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RESEARCH ARTICLE

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The potential distributions of African *Azolla* species and their implications for African wetland ecosystems for the future

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Abstract

Climate change is predicted to affect species in aquatic ecosystems. In Africa, factors that may influence the responses of aquatic species are poorly studied and challenging to predict. In this study, we examined the potential distribution of three aquatic fern species in the genus *Azolla* in Africa under projected climate change scenarios. MaxEnt was used to create ecological niche models of the three species using occurrence data and environmental variables. All models had satisfactory AUC and TSS values, indicating high prediction precision (AUC and TSS > 0.801). Results showed that elevation and precipitation were the most important variables limiting the species' expansion in the future. In addition, we observed significant variations in the climatic niches of the three species and their distinct climatically appropriate regions. The current potential distribution ranges for the species varied between 2,328,726 km^2 and 4,026,363 km^2. According to the model predictions for the current period, the potential range of *Azolla* species extended outside the known and recorded locations; however, under future climate conditions, the species were projected to lose between 8.1% and 48% of their suitable habitats due to climate change. Our findings can be used to develop sustainable conservation measures for aquatic species and raise awareness about the effects of climate change.

KEYWORDS
Africa, *Azolla*, climate change, ecological niche modeling, MaxEnt, wetland ecosystems

TAXONOMY CLASSIFICATION
Conservation ecology; Ecosystem ecology

1 | INTRODUCTION

Climate change is expected to be the primary cause of biodiversity loss in the future (Bellard et al., 2012; Velazco et al., 2019). Ecological Niche Models (ENMs) are the most frequently used technique for predicting the impact of future climate change on species' ranges and distributions. ENMs are used to forecast current and future environmental suitability and provide recommendations for identifying priority areas for protection (Tiamiyu et al., 2021), management, and conservation of species (Nzei et al., 2021), and restoration of habitats (Johnson et al., 2017; Zwiener et al., 2017). As the effects of climate change intensify, the capacity of a species to colonize new suitable habitat is dependent on the individuals' dispersal ability, landing in appropriate habitat, and stable population establishment (Angert et al., 2011; Wolf et al., 2001). Although ferns generally have greater potential to disperse their spores over long distances than seed plants (Ranker & Haufler, 2008), an inability to adapt to the changing environment may lead to local or global extinction (Given, 1993).

Azolla Lam. is a genus of aquatic ferns belonging to the Salviniaceae family, and it has a wide, global distribution. According to the latest classification of ferns and lycophytes (PPG I, 2016), *Azolla* has approximately nine species. Four of these are found in Africa: *Azolla nilotica* (Figure 1) is endemic to Africa and is widespread in East, Central, and Southern Africa; *A. filiculoides* is found in North and Southern Africa; *A. caroliniana* is naturalized in Egypt; and *A. pinnata* subsp. *africana* is also endemic to Africa and is widely distributed throughout continental Africa and Madagascar, except in North Africa (Saunders & Fowler, 1993).

Even though *Azolla* species have been declared noxious weeds in some parts of the world, such as South Africa and Florida in the USA (Janes, 1998; McConnachie et al., 2003; Sadeghi et al., 2013), they have several economic benefits. First, *Azolla* is known to absorb large amounts of heavy metals from contaminated wastewaters (Talebi et al., 2019). In addition, *Azolla* is used as a broiler ingredient in Bangladesh (Basak et al., 2002) and as a source of nitrogen fertilizer in rice production in Ghana, India, and China (Arora & Singh, 2003; Nyalemegbe et al., 1996; Singh & Singh, 1987; Yao et al., 2018). Recent genomic studies in *Azolla* species have provided invaluable insights into the evolution of land plants, cyanobacteria associations, and insecticide resistance (Güngör et al., 2021; Li et al., 2018). Further evidence suggests that *Azolla* species played a key role in global cooling during the middle Eocene, a period described as the *"Azolla Event"* (Speelman et al., 2009). The findings of this previous research underpin ongoing studies to assess whether *Azolla's* remarkable ability to sequester carbon might be harnessed to mitigate current greenhouse gas emissions and global warming (Gunawardana, 2019). Also, Katayama et al. (2008) proposed the potential use of *Azolla* species as part of a space vegetarian diet on Mars alongside beans, rice, and soybeans. The potential uses of this super plant are seemingly endless (see John et al., 2012).

Despite *Azolla's* apparent resilience and ability to become abundant, its future may not be secure in Africa. Evidence of the recent local extinction of *Azolla nilotica* in the Nile delta of Egypt is alarming (Birks, 2002), and should cause concern about the existence of this endemic species and other *Azolla* species in African countries. The most recent occurrence records for *Azolla nilotica* are from Lake Manzala during the 19th century, Edku Lake around the 1920s, and Burullus Lake in the 1960s, all in Egypt (Birks, 2002). Persistent changes in sea level, siltation of Nile distributaries, uncontrolled chemical fertilizer application (Horak et al., 2021), and human interference in diverting Nile waters for irrigation are some of the root causes of *A. nilotica's* extinction (Kendie, 1999). The current water quality preferences of *Azolla* are still unknown, which complicates efforts to understand, manage, and potentially mitigate threats to *Azolla* populations. Today, *Azolla nilotica's* nearest station of occurrence to Egypt is in Central Sudan (Saunders & Fowler, 1992).

In Africa, larger wetlands cover less than 10% of the Sub-Saharan Africa landmass (Mitchell, 2013), and in the recent past freshwater ecosystems have declined at a startling rate (Cohen et al., 2016), either due to expansion for urban development, agriculture or mining activities. This decline threatens aquatic plants because aquatic ecosystems and obligate aquatic plants are inextricably linked. Understanding the appropriate habitat and distribution of aquatic species is required to examine the magnitude of climate change and its ramifications for species decline or increase (Nzei et al., 2021). However, one of the most challenging tasks in ecology is predicting which species will coexist in future and where they will occur (Wisz et al., 2013). This is particularly an uphill battle in Africa, Madagascar, and its surrounding islands

FIGURE 1 *Azolla nilotica* from Lake Baringo, Kenya (photo credit: Professor Gwang-wan hu)

with heterogeneous ecoregions ranging from tropical, subtropical, montane, Mediterranean, deserts, and mangroves. These ecoregions dictate species distribution, and biodiversity threats become unevenly distributed across the continent, making it challenging to predict climatic variations (Burgess et al., 2006). Scarcity of data and unjustifiable absences due to limited sampling are also confounding factors, as available data in museums or herbaria may not have the exact location of a species and limited sampling results in potential biases (Engler et al., 2004). Prolonged weather patterns and temperature can also rapidly change the distribution of aquatic species (Ngarega et al., 2022), which points to the need to better understand and document their species distribution.

Although the impact of global climate change has been assessed in various aquatic species such as *Elodea canadensis* (Heikkinen et al., 2009), *Egeria densa*, *Myriophyllum aquaticum*, and *Ludwigia* spp. (Gillard et al., 2017), *Ottelia* spp. (Ngarega et al., 2022), *Hydrocotyle umbellata* and *Salvinia auriculata* (Heneidy et al., 2019) and water lilies (Nzei et al., 2021), aquatic ferns, particularly in Africa, have remained underexplored. Ecological Niche Modeling is a valuable technique as it can predict suitable habitats both within and outside the current distribution range of a species (Gillard et al., 2020). These tools use machine learning and statistical approaches to link available georeferenced data and environmental variables to predict a species' ecological niche and potentially suitable habitat (Phillips et al., 2006).

Our aims here were to use ENMs to (i) determine environmental variables affecting the distribution of *Azolla* species in Africa, (ii) estimate these species' current possible distribution in Africa based on suitable habitat, and (iii) predict *Azolla's* potential distribution in future under two representative concentration pathway scenarios (RCP 4.5 and RCP 8.5). We hypothesize that the increasing threat to African wetland ecosystems will drastically reduce *Azolla's* habitat in future, and the findings of this research will provide a conceptual and theoretical framework for exploring aquatic ferns for conservation and sustainable use.

2 | MATERIALS AND METHODS

2.1 | Study area and species georeferenced occurrence data

Four species of *Azolla* are found in Africa: *A. caroliniana*, *A. filiculoides*, *A. nilotica*, and *A. pinnata* subsp. *africana* (https://www.fernsofafrica.com/). *Azolla caroliniana* is naturalized in Egypt and was therefore not considered for modeling due to having few occurrences in Africa (a minimum of three samples is required for good model development) (van Proosdij et al., 2016). In addition, several localities for *Azolla pinnata* subsp. *asiatica*, which is predominantly widespread in Asia, were not considered since they were beyond the scope of this study.

The species occurrences were obtained using the "Spocc" R package (Chamberlain et al., 2017). The package allowed us to download occurrence data from the Global Biodiversity Information Facility (http://www.gbif.org), iNaturalist (http://www.inaturalist.org), and the RAINBIO Database (a compilation of 13 databases for georeferenced occurrences of Tropical African plants; Dauby et al., 2016) to extract georeferenced occurrence data for the other three *Azolla* species in Africa. Most localities from the RAINBIO Database (33 localities) contained *Azolla pinnata* subsp. *africana* (20 localities), with the majority being duplicated on GBIF. To correct sample bias and ensure occurrence independence, data were manually filtered and duplicates excluded in Microsoft Excel 2021, followed by a spatial thinning of the remaining data using the SDMToolbox v.2.5 (Brown et al., 2017) extension in ArcGIS v.10.8.1 (Esri, Redlands, CA, USA) to ensure a minimum distance of 5 km between the records.

2.2 | Environmental data

Initially, 19 bioclimatic variables from the WorldClim2.1 database (http://www.worldclim.org; Appendix S1) (Fick & Hijmans, 2017), with a general spatial resolution of 2.5 arc-min that reflected the *Azolla* distribution data collection, were chosen to model the current distributions of *Azolla* species. The elevation layer was also downloaded from the WorldClim2.1 database and added to the variable dataset. The confidence level in future climate change projections is determined by the performance of global climate models (GCMs). We obtained future climate data from one GCM (the Community Climate System Model version 4 CCSM4). This GCM has been used widely to map the region's potential distribution of wetland species (Ngarega et al., 2022; Nzei et al., 2021).

For this GCM, we obtained two Representative Concentration Pathway scenarios (RCP 4.5 and RCP 8.5). RCPs are greenhouse gas concentration prediction scenarios implemented by the Intergovernmental Panel on Climate Change (IPCC) in order for climate change studies and modeling to use a consistent set of metrics (van Vuuren et al., 2011). RCP 4.5 anticipates CO_2 concentrations will increase to around 650 parts per million (ppm) by 2100 before stabilizing, while RCP 8.5 predicts increasing CO_2 concentrations to around 370 ppm by 2100 (van Vuuren et al., 2011). To prevent collinearity (Pearson's $r > 0.8$), we chose one variable per group of intercorrelated variables and examined the relative value of each variable kept with 10 permutations per model replication. Nine bioclimatic variables with a variance inflation factor (VIF) of less than ten were derived (Appendix S2). VIFs greater than ten and an r value greater than 0.8 are considered redundant (Montgomery & Peck, 1992); however, Bio12 (Annual precipitation) and Bio17 (Precipitation of the driest quarter) were incorporated for modeling since these variables have been reported to be potential limiting factors to the distribution of aquatic plants (Ngarega et al., 2022; Symoens, 2009) and different variables may have different biological significance for the distribution of the target species (Mbatudde et al., 2012; Pradhan et al., 2012). Therefore, eleven bioclimatic variables were included in the final models (Table 2).

2.3 | Modeling procedure

The current and future potential distributions of *Azolla* were modeled using MaxEnt 3.4.4 (Elith et al., 2011). This modeling technique has been shown to outdo other presence-only modeling techniques (Elith et al., 2011). MaxEnt estimates the best-fitting probability distribution for simulating habitat suitability using random background points rather than real absences (Phillips et al., 2006). We utilized area under the curve (AUC) statistics (Phillips et al., 2006) and the true skill statistics (TSS) to evaluate model performance (Allouche et al., 2006). The bootstrap replicate run type was used to replicate all models thirty times. For each model run, the species datasets were randomly divided into 70 percent training and 30 percent test datasets, and the final average outputs were employed for further analysis. To understand which climate variables may be important among *Azolla* species, we employed MaxEnt's relative contribution and jackknife tests. In addition, response curves for all variables in the models were investigated to test the response of each species to different variable values.

2.4 | Distribution range changes for *Azolla*

We converted the current and future output raster files for the *Azolla* species into presence-absence (1/0) format using SDMToolbox v.2.5 (Brown et al., 2017) incorporated in ArcGIS v.10.5 (Esri, Redlands, CA, USA). We used the maximum training and sensitivity plus specificity (MTSS) as a threshold, which has been observed to be the most accurate and conservative threshold for distinguishing suitable from unsuitable regions (Liu, Newell, et al., 2016). The binary maps for the two future RCP scenarios were subtracted from the current (baseline) binary maps to account for the range changes between the current and future models. The resulting outputs were then used to show areas of range change in terms of losses, gains, or stability.

3 | RESULTS

The final dataset included 170 occurrences for *A. filiculoides*, 30 for *A. nilotica*, and 160 for *A. pinnata* subsp. *africana* (Figure 2; Appendix S3). Model evaluation under baseline climatic conditions revealed good model performance for the MaxEnt modeling approach for all examined species (Table 1). The most important variables that contributed to the models varied across the three species (Table 2). For the *Azolla filiculoides* model, the most important variables were Bio14 (% contribution = 37.5), Bio9 (% contribution = 33.5), Bio12 (% contribution = 10.0) and elevation (% contribution = 9.2). For the *A. nilotica* model, Bio12 was most important (% contribution = 41.2), Bio13 (% contribution = 15.4), followed by Bio19 (% contribution = 13.2). Lastly the distribution of *A. pinnata* subsp. *africana* was most influenced by Bio13 (% contribution = 29.6), Bio19 (% contribution = 4.4), and elevation (% contribution = 50.2). According to jackknife tests,

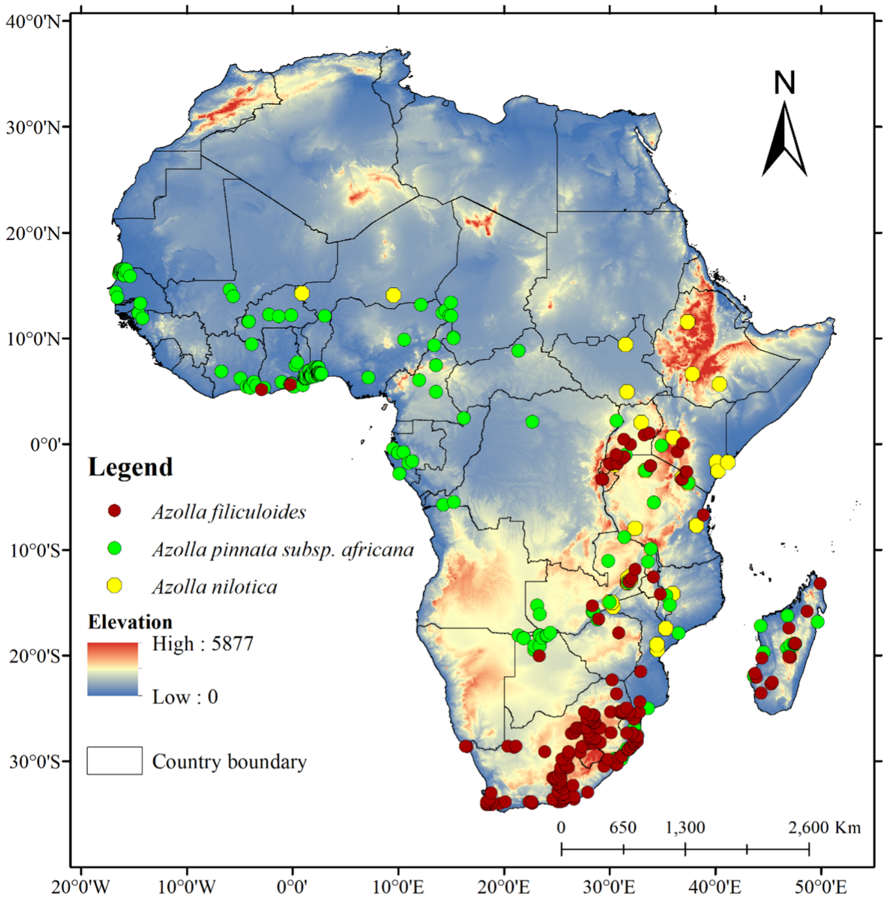

FIGURE 2 Study area and distribution of data points for African *Azolla* species used to create the distribution models

TABLE 1 Number of records and average values per species of the AUC values of the SDMs

Species	No. of records	AUC (*SD*)	TSS
Azolla filiculoides	170	0.968 (003)	0.847
Azolla nilotica	30	0.952 (012)	0.801
Azolla pinnata subsp. *africana*	160	0.934 (011)	0.822

Abbreviations: AUC, area under the curve; *SD*, standard deviation.

TABLE 2 Contributions of environmental variables for each *Azolla* species model in tropical Africa

	Species		
Variable	*Azolla filiculoides*	*Azolla nilotica*	*Azolla pinnata* subsp. *africana*
Bio2	1.3	6.4	2.5
Bio3	4.9	2.5	2.0
Bio8	0.5	0.3	1.1
Bio9	**33.5**	2.1	4.2
Bio10	0.7	0.3	1.3
Bio12	**10.0**	**41.2**	1.6
Bio13	0.5	**15.4**	**29.6**
Bio14	**37.5**	4.5	0.2
Bio15	0.8	0.4	1.9
Bio17	0.6	3.3	0.7
Bio19	0.4	**13.2**	**4.4**
Elevation	9.2	10.6	**50.2**

Notes: In bold, the most important variables (3 largest values) for each model are highlighted. Bio2—mean diurnal range; Bio3—isothermality; Bio8—mean temperature of wettest quarter; Bio9—mean temperature of driest quarter; Bio10—mean temperature of warmest quarter; Bio12—annual precipitation; Bio13—precipitation of wettest month; Bio14—precipitation of driest month; Bio15—precipitation seasonality; Bio17—precipitation of driest quarter; Bio19—precipitation of coldest quarter; Elevation—Altitude above sea level.

Bio9, Bio10, and Bio 14 were important predictors for *A. filiculoides*, while Bio2 was a poor predictor (Appendix S4a). The regularized train gain was observed to reduce most when Bio12 was omitted from the model, indicating that this variable was important in building the *A. filiculoides* model. For *A. nilotica*, Bio12 and Bio13 were the most important predictors. The regularized train gain was observed to reduce most when Bio12 was omitted from the model, indicating that this variable had important information absent in other variables (Appendix S4b). On the other hand, for *A. pinnata* subsp. *africana*, elevation, Bio8, and Bio3 were the most important single predictors (Appendix S4c). When Bio2 and elevation were omitted from the model, the gain was observed to reduce the most, highlighting that these two predictors were important in building the final model for *A. pinnata* subsp. *africana* (Appendix S4c).

Under current climate conditions, the potential range of *Azolla* extended outside the known and recorded locations of the three species (Figure 3). The prediction of current habitats for *A. filiculoides* indicated that highly suitable areas occurred in Kenya, South Africa, Uganda, Mozambique, and Madagascar. The distribution of *A. pinnata* subsp. *africana* was highly correlated with low elevation. Most of the highly suitable areas were located in lowlands and coastal areas in East, Eest, and Southern Africa, including South Africa, Mozambique, Nigeria, Kenya, Somalia, Senegal, Cote d'Ivoire, Ghana, Togo, and Benin. As for *A. nilotica*, highly and medium favorable areas were located almost throughout tropical Africa. The MTSS threshold values that were used to convert the continuous suitability maps into binary are shown in Appendix S5. Of the three species, *A. filiculoides* had the smallest current habitat area of approximately 2.3 million km^2 (Table 3; Figure 3).

The projections of future habitat suitability for *Azolla* varied depending on the RCP scenario and differed for each species (Table 3; Figures 4 and 5). According to the model forecasts under RCP 4.5, *A. pinnata* subsp. *africana* had the largest stable habitat (approximately 3.18 million km^2), while *A. nilotica* had the least stable habitat (approximately 1.82 million km^2). Under RCP 8.5, *A. pinnata* subsp. *africana* had the largest stable habitat (approximately 3.35 million km^2), closely followed by *A. filiculoides* (approximately 2.02 million km^2), and lastly, *A. nilotica* (approximately 1.29 million km^2) (Table 3; Figure 5). The MaxEnt model projections showed that under the most pessimistic scenario (RCP 8.5), *A. nilotica* would be the most vulnerable to climate change and would lose the highest % of its suitable range (% loss = 48%, Table 3).

4 | DISCUSSION

4.1 | Evaluation of model performance

The necessity for an absolute and immediate response to climate change is gaining global attention but predicting which species are highly threatened and where they will shift to evade extinction remains a challenge (Sinclair et al., 2010). Despite the inability of Ecological Niche Models to predict species' capacity to evolve, they can give a glimpse of what factors are likely to induce changes in species' distributions (Ngarega et al., 2021). Several ecological niche model algorithms have been proposed, and MaxEnt has shown its efficacy in terms of model performance (Elith et al., 2011; Elith & Leathwick, 2009), reduced computational time, simplicity, ease of use, and has been used extensively (Heneidy et al., 2019; Kaky et al., 2020; Lissovsky & Dudov, 2021; Ngarega et al., 2022; Nzei et al., 2021).

MaxEnt generates both pseudo-absence and presence-only occurrence data points, which can have an impact on species range predictions. Our method considered both geographical scope and environmental constraints to generate geographically and ecologically balanced pseudo-absence points that potentially predicted the environmental suitability for each species. Our model was accurate, statistically significant, and gave excellent predictions of AUC values of 0.968, 0.952, and 0.934 for *Azolla filiculoides*, *A. nilotica* and *A. pinnata* subsp. *africana*, respectively (Table 1). AUC values less than 0.5 show that the model's performance is no better than what would

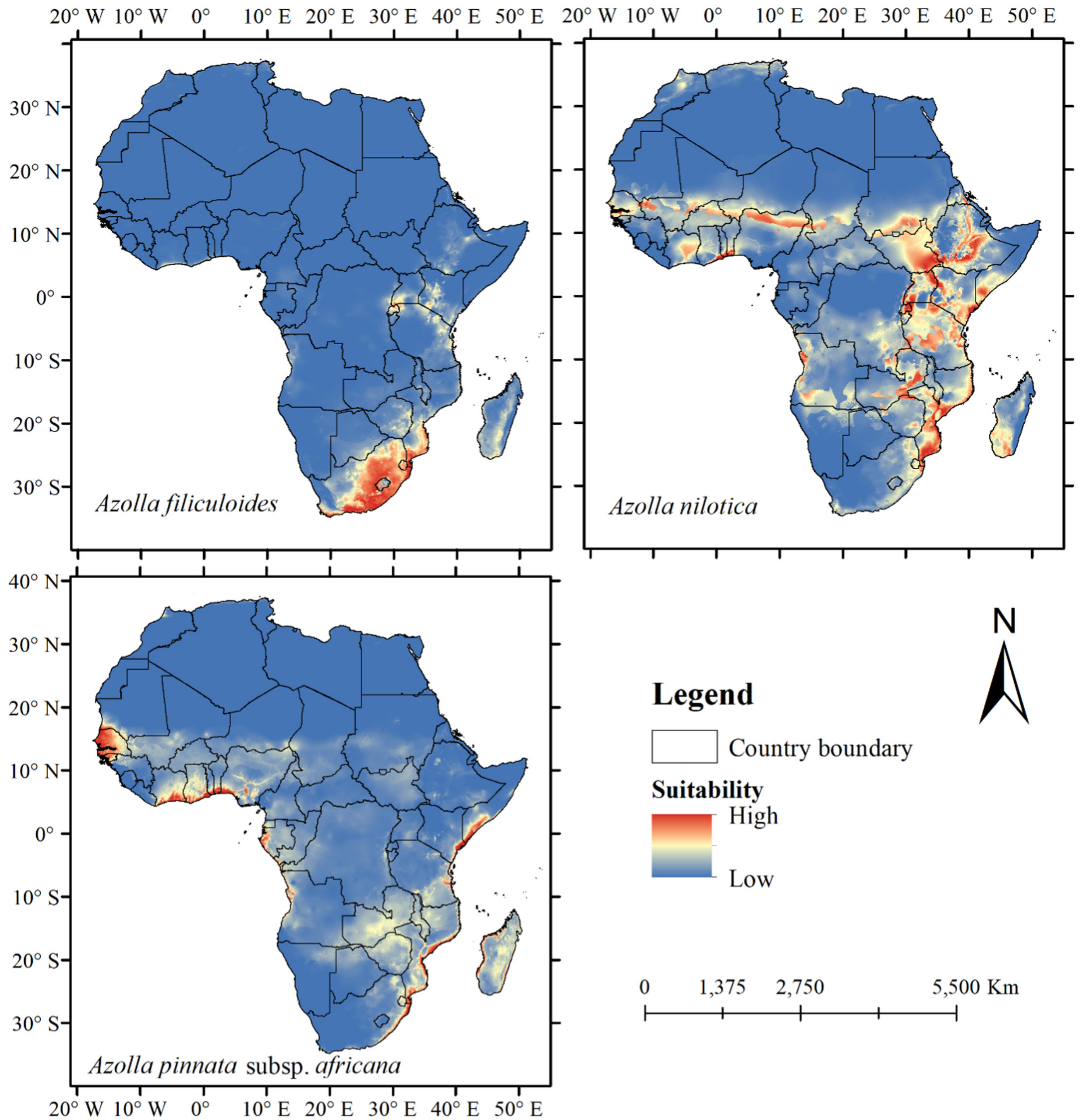

FIGURE 3 Ecological niche models for three *Azolla* species showing potential distribution under current climate conditions

be anticipated by chance, while values closer to one are considered better performance (Hijmans, 2012; Jiménez-Valverde, 2012).

4.2 | Contribution of climate variables to habitat suitability under current climate

In this study, elevation, temperature, and precipitation significantly affected *Azolla* species' climatic distribution, although their relative importance varied among species. Mean diurnal range (Bio2) and mean temperature of the driest quarter (Bio9) were the main temperature variables that dictated *Azollas*' distribution, whereas annual precipitation (Bio12), precipitation of the wettest month (Bio13), precipitation of the driest month (Bio14) and precipitation of the coldest quarter (Bio19) also influenced the distribution (Table 2). Climatic variables such as temperature and precipitation are known to greatly impact community structure, ecosystem functioning, and aquatic plants' distribution (Alahuhta et al., 2017; Elith & Leathwick, 2009; Nzei et al., 2021; Parmesan, 2006). Temperature variables, including isothermality (Bio3), mean temperature of the

TABLE 3 Loss and gain of suitable habitat area in Africa for *Azolla* species under two greenhouse gas emission scenarios for the future (2070)

Species	Habitat current (km²)	Habitat RCP 4.5	Area (km^2)	Area (%)	Habitat RCP 8.5	Area (km^2)	Area (%)
Azolla filiculoides		Loss	189,361.6	8.1	Loss	306,357.5	13.2
	2,328,726	Gain	383,277.8	16.5	Gain	271,186.7	11.7
		Stable	2,139,364	91.9	Stable	2,022,368	86.8
Azolla nilotica		Loss	645,452.8	26.2	Loss	1,175,428	47.7
	2,463,726	Gain	450,855.5	18.30	Gain	524,350.2	21.3
		Stable	1,818,273	73.8	Stable	1,288,298	52.3
Azolla pinnata subsp. *africana*		Loss	8485,16.9	21.0	Loss	672,643.5	16.7
	4,026,363	Gain	732,280.1	18.2	Gain	1,651,839	41.0
		Stable	3,177,846	78.9	Stable	3,353,719	83.3

Note: Percentage (%) loss, gain, and stable were calculated with respect to the current stable area.

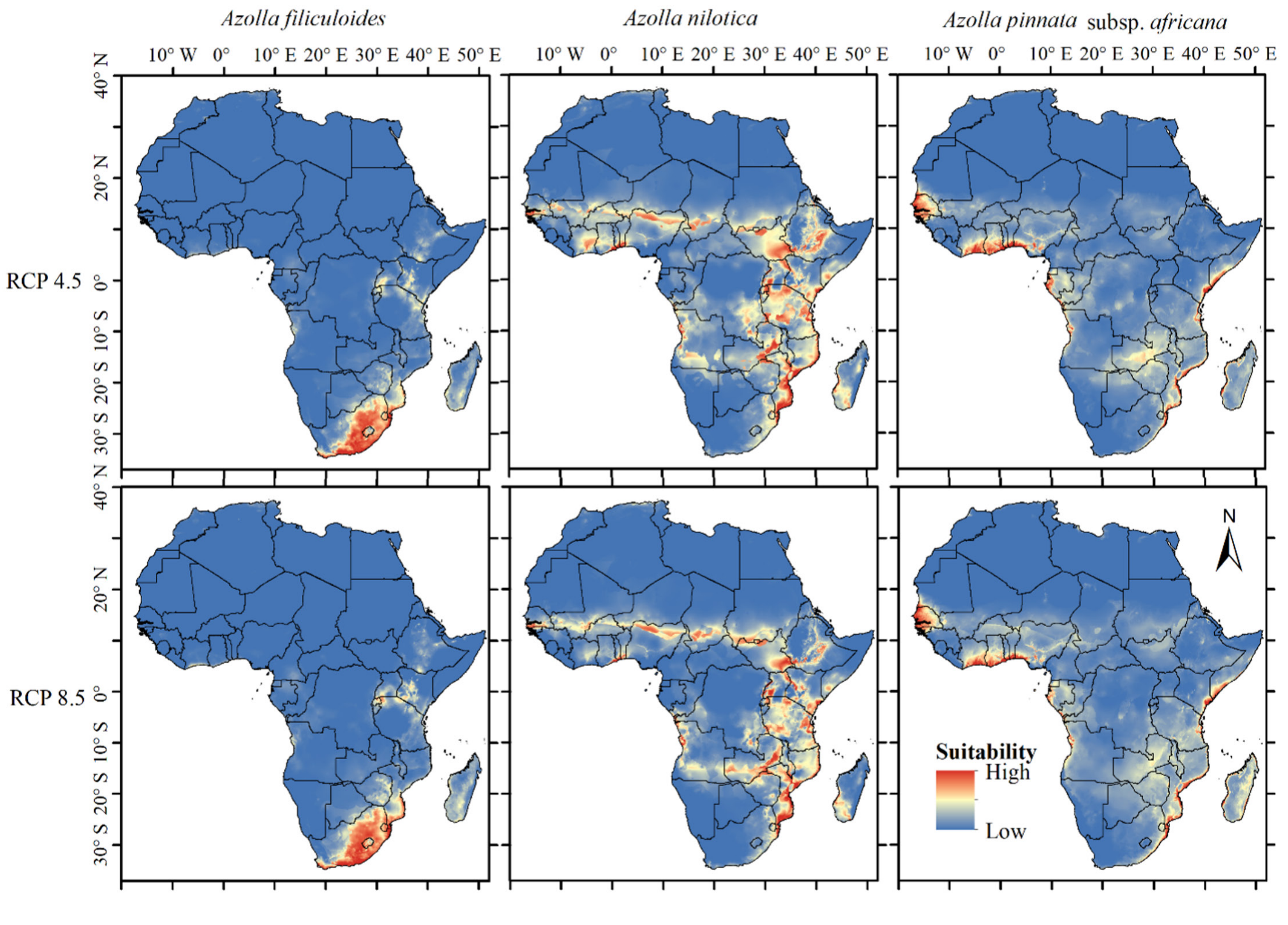

FIGURE 4 Ecological niche models for three *Azolla* species showing potential distribution under two possible future climate conditions (upper panels: less extreme, RCP 4.5; lower panels: more extreme, RCP 8.5) for the 2070s

wettest month (Bio8), mean temperature of the wettest quarter (Bio10), and precipitation seasonality (Bio15), also had a minor impact on *Azollas* species' distributions. Heneidy et al. (2019) and Ngarega et al. (2022) observed a similar trend in the effects of temperature and precipitation variables on aquatic plants, particularly the mean temperature of the driest quarter (Bio9) and precipitation of the driest month (Bio14).

African geography is highly diversified, and the continent has a heterogeneous climate that strongly influences species distributions. Habitat suitability under the present predictions was well supported by the MaxEnt model and largely corresponded with our areas of observation (Figure 3). The suitable habitat for *A. filiculoides* cuts across East and Southern Africa, but its suitability was more concentrated in Southern Africa. This is well supported by high

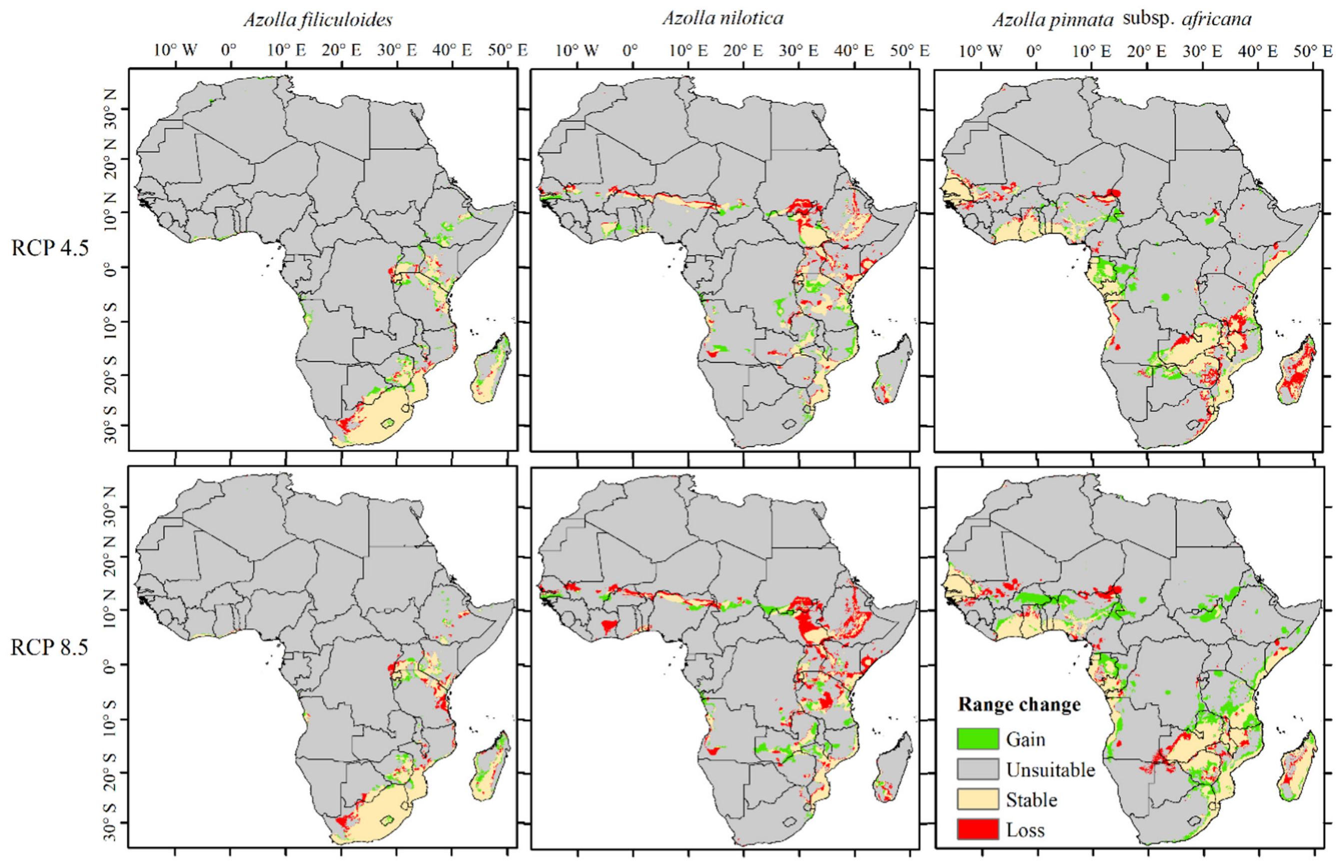

FIGURE 5 Changes in potential distribution ranges for three *Azolla* species under future climate conditions for the 2070s

precipitation values for the driest month (Bio14), a significant percentage of annual precipitation (Bio10), and the mean temperature of the driest quarter (Bio9) compared with other species (Table 2). Talley and Rains (1980) conducted a field experiment on *Azolla filiculoides*, and the growth rate increased with an increased temperature as high as 35 degrees Celsius. Additionally, south-eastern Africa receives summer rains due to changes in the sea surface temperatures along the coast (Nicholson, 2000), which probably favors *A. filiculoides*' habitat. Our model also projected habitats with very low suitability of *A. filiculoides* in northern Africa and the central parts of west Africa.

Azolla nilotica has potential for cosmopolitan distribution in continental Africa and Madagascar. Areas of high suitability for the species were recorded along the Nile River and the Great Rift Valley, in both the Nubian and Somali plates (Figure 3), and its distribution extended to the Central, West, and South-eastern Coast of Africa. Bio2 (mean diurnal range), Bio12 (annual precipitation), and Bio13 (precipitation of the wettest month) (Table 2) were the primary factors influencing its distribution. The regions of high suitability for *A. nilotica* lay mainly within the equatorial latitudes, which experience two rainy seasons (Nicholson, 2000), thus offering optimum conditions for the species. The potential suitable habitat in North Africa can be directly linked to the Mediterranean climate in the region, the presence of the Garâa Sejenane freshwater wetland in northern Tunisia (Rouissi et al., 2018), the Cheliff River in Algeria, the Lac Tonga Ramser site in Algeria, and other wetlands in North Africa. Hygrophytes are rich in species richness and diversity in lower elevations, a phenomenon that could explain the preference of both *A. nilotica* and *A. filiculoides* for low elevation habitats (Liu, Chen, et al., 2016).

Azolla pinnata subsp. *africana* (Table 2) appeared to have a stronger affinity for the highlands along the East and West coasts of Africa, including the Fouta Djallon highlands in Guinea, the Plateau of Yorubaland in Nigeria, the Cameroons highland in West Africa, and the Eastern Highlands in East Africa and Madagascar (Figure 3). These regions are characterized by humid subtropical marine climates, and it is not surprising that precipitation of the wettest month (Bio13), precipitation of the coldest quarter (Bio19), and elevation had a substantial influence on the species. Temperature variables, conversely, had little influence on *A. pinnata* subsp. *africana*'s distribution with the highest record only at 4.2%.

4.3 | Habitat suitability under future climate change

In 2015, more than 190 countries came together, resolved, and unanimously agreed to limit the global temperature increase to 1.5°C (COP21, Clémençon, 2016). Today, greenhouse gas emissions are still increasing. A clear picture emerges from this: Either governments have not met the Paris Agreement goals or have completely failed to deliver. In Africa, only two countries have shown tremendous effort to mitigate carbon emissions, The Gambia, despite being a developing country that has contributed the least to the problem and Morocco, which is increasing its solar power capacity (Azeroual et al., 2018).

Species do not respond to global change averages but instead to local and regional change (Walther et al., 2002). Future model predictions indicated that climate change would significantly impact *Azollas* species' distributions under different Representative Concentration Pathways (RCPs). Depending on the RCP scenario, substantial expansions and contractions of the three species' suitable habitats were predicted (Table 3).

Azolla filiculoides is predicted to remain restricted to its habitat (Southern Africa and some parts of East Africa) but recorded the highest stable habitat both at RCP 8.5 and RCP 4.5 at 91.87% and 86.87%, respectively, and the lowest habitat loss under stabilization climate change scenario (RCP 4.5) (Table 3). Its range of expansion and stability could be favored by higher temperatures and increased nitrogen concentration. Such potential expansions of aquatic species, especially invasive species, have been reported by McConnachie et al. (2003), Rahel and Olden (2008), and Nzei et al. (2021). *Azolla filiculoides*' invasive ability was approximated to cause an economic loss of USD 589 per hectare per year in South Africa (McConnachie et al., 2003), and our distribution model further supports the need to control its invasiveness.

Azolla nilotica's habitat is expected to gain slightly higher suitable areas under RCP 4.5 (2070) compared with *A. filiculoides* and *A. pinnata* subsp. *africana*, but in the extreme case scenario of RCP 8.5 (2070), *A. nilotica* is predicted to lose almost half of its potential future habitat, at 47.7%, against a gain of only 21.3% (Figure 4; Table 3). Central regions of South Sudan, Congo, West Africa, and significant portions of South Africa and Madagascar will be highly affected (Figures 4 and 5). This could be associated with the vulnerability of African wetland systems that are highly seasonal (Langan et al., 2018), while *A. nilotica* prefers a stable environment, and any slight disturbance could lead to its disappearance (Stergianou & Fowler, 1990). It is not surprising that Bio 12 (annual precipitation) had the greatest impact on *A. nilotica* (Table 2).

Azolla pinnata subsp. *africana* is estimated to lose 21.1% and 16.7% of its potential suitable habitat under RCP 4.5 and 8.5, respectively. *Azolla pinnata* also has the potential to tolerate higher temperatures between 25 and 30°C (Sadeghi et al., 2013) and this is well supported by the model as its future distribution records the highest gain at 41% (Table 3). Its expansion is potentially associated with rising global temperatures. Although decreased precipitation increases the salinity of freshwater ecosystems (Jeppesen et al., 2015), *A. pinnata* is least affected by decreased salinity (Masood et al., 2006), and thus remains relatively stable under both scenarios (Figure 4; Table 3).

Among the three species, *A. filliculoides* will be the least affected in terms of loss both at RCP 4.5 and 8.5 scenarios. The ability of this species to withstand harsh climatic conditions potentially confers an adaptive advantage (Sadeghi et al., 2013). *Azolla nilotica* and *A. pinnata* subsp. *africana* tend to share almost similar climatic conditions throughout continental Africa and are predicted to remain comparably stable under RCP 4.5, with the exception of *A. nilotica* losing a higher percentage of 47.7% under RCP 8.5 (Table 3). As expected, the reduction in rainfall and its unpredictable seasonality in the vast Sahara Desert render the climate unsuitable for *Azolla* both under the current and future predictions (Figure 5).

Climate change impacts are inevitable and can inflict physiological constraints on species that will determine their distribution to various degrees. Early understanding of these potential climate change repercussions would aid in anticipating their consequences for species and give time to implement appropriate management strategies (Walther et al., 2002). While the vast majority of African regions have been reported to experience an extreme increase in temperature over the past decades (Easterling et al., 2012), water balance and increased carbon dioxide (CO_2), especially in tropical and subtropical regions (Niang et al., 2014; Nicholson, 2000) also affect species distributions. Spatial temperature and precipitation patterns are expected to shift, leading to a different configuration of vegetation zones and hydrological regions, which will have enormous consequences for aquatic and wetland habitats. This will consequently have lethal ramifications for aquatic life and will likely make some regions less suitable or unsuitable for these species.

Over the past decades, global wetlands have declined considerably. Africa has 10% of the planet's global wetlands area, and 43% of the total global area of Ramsar-designated Wetland Sites, the highest of any of the six Ramsar regions (https://rsis.ramsar.org, accessed on March 19, 2022) (Gardner & Finlayson, 2018). Despite annual meetings of United Nations Climate Change conferences (COPs), the signing of a plethora of legally binding documents over many years, and the establishment of the Ramsar Convention on Wetlands of International Importance treaty in 1971, which was meant to reduce carbon emissions and conserve and protect wetland ecosystems, Africa has lost 42% of its wetlands (Solheim et al., 2018) due to little or no attention from the governments. For example, Lake Ol'Bolossat, the only lake in Central Kenya, is on the verge of extinction, and the future of the disappearing Lake Chad in North-Central Africa is uncertain. Regrettably, this trend is projected to escalate in future (Xi et al., 2021).

Considering the paucity of ferns on the African continent, extinction threats to the tropical African flora (Aldasoro et al., 2004; Sessa et al., 2017; Stévart et al., 2019), and the habitat specificity of aquatic ferns and other plants to freshwater ecosystems, conservation measures are desperately needed. This could be achieved, in part, by using biological approaches to control invasive aquatic species, drilling boreholes as an alternative to using wetlands as sources of water for local people, and respecting and maintaining cultural practices. Some wetlands are considered sacred and protected, and by continuing these local practices, threatened aquatic species will be preserved.

5 | CONCLUSIONS

In this study, we developed MaxEnt models based on occurrence localities and twelve environmental variables to describe the distributions of three *Azolla* species in Africa under present and future climatic scenarios. Environmental variables including elevation, precipitation of the wettest month, precipitation of the coldest quarter, and precipitation of the driest month contributed most to these models' predictions of suitable habitat across the members of this genus. Our findings suggested that under future climate change, *Azolla* species in Africa will suffer the loss of at least 8.1% and as much as 48% of their suitable habitat. The findings of our study can be utilized to develop specialized protection measures for various aquatic species and create awareness of climate change impacts on aquatic plants and African plants generally.

AUTHOR CONTRIBUTIONS

Mwihaki J. Karichu: Conceptualization (lead); data curation (lead); formal analysis (equal); methodology (equal); software (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **Boniface K. Ngarega:** Data curation (equal); formal analysis (equal); methodology (equal); software (equal); visualization (equal); writing – review and editing (equal). **Guy E. Onjalalaina:** Data curation (equal); formal analysis (supporting); methodology (supporting); writing – review and editing (equal). **Peris Kamau:** Conceptualization (supporting); data curation (equal); validation (equal); writing – review and editing (equal). **Emily B. Sessa:** Conceptualization (equal); data curation (supporting); funding acquisition (lead); investigation (lead); project administration (lead); resources (lead); supervision (lead); validation (equal); visualization (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in appendices.

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SUPPORTING INFORMATION

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

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