCZ) and the northeast-southwest oriented Congo Air Boundary (CAB). The ITCZ is a region where the trade winds from the northern and southern hemispheres converge, causing warm, moist air to rise and cool, leading to heavy rainfall. In contrast, the CAB represents a boundary between moist, maritime air from the Atlantic Ocean and drier, continental air from the east. This results in different precipitation regimes along and around the CAB (Schneider et al., 2014). These zones further influence the distribution of species, species' adaptations, and overall biodiversity patterns. During the AHHP, it is conceivable that insufficient precipitation or unstable climatic conditions hindered tree fern recruitment, especially in areas under the influence of CAB. This instability was characterized by sequentially wet and arid phases in much of Africa, and the reported highly seasonal Lake Nile ca. ~20,000–12,500 yr. BP (Street-Perrott et al., 2000) corroborates this claim.

In understanding the distribution of tree ferns in African regions, multiple factors come into play. Notably, elevation and moisture play a significant role in the distribution of some tree ferns. While some *Alsophila* species have been discovered at lower elevations, with examples like *A. dregei* found as low as 400 m, most tree fern species thrive at significantly higher elevations. For instance, *A. humilis* and *A. thomsonii* (both highly affected by elevation, at 25.2 % and 25.3 %, respectively; Table 3) are confined to the East Africa Montane region, specifically in places like the Usambara Mountain in Tanzania, where elevations reach approximately 1030 m above sea level. Similarly, *A. milbraedii* (not included in this study due to few occurrence data points) thrives in even higher elevations, especially in Mt. Ruwenzori in Uganda, where altitudes soar to as much as 3300 m (Holttum, 1981). The Sahara region, though primarily characterized by plateau-like topography with an average elevation of 500 m, has several mountain ranges that are over 1000 m, such as the Aïr, Ahaggar, and Tibesti mountains whose altitudes could potentially support tree ferns if elevation were all that mattered. It is likely, therefore, that moisture (as shown by high values of Bio13, Precipitation of the Wettest Month, and Bio14, Precipitation of the Driest Month; Table. 3) presents the greatest challenge for the growth of tree ferns in this vast region. Furthermore, other factors like ploidy level, reproductive behavior (Chiou et al., 2003; Sessa et al., 2016), and additional biotic factors such as competition from other tropical plants (Page, 2002) may have contributed to the restriction of tree fern distributions in North African regions.

While the magnitude of biome shifts in Africa in the past is still poorly understood (Street-Perrott et al., 2000), a map of African biomes dating back to 6000 yr. BP has shown that Madagascar, along with eastern, southern, and central Africa, experienced minimal changes (Hänninen, 2021) compared to the present time. The potential distribution of tree fern species as modeled in our study also supports this. Major ecological shifts have also been reported north of 15 degrees during the mid-Holocene. The observed range contraction of tree ferns' suitable habitat during the mid-Holocene could be attributed to forest clearance by humans (Finch and Hill, 2008; Mercuri et al., 2011) or shifts in climatic patterns such as changes in temperature and precipitation regimes. Though limited, existing data from equatorial Africa also suggest that the extent of tropical rainforest biome coverage is probably greater now than it was during the mid-Holocene (Lezine and Cazet, 2005). This trend can be confirmed in our study (Fig. 4; Table. 4) where stable habitat for most tree fern species has increased from the mid-Holocene to the present. However, African tree ferns seem to be highly specialized in their habitat requirements and their distribution is notably restricted in refugia that have experienced climatic stability over geological time (Fjeldsa and Lovett, 1997). These findings align with previous model simulations by (Harrison et al. (1998) and Joussaume et al. (1999), which suggest that shifts in the intertropical convergence zone (ITCZ) towards the north during the summer of the northern hemisphere, also likely influenced mid-Holocene seasonal climate.

Typically, most *Alsophila* species underwent slight range expansion during the MH compared to the LGM, a clear indication of an increase in humid conditions during the early and mid-Holocene (corresponding to the AHHP), though this period was characterized by a reduction in seasonality. This habitat gain likely represents an expansion into areas with more favorable (warmer and wetter) conditions with the retreat of the LGM and onset of the AHHP. However, species respond differently to climate change, for instance, *A. thomsonii,* remained relatively unaffected by these climatic shifts and retained significant stable habitat between the LGM and MH across continental Africa. Similar tropical humid plants have been reported to behave independently rather than as a migrating community (Watrin et al., 2009). In contrast, some species like *Alsophila manniana*, which was highly influenced by Bio14 (Precipitation of Driest Month) expanded in the mid-Holocene. These findings emphasize the importance of considering individual species' responses to past climate events to better predict their future distribution patterns in the face of ongoing climate change.

4.3. *Current status of African tree ferns and biological insights*

Understanding the current potential range of species in response to past, present, and future climate scenarios is crucial for predicting species survival and adaptation strategies (Thuiller et al., 2008). In this study, the current habitat suitability of most populations of tree ferns seems stable in Africa. However, Hamilton and Taylor (1991) point out that such assumptions should be met with skepticism as they may overlook potential ecological changes and gradual or unrecognized shifts. In addition, most of these ferns are either found in safe havens (refugia) that have experienced consistent climatic conditions (Fjeldsa and Lovett, 1997) or they predominantly occur in protected areas. While tree fern species are predicted to undergo elevational shifts, these protected areas may fail to adapt accordingly, and with increasing human population pressure and augmented agricultural practices, the future of these protected areas remains largely unknown. Several tree fern populations are dying in Kenya's East African Montane region, a biodiversity hotspot (personal observation). van der Linde and Nel (1996) observed a similar trend in Ngome Forest, South Africa where most colonies of *Alsophila capensis* were dead.

Notably, the current habitat suitability of tree ferns shows the potential role of ecological versatility and ecophysiological traits in the distribution of species as exemplified by *Alsophila dregei* (which occurs both in continental Africa and Madagascar) and *Alsophila manniana* (widely distributed in continental Africa), respectively.

The potential habitat distribution of *Alsophila dregei* within tropical rainforests and savannah grasslands in both continental Africa and Madagascar allows for several conclusions to be drawn. First, tree fern species are not dispersal-limited, as evidenced by the ~400 km shortest distance between continental Africa and Madagascar (Rabinowitz and Woods, 2006). Molecular-based evidence supports the independent colonization of *A. dregei* from Africa to Madagascar through long-distance dispersal events in the Miocene (Janssen et al., 2008). Second, bioclimatic niches and ecological preferences play a major role in influencing tree ferns' habitat suitability (Aldasoro et al., 2004; Janssen et al., 2008). The existence of widespread, shared, and proximate grassland ecosystems between Madagascar and East Africa further supports this. Recent studies, based on soil, animal fossils, stable isotopes, and phytoliths have demonstrated a widespread grassland ecosystem in East Africa 8–10 mya (Peppe et al., 2023). Considering the higher affinity of *A. dregei* to grassland ecosystems, these habitats likely provide suitable conditions for this species' establishment in Madagascar. Also, the dense adventitious roots of *Alsophila dregei* (Edwards et al., 2005) confer fire resistance by providing physical protection and facilitating rapid regeneration, which has enabled the species to continuously exist in fire-prone savanna ecosystems, demonstrating its remarkable ability to withstand fire (Roux, 2003). Recent studies have demonstrated the critical role of fire in driving ecological shifts between different ecosystems (Quick et al., 2024), a possible explanation for the shift of *A. dregei* from tropical rain forests to savannas. Janssen et al. (2008) also demonstrated that Madagascan taxa occupy slightly more seasonal and more humid locations than continental African tree ferns, a phenomenon that explains the absence of many Madagascan tree ferns in Africa and reinforces niche conservatism among scaly tree ferns (Bystriakova et al., 2011).

Ecophysiological traits may also contribute to the vast distribution and habitat suitability of species like *Alsophila manniana* (highly influenced by Bio14, Precipitation of the Driest Month) in continental Africa. Firstly, *A. manniana* occupies a broad elevational gradient from 200 to 2700 m (the highest of all species in this study) (Table 1) (Edwards et al., 2005; Palmer-Newton, 2018). This allows the species to occupy different niches within montane forests, adjusting to variations in temperature and humidity across its range (McCain and Grytnes, 2010). Secondly, the species is shade tolerant (Edwards et al., 2005), allowing it to thrive under the canopy of dense forests, which may increase consistent access to water. Thirdly, the presence of spines on the caudex (the "woody" stem at the base of the fern) of *A. manniana* (Holttum, 1981) plays a crucial role in retaining moisture by reducing water loss through transpiration (Pei et al., 2024), and can protect it from browsing damage from herbivores. Similarly, *A. manniana* may possess genetic adaptations that allow it to thrive in a range of climates or to tolerate climatic fluctuations better than other species. These traits could confer remarkable adaptability to changing conditions, resulting in its wide distribution in continental Africa.

In addition to ecological versatility and ecophysiological traits, other evolutionary and life history traits likely also affect different ferns' responses to climate change. Recent findings by Karichu et al. (2022) on the impact of climate change on *Azolla* (an aquatic and obligately outcrossing heterosporous fern genus) highlight the significant influence of differences in temporal scale, habitat, and reproductive strategy. These differences play a crucial role in how fern species respond to environmental variables, potentially leading to contrasting predictions of range expansion and contraction under climate change scenarios. While Karichu et al. (2022) predicted a potential negative impact of climate change on several species of *Azolla* in Africa due to their specific water needs and sensitivity to precipitation and elevation, the current study predicts an increase in the range sizes of some tree ferns (which are terrestrial and homosporous, meaning they produce one type of spore and can potentially self-fertilize) (Sessa et al., 2016). These differences in life history strategy – potentially selfing vs. obligately outcrossing – as well as lower rates of molecular evolution in the tree ferns (Loiseau et al., 2020) may differentially affect the ability of species in these groups to adapt to or tolerate temperature variations and changing precipitation patterns. However, the shared importance of variable Bio13 (precipitation of the wettest month) between the two studies signifies the critical role of water availability during the peak precipitation period for both aquatic and terrestrial ferns.

Overall, our analyses of current habitat suitability and range dynamics reveals varied patterns among tree fern species. While several species, such as *A. camerooniana*, *A. humilis*, and *A. thomsonii*, show a potentially large stable habitat, there are also notable areas of loss and gain, reflecting ongoing habitat shifts. These dynamics are likely influenced by local environmental changes, species-specific traits and adaptability, and the impacts of human activities.

4.4. Looking ahead: future distribution of tree ferns in Africa under RCP 4.5 and RCP 8.5 Scenarios

Representative Concentration Pathways (RCPs) are scenarios used to project future climate conditions based on different greenhouse gas concentration trajectories (van Vuuren et al., 2011). Specifically, RCP 4.5 and RCP 8.5 represent two contrasting climate futures: RCP 4.5 assumes a stabilization scenario with moderate emissions, while RCP 8.5 assumes a high-emission trajectory with significant warming. Based on the results of this study, it seems that the studied tree fern taxa will have differential responses to global climate change in continental Africa under RCP 4.5 and RCP 8.5 (Figs. 4 and 5), shaped by historical and ecological factors. For example, *Alsophila dregei*, *A. humilis*, *A. manniana,* and *A. thomsonii* are predicted to gain suitable habitat in both RCP 4.5 and RCP 8.5 scenarios (Table 4), presumably because warmer temperatures will expand their suitable range into higher elevations, more northern latitudes, or areas that were previously dominated by other vegetation types. On the other hand, *A. camerooniana* is predicted to lose more of its suitable habitat in both future scenarios than it will gain (Table 4). One possible explanation for this observed trend is that tree ferns are often associated with higher elevations where conditions are cooler and more humid (Kluge and Kessler, 2007), and this species occupies the narrowest, and one of the highest, elevational ranges of the species studied (Table 4). If rising temperatures make the lower elevations of its range less suitable for *A. camerooniana*, its potential habitat will be even more limited, and its range will likely contract.

4.5. Conclusions and further African ferns ecological research

In this study, we utilized maximum entropy modeling (MaxEnt) to assess the effects of global climate change on five *Alsophila* species. The resulting models demonstrated a high predictive capacity (with excellent TSS and AUC scores), thereby exhibiting high reliability. While the current distribution of the studied taxa aligns closely with the predicted suitable regions in the MaxEnt models, it is imperative to note the existence of uncertainties related to non-climatic factors (Vacchiano and Motta, 2015), such as the dispersal limitations of species, interspecific competition, the availability of nutrients, and continued direct destruction of habitats by humans.

While most tree ferns have demonstrated remarkable resilience and adaptability in Africa across time periods (LGM, MH, current, and expected in the future), it is possible that, considering the slow rate of evolution in tree ferns (Loiseau et al., 2020), their high endemism levels, and the unpredictability of local climate change impacts, some of these species may not be able to keep pace with these changes, leading to reduced population sizes and even probable local extinction. Our study demonstrates the variable responses of different tree fern species to climate change. This variation underscores the complexity of species' responses to changing climatic conditions and emphasizes the need for tailored conservation efforts to ensure the survival of diverse species in the face of environmental challenges and anthropogenic pressures.

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Author contributions

MJK and EBS designed the study; EBS secured funding and supervised the study; MJK, BKN, and EBS performed data analysis; MJK wrote the initial manuscript draft; all authors interpreted the results and contributed to the final version of the manuscript.

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Declaration of competing interest

The authors declare that they have no competing interests related to this research.

Data availability

All data sets used in this study are provided as supplementary files.

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