

# Environmental determinants of the current and future distribution of seven *Ottelia* Pers. species in African freshwater bodies

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## Research Article

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# Abstract

Understanding the influence of environmental covariates on plants' distribution is critical, especially for aquatic plant species. Climate change is likely to alter the distribution of aquatic species. However, knowledge of this change on the burden of aquatic macroorganisms is often fraught with difficulty. *Ottelia* Pers., a model genus for studying the evolution of the aquatic family Hydrocharitaceae, is mainly distributed in slow-flowing creeks, rivers or lakes throughout the world's pantropical areas. Due to recent rapid climate changes, the natural *Ottelia* populations have declined significantly. In the present study, we use maximum entropy (MaxEnt) to explore the environmental drivers of seven *Ottelia* species distribution in African freshwater bodies. The models use known background points to determine how environmental covariates vary spatially and produce continental maps of these species' distribution. We also estimate the possible influences of the optimistic and extreme pessimistic Intergovernmental Panel on Climate Change (IPCC) pathway scenarios and identify high suitability areas under these scenarios. Model performances were statistically significant than random expectations with Area Under Curve (AUC) values above 0.831, indicating the good performance of the models. We observe that our studied *Ottelia* species had distinct spatial patterns influenced by climate variations (e.g. Bio9- mean temperature of driest quarter, Bio12- annual precipitation, and Bio14- Precipitation of the driest month). While there is a lack of accord in defining the limiting factors for the distribution of the seven species, it is clear that water-temperature conditions have promising effects when kept within optimal ranges. Niche overlap analyses showed that most *Ottelia* species have similar but not equivalent climatic niches. In addition, considering the expected warming in the future, the persistence and survival of the *Ottelia* species in Africa could be compromised. The present findings provide a theoretical basis for the distribution of various *Ottelia* species in Africa.

## 1. Introduction

The world is evolving rapidly, affecting biodiversity in several ways (IPCC, 2014). Apart from the habitat loss known to threaten most species (Hanski et al., 2013), the increased human emissions of CO<sub>2</sub> from burning fossil fuels and other greenhouse gasses that cause climate change (IPCC, 2014) also affect living creatures. Similarly, the loss of biodiversity has been identified as one of the most significant threats to ecosystems, endangering human well-being and ecosystem resilience (Butchart et al., 2010; Hoekstra et al., 2005).

Aquatic ecosystems are among the most diverse and sophisticated ecosystems around the world. Due to human growth and development, these habitats face a slew of challenges, including habitat loss, degradation, and fragmentation (Murphy et al., 2019). Regardless of the importance of aquatic communities and their looming challenges, assessing aquatic assemblages for conservation reasons has proven extremely difficult, particularly given limited resources (Wilson et al., 2006). The instability generated by climate change trends is among the most significant problems facing conservation policies, as any policy must forecast the circumstances that habitats will likely encounter in the future (Pressey et al., 2007). Therefore, understanding the current aquatic biodiversity status, extinction trend threats, and

formulation of conservation strategies requires prior knowledge of the species distribution (McCarthy et al., 2008; Bailie 2004), and to deal with these uncertainties, several researchers have attempted to model the distribution of aquatic species in the future in order to offer conservation measures.

Over the past few decades, Africa has observed regional and continental climate change that has severely affected the water systems in the region (Serdeczny et al., 2017; Cavé et al., 2003). The future projections have suggested that there will be periods of shifts from decrease to increase in precipitation (Shepard, 2019; Serdeczny et al., 2017). Generally, sea levels, river flows, and direction and rainfall patterns will be majorly affected worldwide as predicted by the IPCC report (Bernstein et al., 2008), as well as the expected increased frequencies of heat waves (IPCC, 2014). Africa faces the risk of losing ~ 17% of the drainage due to the 10% drop in precipitation by 2050 (Misra, 2014; Nyong and Niang-Diop, 2006). These changes foretell significant potential alterations in the ecology and distribution of wetland species, coupled with expansion and shifts of ranges where species occur (Thornton et al., 2011; De Wit and Stankiewicz, 2006). Even so, these wetland species face risks of losing their habitats, and accelerated climate change may drive them into extinction (McLaughlin et al., 2017; Corlett, 2016).

Genus *Ottelia* includes aquatic species possessing a wide distribution in tropical, subtropical, and temperate regions of the globe (Cook and Urmi-König, 1984; Cook et al., 1983). Cryptic speciation observed among specific species recently has heightened interest for further research on the genus (Li et al., 2020; Li et al., 2019; Ito et al., 2019). Irrespective of the high diversity of the *Ottelia* species (Fan et al., 2019; Guo et al., 2019; Li et al., 2019; Zhai et al., 2018), few studies have used georeferenced data and statistical models to assess the effect of climate on the expansion or reduction of the geographical distribution of *Ottelia* species (Guo et al., 2019). In Africa, this genus has been assessed on a molecular and taxonomical basis (Li et al., 2020; Symoens, 2009). However, no previous studies on the continent have evaluated the ENMs of the genus, and only *O. acuminata* has received attention regarding ENMs elsewhere (Guo et al., 2019). This species' future projections have shown a general stable habitat under the extreme greenhouse gas emission scenario RCP 8.5, with a slight shift of the range polewards. In addition, tropical Africa possesses a unique topography, and different ecoregions typically bear different environmental characteristics (Murphy et al., 2019). It is anticipated that every plant species in this region will show a complex feedback mechanism to climate change (Corlett, 2016). Niche separation among *Ottelia* populations of sympatric species favors long-term coexistence, and the resultant features or the niche disparities cause higher competition within a species' populations than that with other species populations (Li et al., 2020; Chesson, 2000). Therefore, there is the need to assess ENMs for the genus *Ottelia* to discourse factors that would influence the distribution, and diversification of this genus, as a case study in African freshwater environments, on a climate change basis.

Ecological niche models (ENMs) are powerful tools widely used in assessing the impacts of climate and environmental change on species, as well as their habitat suitability (Elith and Leathwick, 2009; Hirzel et al., 2006). The maximum entropy (MaxEnt) is preferred among the presence-only models since it has prior positive outcomes and has been used widely (Elith et al., 2011; Phillips et al., 2006). has been shown to outdo the genetic algorithms and the regression models in SDM (Heikkinen et al., 2006; Elith et al.,

2006) and could account for the complex interactions between geographical features responsible for the absence or presence of water basins (Phillips and Dudik, 2008). Furthermore, MaxEnt can predict species' habitat suitability in the unknown wetlands/basins using presence-only data and has been successfully conducted in several wetland species, such as *O. acuminata* (Guo et al., 2019) and *Hydrocotyle umbellata* and *Salvinia auriculata* (Heneidy et al., 2019).

Our study focuses on using the ENMs to estimate the influence of environmental change on seven African *Ottelia* species and to detect the impact of climate change by 2050s under moderate and extreme greenhouse gas emissions using MaxEnt (Phillips et al., 2006). Additionally, we highlight the relative increases and decreases of areas of habitat suitability for studied seven *Ottelia* growing regions under current and future periods and further discuss the niche overlap among the species in the region and probe the reasons for the patterns. While this study focuses on *Ottelia*, some of its results are significant and may apply to other macrophytes at a vast scale.

## 2. Materials And Methods

### 2.1. Study area and species

Tropical Africa is characterized by abundant reservoirs that include basins such as the Lake Victoria, Congo, and Zambesi Basins, with large rivers that include Niger, Zambezi, and Congo (Lewis and Berry, 2012). The availability of these extensive water systems that are widely interconnected provides an excellent opportunity to assess their complexity due to topography (De Dominicis et al., 2015). Worthy to note is that a significant percentage of the freshwater and river basins are restricted to two or more countries. An array of climates characterizes this region, for instance, semiarid, desert, tropical monsoon equatorial climate. We divided the study area into 10 × 10 Km grid cells. The distribution of seven Africa *Ottelia* species viz. *O. cylindrica* (T.C.E.Fr.) Dandy, *O. muricata* (C.H. Wright) Dandy, *O. kunenensis* (Gurke) Dandy, *O. fischeri* (Gurke) Dandy, *O. ulvifolia* (Planch.) Walp, *O. exserta* (Ridl.) Dandy and *O. verdickii* Gurke were modeled and projected to evaluate future climate change impacts on water systems in tropical Africa. Lastly, modeling the distributions of *O. luapulana*, *O. lisowskii* Symoens, *O. scraba* Baker, *O. somalensis* Chiov., and *O. alismoides* (L.) Pers. which had less than few occurrences, was not possible. For accurate modeling and producing fitting models, a species requires more than three occurrence records (van Proosdij et al., 2016).

### 2.2. Collection of occurrence data

The African *Ottelia* species occurrence data and localities were obtained from different sources, including the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>, accessed on March 2020), TROPICOS (<http://www.tropicos.org/>, accessed on March 2020), Zambia Flora (<https://www.zambiaflora.com/>, accessed on March 2020), hitherto published literature (Kennedy et al., 2015) and our fieldworks (2018–2019). Notably, there is substantial ambiguity present in the taxonomical literature of the genus *Ottelia* in Africa due to the tantamount use of various names to identify one species, e.g., *O. ulvifolia*, *O. exserta*, among others (Ferrer-Gallego et al., 2016). Therefore, to

evade any misperception arising from this taxonomic uncertainty, only the literature information with listed specific epithet according to Plant List (IPNI; The Plant List, 2010) was considered, discarding all the synonyms that refer to one species. We cross-checked all herbarium specimens for probable misidentification and noted the locality information on label data. For the herbarium records that lacked geographic coordinates but had locality occurrence descriptions, we used Google Earth™ to georeference them at three decimal degrees accuracy levels. With the data obtained, including a combined dataset 505 for all species records for the study area, a spatial rarefying of each species' localities was performed on R package "spThin" v. 0.1.0 (Aiello-Lammens et al., 2015) to reduce the autocorrelation between the points at each grid cell of ten by ten km. Occurrence data and field survey localities are shown in Table S1, and displayed in Fig. 1.

## 2.3. Environmental variables

Climatic data variables attained from the period 1950–2000 were obtained from the WorldClim database (<https://www.worldclim.org/bioclimate>) at a resolution of 2.5-arcmin from the equator (Hijmans et al., 2005). This dataset (19 variables) includes a summary of information on average, extremes, and seasonality patterns of precipitation and temperature. We ran a Pearson correlation test on the 19 bioclimatic factors to exclude the collinear ones since presence-only models are generally affected by collinearity between variables (Dormann et al., 2007). We used a threshold-dependent variance inflation factor (VIF) correlation at a threshold of 0.7 using the "cor" function in R 3.6.2 (R-Core-Team, 2019). Nine variables were selected following their restricted collinearity and used for preceding analyses (Table S2). *Ottelia* is an aquatic genus, and due to its dependency on water, we included precipitation of the driest quarter (Bio17) and annual precipitation (Bio12) as relevant to water availability for the genus. We also incorporated elevation (<http://srtm.csi.cgiar.org/>) as an extra variable since *Ottelia* is affected by geography (Symoens, 2009). It is worthy to note that altitude affects freshwater aquatic species since they are restricted to basins bearing certain features, and elevation plays a vital role in these features, for instance, available vegetation in the surrounding, nutrients, speed of flow, among others (Nori and Rojas-Soto, 2019). In addition, different *Ottelia* species have been associated with their type habitat and observed to be affected by the direction of water movement (Kennedy et al., 2015); therefore, we calculated 'slope' in ArcGIS v. 10.5 and added the raster variable. The Land use was obtained from <http://www.fao.org/faostat/en/#data/RL>, population density from <http://sedac.ciesin.columbia.edu/data/collection/gpw-v4> (CIESIN, 2017), and water area from HydroSHEDS dataset (<http://hydrosheds.cr.usgs.gov>). Future prediction variables included the global climate models (GCM) from the Community Climate System Model (CCSM; Gent et al., 2011) at 2.5 arcmin according to McSweeney et al. (2015) for the periods 2041–2060, commonly referred to as period "2050". Two representative concentration pathways (RCP) were selected for each period (CCSM) to represent the moderate (RCP 4.5) and extreme climatic changes (RCP 8.5). RCP 8.5 assumes no climate policies will be undertaken either in the future or present, and it reflects very high emissions scenarios (~1370-ppm CO<sub>2</sub> equivalent by 2100; van Vuuren et al., 2011). Due to the future complexities and obtaining

data for these periods, all the social variables remained constant, and were therefore used the current and future projections.

## 2.4. Ecological modeling and validation

Here, the maximum entropy algorithm applied in MaxEnt v. 3.4.3.e (Phillips et al., 2006) was used to appropriate the seven *Ottelia* species' distribution likelihood across our study area, subjecting it to constraints imposed by the environmental characteristics of the current data coordinates (16 variables, Table 1). We used the ENMeval package in R v. 3.6.2 (Muscarella et al., 2014) to perform a tuning experiment of our MaxEnt models. Using defaults for MaxEnt has resulted in poor-performing models (Radosavljevic and Anderson, 2014; Warren and Seifert, 2011). The 'block method', which divides data (presence points) into  $k$  = folds (Wenger and Olden, 2012), was employed to make the localities data into independent spatial test and training data sets. The regularization multipliers were set from 0.5 to 5 with increments of 0.5 in the  $k$  of MaxEnt models. The feature combinations used were L, H, LQ, LQH, LQHP, and LQHPT; where P = product, H = hinge, T = threshold, Q = quadratic, and L = linear. The tuning experiment was applied for all the seven *Ottelia* species, then MaxEnt was run with the following parameters: 10 cross-validate replicates with 75% training and 25% test data, 10,000 background points, and 5,000 iterations. Validation of the models included performing the receiver operating characteristics (ROC) curve analysis to estimate the values of AUC<sub>test</sub> and AUC<sub>train</sub> (Warren and Seifert, 2011). We also included the jackknife tests to analyze the relative importance of the selected variables. The models' results were given as averages of the ten replicates and converted into binary layers with 1 (presence) and 0 (absence) values for each species using the maximum training and sensitivity plus specificity (MTSS) as a threshold. MTSS is recommended as a conservative approach that minimizes commission and omission errors (Guisan et al., 2017; Liu et al., 2016). This analysis was performed in ArcGIS v. 10.5. Thus, for each species, one baseline (current) and two potential distribution layers were created based on the two scenarios and one GCM. Future habitat suitabilities were based on the current records and variables described before. For assessing the influence of climate on the distribution of *Ottelia*, we analyzed the distributional changes in habitat suitability for the seven species between the current and future thresholded models.

## 2.5. Niche overlap assessment

To assess the niche overlaps between *Ottelia* species, we used *Schoener D* (Schoener, 1968) and *Hellinger I* (Warren et al., 2008) statistics, implemented in ENM-tools v. 1.4.4 (Warren and Seifert, 2011). These two metrics compare niches overlaps of two species with values from 0 to 1, with 1 signifying resemblance in the two niches and 0, no overlaps (Waren, 2010). We excluded 5% of the occurrence data to account for probable errors in the data.

## 3. Results

### 3.1. *Ottelia* distribution in Africa and model performance

The correlation analysis indicated the following variables to be the best for predicting habitat suitability for the genus *Ottelia*: mean diurnal range (Bio2), mean temperature of the wettest quarter (Bio8), Isothermality (Bio3), mean temperature of the driest quarter (Bio9), precipitation of wettest month (Bio13) precipitation of driest month (Bio14), precipitation seasonality (Bio15), precipitation of warmest quarter (Bio18), and precipitation of coldest quarter (Bio19; Table S2). The AIC values of *Ottelia* species were considered to have the best effects when MaxEnt features were as follows: *O. cylindrica*, L, Q, H, P and RM = 1.5; *O. exserta*, L, Q, H, P, T, and RM = 1.5; *O. fischeri*, L, Q, H, P, and RM = 4; *O. kunenensis*, L, Q, H, and RM = 1.5; *O. muricata*, L, Q, H, P, T, and RM = 2.5; *O. ulvifolia*, L, Q, H, P, T, and RM = 1; and *O. verdickii*, H and RM = 0.5. The MaxEnt AUC models were considered bad if the values were lower than 0.6, good when the values ranged from 0.6 to 0.8, and excellent with values from 0.8 to 0.987 the highest (Warren and Seifert, 2011). The current distribution of the seven species gave satisfactory AUC values as follows: *O. cylindrica*, AUC = 0.973; *O. exserta*, AUC = 0.958; *O. fischeri*, AUC = 0.967; *O. kunenensis*, AUC = 0.980; *O. muricata*, AUC = 0.964; *O. ulvifolia*, AUC = 0.827; and *O. verdickii* AUC = 0.987 (Table 2). Under the MaxEnt models, the genus *Ottelia* ENMs were, to a large extent, affected by the following set of three bioclimatic variables; Bio9 (mean temperature of the driest quarter), Bio12 (Annual precipitation), and Bio14 (Precipitation of the driest month), as well as elevation (Table 3). In the case of *O. cylindrica*, *O. ulvifolia*, and *O. verdickii*, Bio12 highly contributed to their habitat suitability. Bio9 contributed highly to *O. exserta*, *O. muricata*, and *O. ulvifolia* models. Elevation mostly influenced the distribution of *O. exserta*, *O. fischeri*, *O. kunenensis*, and *O. verdickii*. *O. cylindrica*, *O. kunenensis*, and *O. muricata* distribution appeared to be limited by Bio14. The land use and Bio12 variables considerably influenced the distribution of *O. cylindrica* and *O. fischeri*, respectively, while the Water area variable highlighted its importance in affecting the distribution of *O. exserta*, *O. fischeri*.

## 3.2. Predictions of potential distribution in the current and future climate change

The current potential distribution indicated that *O. ulvifolia* occupied the greatest extent in Tropical Africa (Fig. 2). *O. fischeri* had the second-highest potential distribution, followed by *O. muricata*, *O. exserta*, *O. cylindrica*, *O. kunenensis*, and *O. verdickii* in that order. In Madagascar, where only *O. ulvifolia* occurs, revealed suitable high habitats for *O. exserta* and *O. fischeri*, with low suitability for *O. cylindrica*. Zambia, Angola, Botswana, south of DR Congo were revealed to be hotspots for the *Ottelia* species. New areas, including northern Sudan and Cameroon, revealed potential habitats for several *Ottelia* species with no previous records (Fig. 2, 3, S1).

Table 1  
Environmental covariates used in modeling the distribution *Ottelia*

Category	Code	Variables	Unit	Source	
Bioclimatic	Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	°C * 10	WorldClim	
	Bio3	Isothermality	-	WorldClim	
	Bio8	Mean Temperature of Wettest Quarter	°C * 10	WorldClim	
	Bio9	Mean Temperature of Driest Quarter			
	Bio12	Annual precipitation	mm/month	WorldClim	
	Bio13	Precipitation of Wettest Month	mm/month	WorldClim	
	Bio14	Precipitation of Driest Month	mm/month	WorldClim	
	Bio15	Precipitation Seasonality (Coefficient of Variation)		WorldClim	
	Bio17	Precipitation of Driest Quarter	mm/quarter	WorldClim	
	Bio18	Precipitation of Warmest Quarter	mm/quarter	WorldClim	
	Bio19	Precipitation of Coldest Quarter	mm/quarter	WorldClim	
	Topographic	Elevation	Elevation	m. a.s.l.	STRM
		Slope	Slope	% degree	Derived from elevation
	Social	Land use	-	-	FAO
Population density		-	People/km2	SEDAC	
Water area		-	Water are cover/km2	HydroSHEDS	

Different *Ottelia* species observed and responded differently under future moderate and extreme greenhouse gas emissions for future potential distributions. Generally, there was an overall decrease in habitat suitability for all *Ottelia* by the 2050s under both RCP 4.5 and RCP 8.5 (Fig S2, Fig. 4). However, the latter observed a tremendous loss, as observed by reduction and increase in pixels, respectively (Table S3, Fig. 4). Moreover, under RCP 8.5, potentially suitable habitats in Madagascar and Angola for *O. ulvifolia* and *O. exseta* are lost (Fig. 4); however, they are minimally reduced in RCP 4.5 (Fig S2). Interestingly, *O. verdickii* showed the most gain in suitable areas under the extreme scenario RCP 8.5 compared to the other species (Fig. 4). We also observed a certain trend in both RCP scenarios where all species move towards the North Pole under, indicated by range expansion (Fig. 4, Fig S2)



Table 2

Characteristics of the *Ottelia* species' spatial records used as predictors to model the tropical African freshwater SDMs, including model performance based on AUC values and standard deviation in parentheses

Species	Elevation	No. of presences	AUC (mean)		
			Current	2050s (RCP 8.5)	2070 (RCP 8.5)
<i>Ottelia cylindrica</i>	1100–1900	20	0.988 (0.021)	0.989 (0.002)	0.974 (0.019)
<i>Ottelia exserta</i>	40-1200	87	0.974 (0.019)	0.980 (0.003)	0.954 (0.025)
<i>Ottelia fischeri</i>	1200–1600	12	0.987 (0.015)	0.962 (0.021)	0.878 (0.102)
<i>Ottelia kunenensis</i>	1030–1200	22	0.989 (0.021)	0.970 (0.033)	0.969 (0.035)
<i>Ottelia muricata</i>	1000	53	0.969 (0.019)	0.980 (0.006)	0.957 (0.016)
<i>Ottelia ulvifolia</i>	183–1800	274	0.919 (0.028)	0.926(0.006)	0.831 (0.034)
<i>Ottelia verdickii</i>	1150–1350	33	0.987 (0.015)	0.990(0.009)	0.989 (0.008)

Table 3

Mean relative contribution of each variable to the final model of the current distribution for each *Ottelia* species studied

Species	<i>Ottelia cylindrica</i>	<i>Ottelia exserta</i>	<i>Ottelia fischeri</i>	<i>Ottelia kunenensis</i>	<i>Ottelia muricata</i>	<i>Ottelia ulvifolia</i>	<i>Ottelia verdickii</i>
Bio2	3.5	2.7	<b>12.3</b>	4.6	0.5	3.5	4.7
Bio3	0.3	2.9	0.9	6.2	2.9	4.8	0.5
Bio8	9.4	0.6	0.0	0.0	0.0	2.6	0.1
Bio9	2.5	<b>23</b>	0.7	3.6	<b>24.9</b>	<b>10.3</b>	0.0
Bio12	<b>12.2</b>	8.2	4.4	4.6	4.0	<b>16</b>	<b>18.6</b>
Bio13	2.3	0.7	0.1	0.2	0.2	<b>21.9</b>	0.0
Bio14	<b>27.3</b>	1.0	2	<b>21.1</b>	<b>32.1</b>	2.3	14.5
Bio15	0.7	2.5	0.1	0.0	0.6	1.5	0.4
Bio17	3.5	1.3	2.7	2.5	1.5	1.9	<b>14.7</b>
Bio18	3.0	9.8	1.5	9.7	<b>10.5</b>	4.7	6.1
Bio19	1.9	8.9	2.3	4.7	1.0	2.2	3.9
Elevation	9.5	<b>15.1</b>	<b>37.6</b>	<b>25.5</b>	9.0	5.1	<b>22.1</b>
Slope	1.3	6.0	8.9	<b>10.9</b>	3.1	3.6	5.1
Water area	0.6	<b>9.6</b>	<b>10.5</b>	5.2	8.8	6.8	2.2
Population Density	0.1	1.1	10.4	1.8	0.3	2.8	1.4
Land use	<b>22</b>	6.7	5.3	1.7	0.8	10.2	5.7

### 3.3. Niche overlap analyses

The overall niche overlap analysis indicated that Tropical African *Ottelia* species overlap considerably, according to *D* statistics (Table 4). However, *I* statistics revealed an average overlap among all pairwise combinations (randomized values < 0.5) (Table 4). *O. fischeri* observed the highest overlap with all the *Ottelia* species except for *O. cylindrica*, according to *I* value (randomized values < 0.5, Table 4). There was almost complete overlap between *O. kunenensis* and *O. muricata*, and more or less none between *O. kunenensis* with *O. verdickii* ( $D = 0.7011$  and  $0.0963$ , respectively; Table 4).

Table 4  
Niche overlap *D* statistics (above diagonal) and *I* statistics (below diagonal)

Species	<i>O. cylindrica</i>	<i>O. exserta</i>	<i>O. kunenensis</i>	<i>O. muricata</i>	<i>O. ulvifolia</i>	<i>O. verdickii</i>	<i>O. fischeri</i>
<i>O. cylindrica</i>	0.336	0.283	0.482	0.334	0.304	0.441	
<i>O. exserta</i>	0.554	0	0.305	0.426	0.411	0.159	0.498
<i>O. kunenensis</i>	0.537	0.532	0	0.701	0.290	0.096	0.312
<i>O. muricata</i>	0.671	0.620	0.789	0	0.368	0.183	0.458
<i>O. ulvifolia</i>	0.560	0.619	0.533	0.597	0	0.128	0.591
<i>O. verdickii</i>	0.557	0.439	0.384	0.458	0.423	0	0.169
<i>O. fischeri</i>	0.635	0.660	0.552	0.643	0.724	0.453	0

## 4. Discussion

Mapping the habitat suitability in an ENM approach is advantageous because it offers critical notes on species management and conservation (Elith et al., 2011). Our current study highlighted the importance of assessing the ENMs of the *Ottelia* species for the current and future, using environmental covariates. All models for all species had AUC values above 0.831, which was satisfactory and yielded insights into these species' future distribution with high accuracy levels (Table 2).

Predictions of MaxEnt Modeling for the seven *Ottelia* species' current distribution inferred that the present models predicted the habitat suitability of the *Ottelia* species distribution correctly (Fig. 2). Specifically, all species had higher suitabilities in southern Africa except *O. ulvifolia*, which was widely distributed in tropical Africa. Sighting higher suitable areas for the *Ottelia* species in northern and western Africa where no previous records were made was impressive, highlighting that these species might be present or persist in those regions. Nevertheless, our training tests of the models revealed that modeling using pseudo-presence models was not very precise. The likely explanation is that not all habitats within the range of occurrence are suitable for a species persistence (Verberk, 2011).

Environmental variables directly or indirectly affect SDMs (Austin, 2002). Direct variables, e.g., precipitation and temperature, may influence the survival of organisms and their physiology. On the other hand, elevation and water area (indirect variables) affect the abundance and geographical distribution of species; however, they do not significantly influence their physiology. Therefore, from our VIF correlation analyses and choice of variables in the present study, both the direct and indirect variables were observed to affect the distribution of *Ottelia*.

The climatic variables making the highest contribution to the current habitat suitability and distribution of *Ottelia* differed between the species (Table 3). For *O. cylindrica*, a blend of Bio12 (annual precipitation), Bio14 (precipitation of the driest month), and land use variables explained its distributional range in the southern hemisphere. For *O. ulvifolia*, the combination of Bio9 (mean temperature of the driest quarter), Bio12 (annual precipitation), and Bio13 (precipitation of wettest month) inferred tolerance of a wide range of precipitation and temperature that illuminated its broad distributional range in Tropical Africa. Nevertheless, most species shared the variable related to elevation (*O. exserta*, *O. fischeri*, *O. kunenensis*, and *O. verdickii*), annual precipitation (Bio12) (*O. cylindrica*, *O. ulvifolia*, and *O. verdickii*), and precipitation of the driest month (Bio14) (*O. cylindrica*, *O. kunenensis*, and *O. muricata*). These factors and the others included in the current study are possibly linked to ecosystem competence and, in particular, the availability of nutrients (Zhang et al., 2020; Crossley et al., 2002). Climatic variations can aid evolutionary divergence (Petean et al., 2020; Rissler and Apodaca, 2007) by fostering species adaptation to new climatic environs (Iannella et al., 2019). In addition, the cosmopolitan distribution of *O. ulvifolia* in Africa is supported by our simulations, which show that the species can persist in a broad range of environmental conditions.

Future projections showed that *Ottelia*'s responses to climate change are highly variable (Fig. 3, Fig S1). Although certain species are expected to be largely untouched by climate change (e.g., *O. verdickii*, in RCP 8.5, Fig. 3), others, especially in the RCP 8.5, are expected to lose a significant amount of appropriate habitat ranges (Fig. 4). The loss of appropriate ranges for a species means, at the very least, a rise in environmental pressure supporting mortality over the establishment in certain areas, which could result in local extinctions (Parmesan et al., 2015; Walck et al., 2011). The different responses to global climate change among closely related *Ottelia* species also indicate that macrophyte populations may disaggregate in the future, affecting the function and structure of the macrophyte assemblages they form (Alahuhta et al., 2020; García-Girón et al., 2020; Murphy et al., 2019).

Our observations from the niche overlap analyses show that most *Ottelia* species have similar but not equivalent climatic niches (Table 4). Despite a low to average overlap between the *Ottelia* species (Table 4), only *O. exserta* and *O. fischeri* shared two identical environmental variables (elevation and water area) that contributed significantly to their distribution (Table 3). While all these species were revealed to have different ecological requirements, their habitat suitability was mostly temperature and precipitation-dependent (Table 3). The low to average niche overlap between the *Ottelia* species may imply that they are distinguished from one another by a variety of abiotic factors. While in the current study, we evaluated the niche overlaps of the seven *Ottelia* species based on bioclimatic characteristics, complex and competitive interactions, on the other hand, which may shape macrophyte assemblages (Murphy et al., 2019; Kennedy et al., 2015).

The present study did not include the effects of pH and nutrient availability of water bodies where species occur and their influence on aquatic species. Therefore, future studies should assess the effects of pH and nutrient availability on the distribution of aquatic macrophytes. Regardless, the observed areas of high habitat suitability for the *Ottelia* species could be observed as potential future refuges. In order to

anticipate the intricate impacts that climate change will have on community assemblages, it is crucial to locate the areas that will most likely persist under adverse future climate change (Pennino et al., 2020; Monsarrat et al., 2019).

Usually, when performing ENMs, the occurrence data should be independent of each other and obtained in an unbiased and random manner (Graham et al., 2004). However, given the inaccessibility of certain African countries/regions, collecting data to meet these criteria is often difficult, and direct sampling of aquatic macrophytes found in deep forests (e.g., Congo) or politically unstable areas could be impossible (Murphy et al., 2019). Furthermore, other water bodies may be home to hippos and crocodiles, making occurrence records for aquatic macrophytes challenging to obtain (Kennedy et al., 2015). Finally, complex river channels can be challenging to traverse. Given this, sampling the whole African continent might not be optimal for the reasons mentioned. The presence records used in the present study were obtained from credible sources *viz.* GBIF, museum herbariums, and published literature. The possibility of selection bias was low in this case was therefore independent. Nonetheless, due to the limitations of the sampling efforts in Africa, this data remains somewhat biased. Even so, the modeling analyses used 10,000 background points (absence data) that were generated randomly by MaxEnt. Background points increase the chances of producing the best fitting probability distribution for estimating habitat suitability (Elth et al., 2011). Also, the modeling approach's environmental covariates were cautiously selected to reduce omission and commission errors. Integration of many predictive covariates in ENM generates overfitting, constraining the spatial range of predictions (Beaumont et al., 2005). Therefore, an optimum number of predictors must be calculated to maximize the effectiveness of the analysis. Regardless of the challenges, we modeled the distribution of seven *Ottelia* species using Maxent and presence-only data and produced reliable models similar to Guo et al. (2019), as well as other aquatic macrophytes (Heneidy et al., 2019; McGarvey et al., 2018).

The current study assessed the probable effects of future climate change on the distribution of seven *Ottelia* species in African freshwater basins. Studies such as this, which use predictive models based on recorded data, established biological parameters, and best possible climate simulations representing the full spectrum of outcomes, offer policymakers and experts critical knowledge to set goals for mitigation and conservation in the future. The present findings highlighted that among the most vital variables influencing the distribution of *Ottelia* were elevation, annual precipitation (Bio12), and precipitation of the driest month (Bio14). Future projections of the habitat suitability showed that the currently suitable area of the *Ottelia* species would decline by 2050s under both climate scenarios RCP4.5 and RCP 8.5, with the pessimistic scenario having a tremendous loss. Extensive reductions in suitable areas under the future climate scenarios indicate the probability of the species being threatened or endangered if the *Ottelia* habitats' keen management and conservation are not observed. While the characteristics of the *Ottelia* species' distribution are pretty satisfactory from this study, more surveys are encouraged throughout tropical Africa to assess the *Ottelia* species distribution.

Generally, we have demonstrated that global climate change would constitute a severe threat to *Ottelia* species, even though the current distribution ranges of most species are closely bound to the water

bodies of the greater central-southern African region, where the local communities are highly dependent on natural water bodies for water. This situation renders many species in decline situations, covering areas where conservation management and scientific research are yet to be undertaken and becoming increasingly vulnerable to various threats. While the current study concentrated on genus *Ottelia*, and particularly the African species, we acknowledge that many aquatic macrophytes need similar careful consideration. As a result, although we recommend more proactive attempts to safeguard *Ottelia* from increasing threats, we also recommend that initiatives be made to evaluate and utilize accessible data continuously (e.g., checklists), together with countrywide level assessments (e.g., Kennedy et al., 2015), to enhance conservation protection of aquatic macrophytes in Africa. Such discussions are currently underway in the African region and are imperative to building preparedness capacity for the ongoing effects of climate change on African waterbodies. Therefore, results from this study are especially pertinent to elaborate the conservation schemes for aquatic macrophytes. Lastly, our findings call for further research into the genus *Ottelia* from a variety of viewpoints, including not only the ENMs and ecological aspects but also the genus' taxonomy, physiology, and molecular barcoding.

## Declarations

### Conflicts of Interest

The authors declare no competing conflict of interests

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## Figures

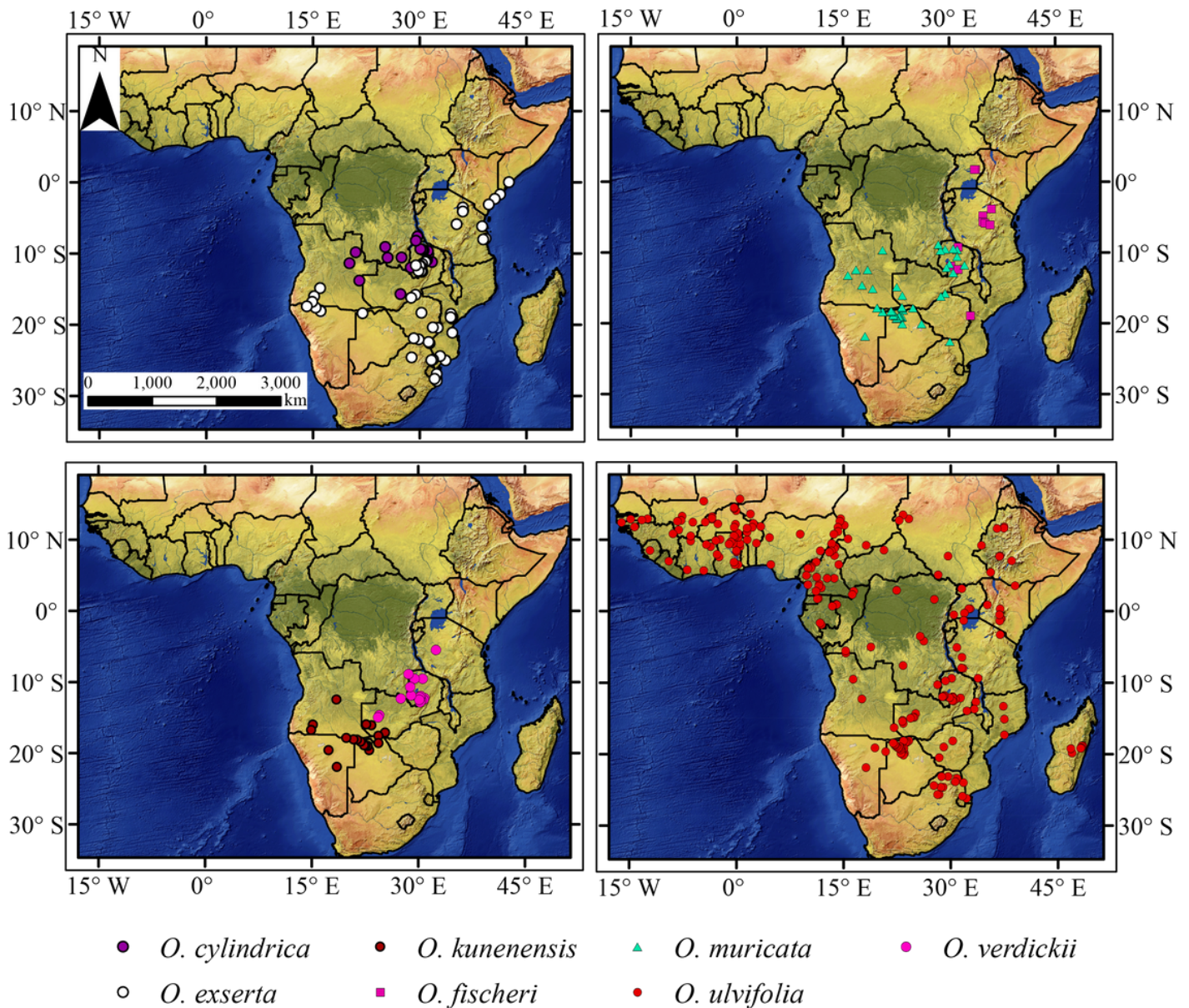


Figure 1

Map of the occurrences of *Ottelia* spp. Occurrences of *Ottelia cylindrica* (n=20), *O. exserta* (n=87), *O. fischeri* (n=12), *O. kunenensis* (n=22), *O. muricata* (n=53), *O. ulvifolia* (n=274), *O. verdickii* (n=33) used for modeling

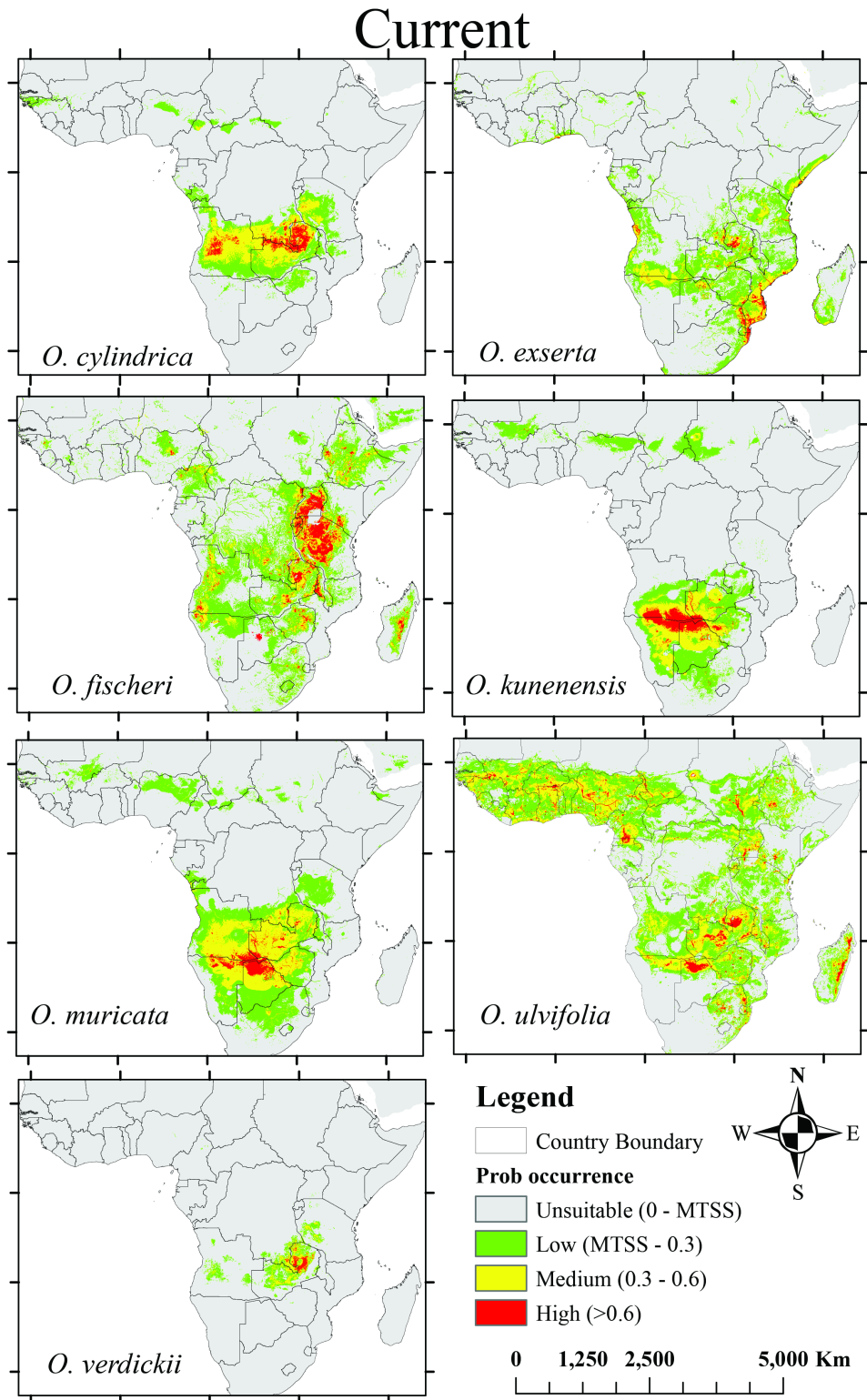
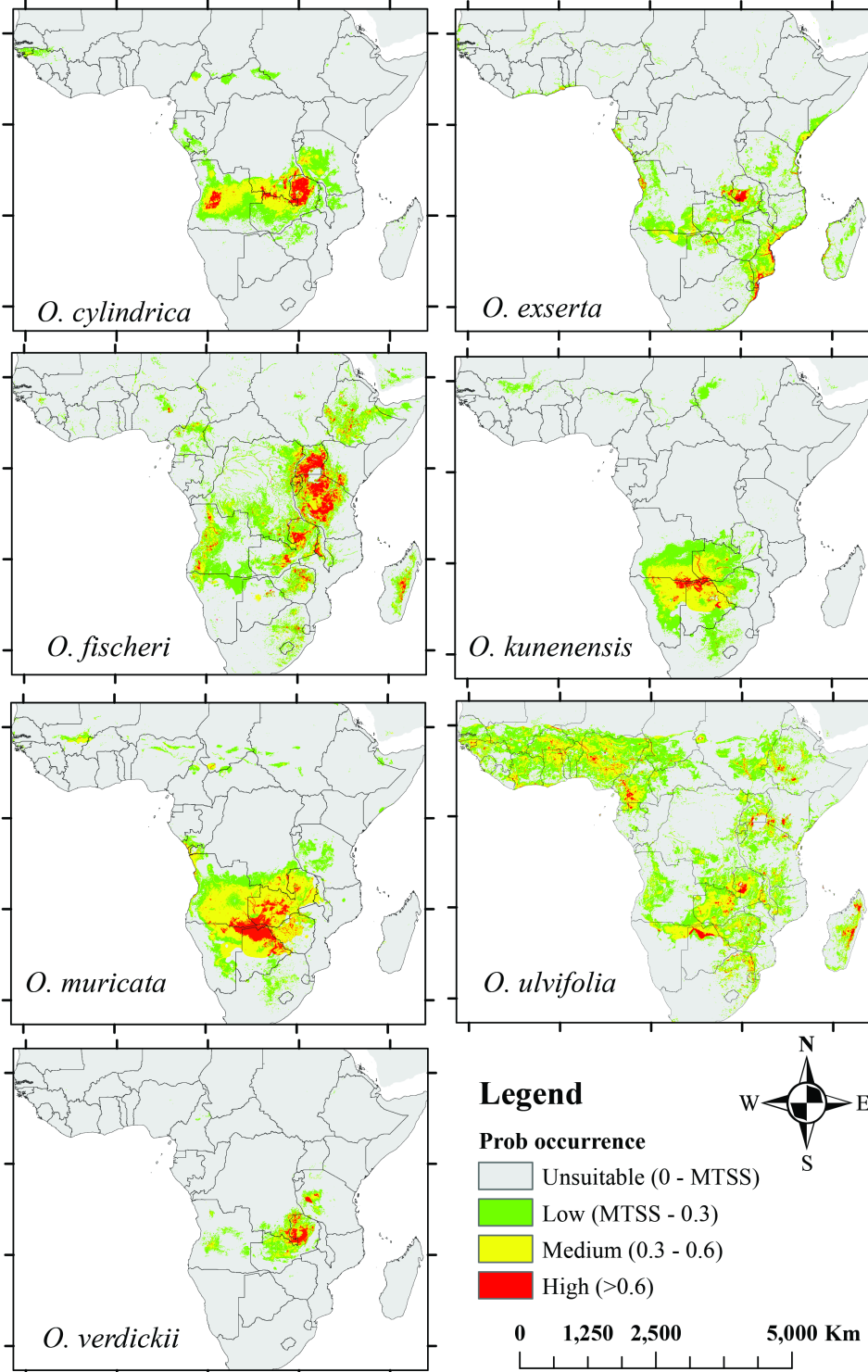


Figure 2

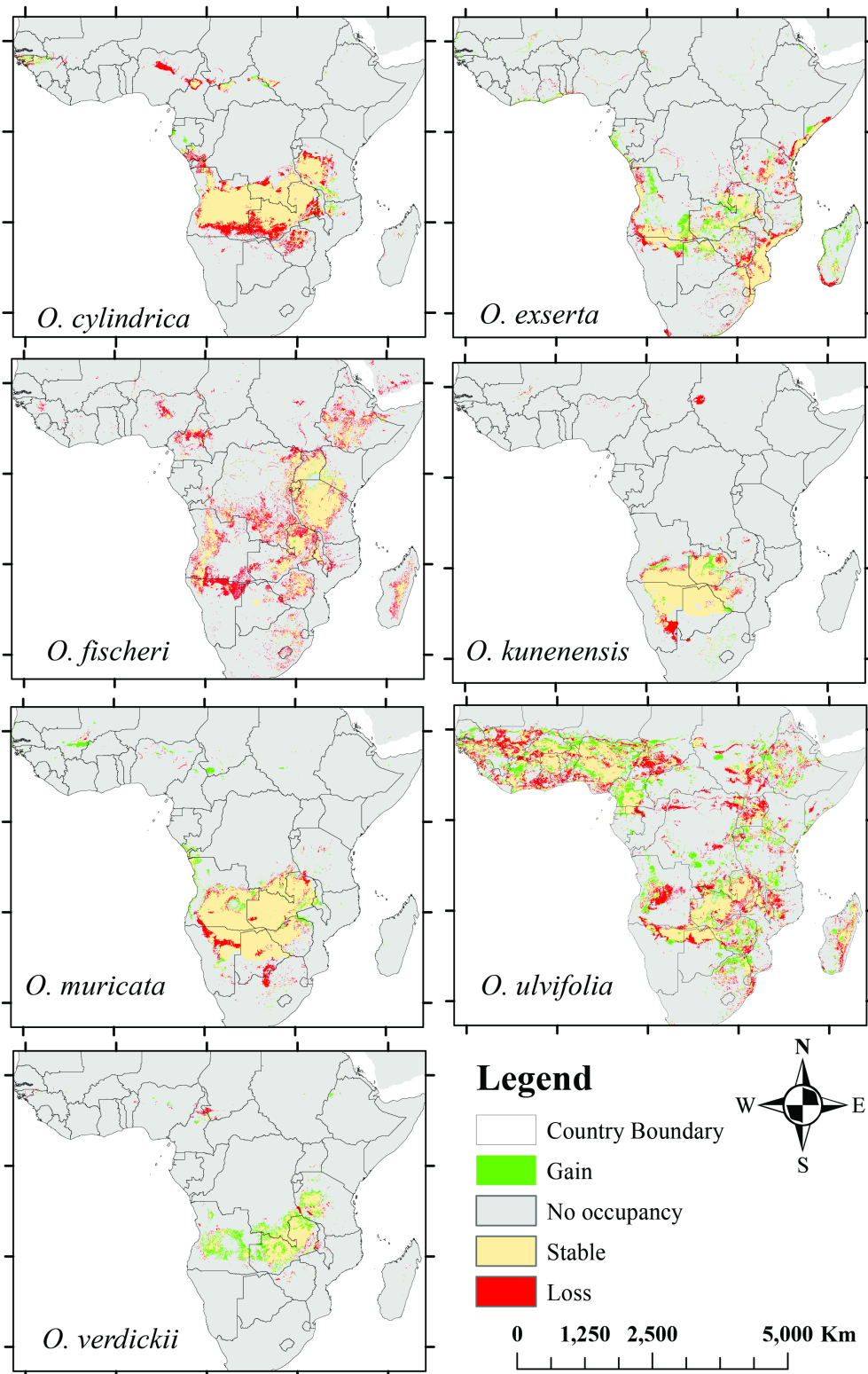
Current potential distribution of *Ottelia* species in Africa. Potential distributions were based on different environmental variables

## 2050 RCP 8.5



**Figure 3**

Predicted potential distribution of the *Ottelia* species in the 2050s for the RCP 8.5 using the Maxent models



**Figure 4**

Predicted change in the distribution of *Otelia* species under RCP 8.5 scenario for the year 2050s

## Supplementary Files

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