frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 28 January 2026
DOI 10.3389/fevo.2025.1715912

Phylogenetic relationships and climate-driven range shifts of Lemnaceae in South Africa

Unarine Honest Ndou[1,2], Thulani Tshabalala[3],
Ledile Thabitha Mankga[3]* and Bezeng Simeon Bezeng[3,4]

[1]South African National Biodiversity Institute, Walter Sisulu Botanical Garden, Roodepoort, South Africa, [2]Department of Agriculture and Animal Health, University of South Africa, Science Campus, Florida, South Africa, [3]Department of Life and Consumer Sciences, University of South Africa, Science Campus, Florida, South Africa, [4]Flyway Conservation Programme, Royal Society for the Protection of Birds, Sandy, United Kingdom

EDITED BY
Emmanuel Chukwuma,
Forestry Research Institute of Nigeria, Nigeria

REVIEWED BY
Bashir Bolaji Tiamiyu,
University of Ilorin, Nigeria
Daniel Zhigila,
University of Cape Town, South Africa
Leone Ermes Romano,
University of Naples Federico II, Italy

*CORRESPONDENCE
Ledile Thabitha Mankga
✉ mankglt@unisa.ac.za

RECEIVED 30 September 2025
REVISED 26 December 2025
ACCEPTED 29 December 2025
PUBLISHED 28 January 2026

CITATION
Ndou UH, Tshabalala T, Mankga LT and Bezeng BS (2026) Phylogenetic relationships and climate-driven range shifts of Lemnaceae in South Africa. *Front. Ecol. Evol.* 13:1715912. doi: 10.3389/fevo.2025.1715912

Duckweeds (Lemnaceae) are among the smallest flowering plants with ecologically significant components of freshwater ecosystems, yet their extreme morphological reduction complicates species identification, biogeographic classification, and invasion assessments. This study integrates multi-locus molecular phylogenetics and species distribution modeling (SDM) to clarify the evolutionary relationships, native versus non-native status, and climate-driven range dynamics of duckweed species in South Africa. Phylogenetic reconstruction based on five plastid markers (*matK, rbcL, rpl16, trnK-3'*, and *trnK-5'*) resolved two well-supported subfamilies (Lemnoideae and Wolffioideae) and confirmed the monophyly of the genera *Lemna*, *Landoltia*, *Spirodela*, *Wolffia*, and *Wolffiella*. Of the 38 taxa analysed, nine were identified as native and 29 as non-native, providing new evidence that *Lemna minor* and *Lemna gibba*, previously regarded as invasive in South Africa, are native species. Ecological niche models developed using MaxEnt and bioclimatic variables projected current and future habitat suitability under four Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5, SSP3-7.0, SSP5-8.5) across three global climate models (MIROC6, EC-Earth3-Veg, and UKESM1-0-LL). Current suitability was found to be the highest in the coastal provinces (KwaZulu-Natal, Eastern Cape, and Western Cape). Future projections revealed model-dependent outcomes, with MIROC6 and EC-Earth3-Veg predicting net expansion of climatically suitable habitat, particularly in inland provinces such as Mpumalanga, Limpopo, North-West, and Gauteng while UKESM1-0-LL consistently predicts contraction. The congruence between phylogenetic identity and projected range shifts highlights regions and freshwater systems vulnerable to future duckweed invasions. By integrating evolutionary history with climate projections, this study provides a robust framework for refining invasive species management, conserving native freshwater flora, and guiding adaptive conservation planning under climate change in South Africa.

KEYWORDS

climate change, duckweed, freshwater ecosystems, invasive aquatic plants, lemnaceae, phylogenetic tree, species distribution modeling (SDM)

1 Introduction

Freshwater ecosystems cover less than 1% of the Earth's surface supporting over 12% of all faunal and floral species (Dijkstra et al., 2014; Ahmed et al., 2022). Despite their significant ecological and socio-economic value, these ecosystems represent some of the most vulnerable ecosystems globally. This is primarily due to factors such as habitat degradation, pollution, overexploitation, biological invasions, and climate change impacts (Ahmed et al., 2022; Bănăduc et al., 2023). Biological invasions and climate change are synergistic drivers of biodiversity loss, particularly in aquatic environments (Weiskopf et al., 2020; Carosi et al., 2023). Invasive aquatic plants, such as duckweeds (family Lemnaceae), exemplify this threat.

Duckweeds are the world's smallest angiosperms with a size range of 1–15 mm (Edelman et al., 2020; Ziegler et al., 2023). They are fast-growing plants that can double their biomass within 30 hrs and are free-floating macrophytes that are capable of forming dense water surface mats (Wang et al., 2014). Duckweed blooms usually disrupt native biodiversity, alter nutrient dynamics, and impair water quality (Ceschin et al., 2019; Zhou et al., 2023). Furthermore, their morphological simplicity and rapid vegetative reproduction make them both ecologically impactful and taxonomically challenging (Senayai et al., 2025).

The accurate classification of aquatic plant species, particularly duckweeds, is fundamental to effective ecosystem management and biodiversity conservation (Friedjung Yosef et al., 2022). Native duckweeds contribute to ecosystem functioning and biodiversity, whereas non-native species often disrupt ecological processes and increase management costs (Ceschin et al., 2019). However, misclassification between the two can lead to inappropriate interventions, including the removal of native species mistakenly identified as invasive. Accurate identification of species is essential for setting conservation priorities, implementing effective invasive species control measures, and improving predictive modeling of ecosystem responses to climate change (Hoveka et al., 2016; Konwar et al., 2023). Moreover, understanding species origins and evolutionary relationships provides insight into introduction pathways and adaptive traits linked to invasiveness (Qi et al., 2023).

According to Hill et al. (2020), South Africa is recognized as one of the most biologically invaded countries in the world and is particularly vulnerable to aquatic invasions. Duckweed species have been introduced through anthropogenic pathways such as the ornamental plant trade, wastewater discharge, and agricultural runoff (Martin and Coetzee, 2011; Hill et al., 2020). Compounding this issue is the accelerating pace of climate change, which is expected to shift the climatic suitability of habitats, potentially facilitating the expansion of invasive species into new regions (Hoveka et al., 2016). In response to these shifting environmental conditions, predictive tools are becoming increasingly vital for anticipating the potential spread of invasive species.

Species Distribution Models (SDMs), particularly those based on the Maximum Entropy (MaxEnt) algorithm, have emerged as powerful tools for predicting species distributions under current and future climatic scenarios (Mahmoud et al., 2025). This is usually done by linking known species occurrences with environmental factors such as climate and topography (Benavides Rios et al., 2024). This has enabled researchers to understand and predict habitat suitability. When integrated with molecular phylogenetic data, SDMs can provide insights into both evolutionary relationships and ecological responses of species to environmental change (Lu and Rao 2024). However, few studies have applied this integrative approach to aquatic plants in Africa, and even fewer have focused on duckweeds.

Therefore, this study integrates molecular phylogenetics and ecological niche modeling to first accurately delineate species and clarify their native or non-native status using a multi-locus phylogenetic approach, and then to project how climate change may alter their distributions in South Africa. Specifically, the objectives of this study were to reconstruct the evolutionary relationships among duckweed species using five chloroplast DNA markers (*matK*, *rbcL*, *rpl16*, *trnK 3'*, *trnK 5'*) and to distinguish between native and non-native duckweed taxa in South Africa. This study also assessed the current and future distribution of duckweed species under multiple climate change scenarios using SDMs. Finally, the study identifies regions and freshwater bodies at risk of future duckweed invasions to inform conservation planning and invasive species management. By elucidating the phylogenetic structure and climate-driven distribution dynamics of duckweeds, this study provides a critical foundation for biodiversity conservation and development of adaptive management strategies in the face of global environmental change.

2 Materials and methods

2.1 Molecular data collection and sampling

Molecular datasets were compiled using previously published sequences and newly collected data. A total of 33 taxa (165 samples) were obtained from GenBank/NCBI based on previously published sequence data (Les et al., 2002). Field-collected specimens were obtained between March and May 2021 from three provinces in South Africa (Figure 1): North-West (Hartebeespoort Dam, GPS: -25.7386, 27.8725), Gauteng (Walter Sisulu Botanical Garden, GPS: -26.0933, 27.8372; Florida Dam, GPS: -26.1711, 27.8914) and Mpumalanga (Bankenveld Golf Club, Emalahleni, GPS: -25.8742, 29.2331). Duckweed specimens were isolated from natural surface mats collected from freshwater bodies. Upon collection, fronds were rinsed in sterile distilled water to remove debris and loosely attached organisms. Surface sterilization was performed using a 1% sodium hypochlorite (NaOCl) solution for 2 minutes, followed by three rinses in sterile distilled water. The collectors comprised of representatives from South African National Biodiversity Institute (SANBI), Water Research Council (WRC), and the Department of Water Affairs. Habitat notes were recorded for each site, indicating slow-moving freshwater bodies with high nutrient loads and duckweed prevalence.

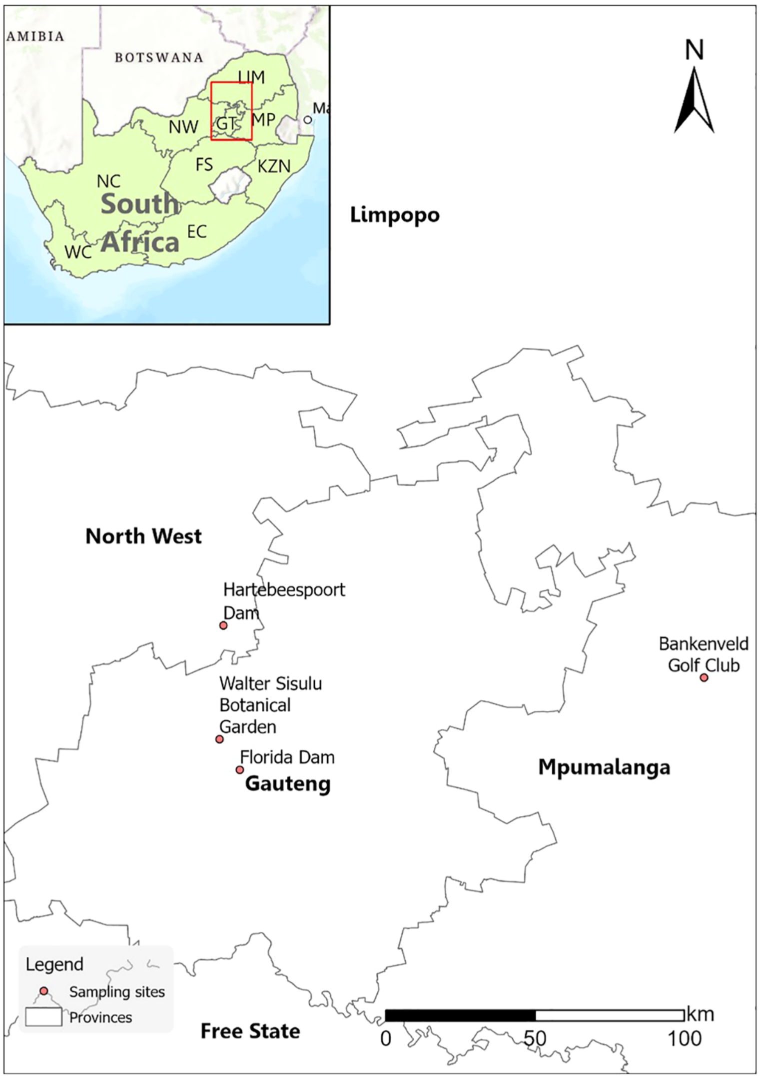

FIGURE 1
Sampling locations of duckweed species across South African provinces. NC, Northern Cape; WC, Western Cape; FS, Free State; MP, Mpumalanga; GT, Gauteng; NW, North-West; LIM, Limpopo; KZN, KwaZulu-Natal; EC, Eastern Cape.

We collected 20 taxa during field surveys, with approximately 10 individual fronds sampled per taxon from different habitats within each province (North-West, Gauteng, Mpumalanga). These replicates were intended to capture intraspecific genetic variation and reduce the risk of contamination or misidentification, given the high morphological similarity among duckweed species. This approach was necessary to ensure robust phylogenetic resolution and minimize errors caused by cryptic hybrids or mixed mats. Field collection was conducted under ethics clearance granted by the University of South Africa-College of Agriculture and Environmental Science Health Research Ethics Committee (Permit ID: 2021/CAES_HREC/130), valid from 06/09/2021 to 31/08/2024. All specimens were pressed, labelled, and deposited at the University of South Africa Herbarium.

DNA extraction was performed using Zymo Research kits, and sequencing was conducted by Inqaba Biotechnical Industries, Pretoria, South Africa. For phylogenetic reconstruction, PCR products were directly Sanger sequenced. Subcloning was not employed, as this study utilized non-recombining plastid DNA regions where direct sequencing is the standard method for recovering the predominant haplotype for species-level phylogenies (Les et al., 2002). Voucher numbers for field-collected specimens are listed in Supplementary Table S1 and marked with asterisks (*). GenBank accession numbers for previously published sequences by Les et al. (2002) are also included. The molecular matrix is available as Supplementary Material (DNA matrix; available at https://doi.org/10.6084/m9.figshare.31095493 and https://doi.org/10.6084/m9.figshare.31073842).

2.2 DNA extraction, amplification and sequencing

Genomic DNA was extracted from 0.1 - 0.15 g of fresh plant tissue using the Plant/Seed DNA MiniPrep Kit (Zymo Research, USA) following the manufacturer's protocol. To assess genetic variation, five chloroplast DNA regions, *matK*, *rbcL*, *rpl16*, *trnK* (3′), and *trnK* (5′) - were amplified using ReadyMix Master Mix (Advanced Biotechnologies, UK) supplemented with 3.2% BSA to enhance PCR efficiency. The selection of these five plastid regions was based on their established utility and proven effectiveness for resolving phylogenetic relationships within the Lemnaceae family (Les et al., 2002; Tippery and Les, 2020). This specific combination of markers provides a range of evolutionary rates, which helps in resolving relationships at both deep and shallow taxonomic levels within the duckweed phylogeny. Furthermore, using this standardized set of loci allowed for the direct integration of our new sequence data with the extensive published dataset from (Les et al., 2002), ensuring robust phylogenetic inference and comparability. Each 25 µL PCR reaction contained: 12.5 µL ReadyMix Master Mix (containing Taq DNA polymerase, dNTPs, and buffer), 0.5 µL of each primer (10 µM), 0.8 µL BSA (3.2% w/v), 2 µL template DNA (~20 ng), and nuclease-free water to volume. Thermal cycling profiles were optimized per locus:

*mat*K and *rbc*L: Initial denaturation at 95°C for 1 min 15 s; 30 cycles of 95°C for 30 s, 55°C for 2 min, 72°C for 2 min 15 s; final extension at 72°C for 5 min.

rpl16 and *trnK* introns: Initial denaturation at 95°C for 45 s; 35 cycles of 95°C for 45 s, 52°C for 45 s, 72°C for 45 s; final extension at 72°C for 5 min.

PCR products were verified on 1% agarose gels stained with ethidium bromide and sequenced by Inqaba Biotechnical Industries (Pretoria, South Africa). The same five plastid markers (*mat*K, *rbc*L, *rpl*16, *trn*K-3′, *trn*K-5′) used for PCR amplification were also employed for sequencing. This ensured consistency between amplification and downstream phylogenetic analysis.

Overall, the final dataset included 39 currently recognized taxa representing five genera: *Wolffiella, Wolffia, Lemna, Spirodela*, and *Landoltia* which are within the Lemnaceae family. These taxa encompassed representatives from both subfamilies, Lemnoideae and Wolffioideae, resulting in a total of 195 samples used for phylogenetic analyses.

2.3 Phylogenetic analysis

Sequences were assembled and edited using Sequencher® version 5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA). Alignments were performed using MUSCLE and manually refined using PAUP* v4.0b10 (Swofford, 2002). In addition, Maximum Parsimony (MP) analyses were conducted using heuristic searches with 1000 random addition replicates and tree bisection-reconnection (TBR) branch swapping and bootstrap support was estimated using 1000 replicates. Bayesian Inference (BI) was performed in MrBayes v3.2.7 (Ronquist and Huelsenbeck, 2003) using four Markov Chain Monte Carlo (MCMC) chains run for 10 million generations. The best-fit substitution model was then determined using the jModelTest. Trees were visualized in FigTree v1.4.4 (Rambaut, 2018) and consequently the taxonomic status (native vs. non-native) was verified following the guideline of Germishuizen and Meyer (2003). The phylogenetic tree was rooted using *Spirodela intermedia*, *Spirodela polyrrhiza* and *Landoltia punctata* (Tippery et al., 2021) that provided an appropriate evolutionary baseline for rooting and ensuring accurate inference of character polarity.

2.4 Determination of biogeographic status

The determination of native or non-native status to the duckweed species identified in our phylogeny was based on a synthesis of authoritative regional references. The primary source for status classification was the comprehensive floristic checklist of Germishuizen and Meyer (2003). To account for more recent taxonomic and distributional updates, this was supplemented by consulting the South African National Biodiversity Institute (SANBI) Red List assessments (e.g. Cholo and Foden (2006); Mtshali et al. (2017)), and invasive species alerts (ARC-PPRI, 2010). As well as the most recent global taxonomic authority, Plants of the World Online (POWO, 2025). In cases of conflicting information between sources, priority was given to the most recent SANBI Red List assessment, as it represents the current expert consensus on a species' status and threat level.

2.5 Species occurrence and environmental data

The occurrence records of duckweed species in South Africa were retrieved from the Botanical Research and Herbarium Management System (BRAHMS; https://herbaria.plants.ox.ac.uk/bol). All duplicate entries were identified and excluded from the dataset prior to the analysis the final curated dataset comprised a total of 87 unique occurrence records.

Climatic data for both current and future scenarios were obtained from the WorldClim database (Fick and Hijmans, 2017). The current climate data (representing 1970–2000) and the future climate projections for 2080 were sourced at a uniform spatial resolution of 30-second (~1 km²) This ensured consistency in the grain of analysis between current and future scenarios. The future projections were based on three Global Circulation Models (GCMs): Model for Interdisciplinary Research on Climate (MIROC6) (Tatebe et al., 2019), Earth Consortium System Model (EC-Earth3-Veg) and UKESM1-0-LL. MIROC6 was selected as a representative of high climate-sensitivity models (Tatebe et al., 2019), EC-Earth3-Veg was chosen for its integrated vegetation-climate feedbacks relevant to habitat modeling (Döscher et al., 2022), and UKESM1-0-LL was included for its comprehensive Earth System processes and detailed aerosol modeling, which are critical for simulating Southern African rainfall (Sellar et al., 2019). All environmental variable rasters (Table 1) were subsequently processed in ArcGIS Pro 2.8.3 (Environmental Systems Research Institute, Redlands, CA, USA) to ensure identical geographic bounds and alignment for the study region.

The study utilised four Shared Socioeconomic Pathways (SSPs), which represent alternative scenarios of greenhouse gas emissions

TABLE 1 Bioclimatic variables applied in species distribution models (SDMs) to predict the occurrence of duckweed species in South Africa.

Bioclimatic variable code	Meaning
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (×100)
BIO4	Temperature Seasonality (standard deviation ×100)
BIO5	Maximum Temperature of Warmest Month
BIO6	Minimum Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
-BIO19	Precipitation of Coldest Quarter

and socio-economic development (Meinshausen et al., 2020). SSP126 describes a low-emission pathway with strong climate mitigation and sustainable development whereas SSP245 represents an intermediate pathway with moderate emissions and development (Van Vuuren et al., 2017). SSP370 is a high-emission pathway associated with regional rivalry and limited climate action, and SSP585 represents a very high-emission, fossil-fuel-intensive future with minimal mitigation (Tang et al., 2023). The values of minimum temperature, maximum temperature, and precipitation were processed for four Shared Socioeconomic Pathways (SSPs: 126, 245, 370, and 585) to assess potential changes in climatic suitability across South Africa.

2.6 Ecological niche modeling

Species distribution models for current and future distributions of duckweed species were developed using MaxEnt version 3.4.4 (Phillips et al., 2017). The software was accessed via the American Museum of Natural History's biodiversity informatics portal (https://biodiversityinformatics.amnh.org/open_source/maxent/). The software estimates species distributions by applying the principle of maximum entropy to presence-only data (Phillips et al., 2006). Prior to model development, all environmental variables were tested for spatial autocorrelation to address issues of multicollinearity. To mitigate the effects of multicollinearity, we performed a sequential variable selection process. Firstly, all 19 bioclimatic variables were initially screened in a preliminary MaxEnt run, and only those with a non-zero contribution to the model were retained (Table 2). All the variables had an above zero contribution to the modeling. We removed two variables from further modeling Bio 1 and Bio 7 because they contributed 0 to model permutation importance. The distribution of duckweed species were mainly influenced by Bio 2 (Mean Diurnal Range (Mean of monthly (max temp - min temp))), Bio 12 (Annual Precipitation) and Bio 14 (Precipitation of Driest Month). Secondly, these retained variables were subjected to a pairwise Pearson's correlation analysis (Figure 2). Following established thresholds (Dormann et al., 2013; Zeng et al., 2016), any variable pair with a correlation coefficient of $|r| > 0.8$ was considered highly collinear (Graham, 2003; Dormann et al., 2013). From each correlated pair, the variable with the greater relative contribution from the preliminary model run was retained for final analysis. This procedure ensured that the final set of predictors used in the conclusive MaxEnt models was both ecologically informative and statistically robust.

To mitigate the effects of spatial sampling bias, where occurrence records are clustered in easily accessible areas, we implemented a bias correction method. We created a spatial bias file by generating a kernel density surface from all duckweed occurrence records in our dataset. This file was then used in MaxEnt to weigh the selection of background (pseudo-absence) points, ensuring they were drawn from a similar spatial bias as the presence data. This approach, known as target-group background sampling, helps the model distinguish the environmental niche of a species from the underlying bias in collection effort (Phillips et al., 2009). For model calibration, 75% of occurrence records were randomly selected for training and 25% reserved for testing, with 15 subsampling replicates run to assess variability in model performance. The maximum number of iterations was set to 5000 to ensure convergence. Model outputs were generated in a logistic distribution, yielding probability scores ranging from 0 (climatically unsuitable) to 1 (highly suitable), and prediction maps were produced using the 10th percentile training presence threshold (Phillips and Dudík, 2008). Model performance was evaluated using both threshold-dependent and threshold-independent methods, with the area under the curve (AUC) metric serving as the primary measure of accuracy. However, recognizing that AUC weights commission and omission errors equally and may overestimate performance (Escobar et al., 2018), our primary ecological inferences were based on a threshold-dependent analysis. We used the 10th percentile training presence threshold to generate binary habitat suitability maps, which allowed us to directly quantify range shifts in terms of habitat gain and loss. Values of 0.5 - 0.7 were interpreted as poor, 0.7 - 0.9 as acceptable, and >0.9 as high performance (Peterson et al., 2011). The relative contribution of predictor variables was further assessed using the jackknife test, which generates models by excluding, including, or

TABLE 2 Bioclimatic variables contributions to duckweed habitat suitability modeling in South Africa.

Variable	Percent contribution	Permutation importance
Bio 2	29.2	15.3
Bio 12	19.6	0.5
Bio 19	14.9	4.5
Bio 6	7.9	5.4
Bio 14	6.9	17.4
Bio 3	5.5	7.9
Bio 4	4.1	1.9
Bio 13	2.6	9.2
Bio 5	2.3	11.2
Bio 15	1.7	8.5
Bio 11	1.4	5.1
Bio 7	1.2	0
Bio 18	0.6	4
Bio 8	0.5	1.2
Bio 10	0.5	1.4
Bio 9	0.4	3.4
Bio 17	0.2	1.7
Bio 1	0.1	0
Bio 16	0.1	1.3

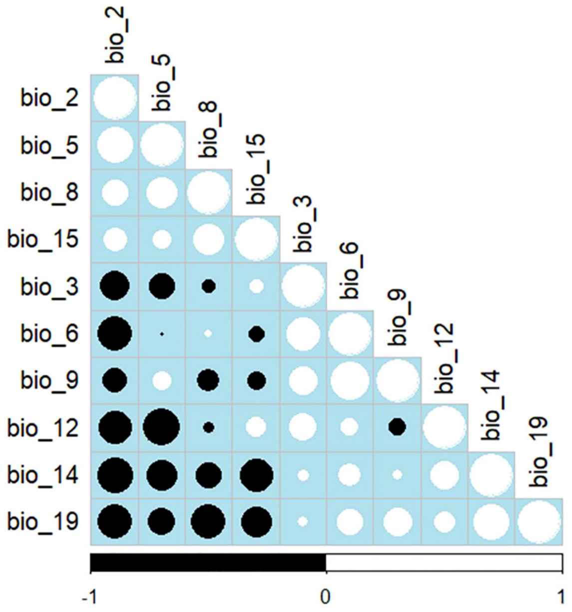

FIGURE 2
Pearson correlation coefficients for the environmental variables retained for the maximum entropy (MaxEnt) distribution modeling of Duckweeds in South Africa.

combining individual predictors to quantify their influence on training gain (Liao et al., 2017). This approach identified the most influential climatic variables for duckweed distribution under both the current and projected future climate scenarios.

2.7 Habitat suitability and range shift analysis

MaxEnt outputs for both current and future climate projections were converted from ASCII to the raster float format using ArcGIS Pro 2.8.3 (Environmental Systems Research Institute, Redlands, CA, USA). MaxEnt outputs for both current and future climate projections were converted from ASCII to raster format and all subsequent spatial analyses were performed using ArcGIS Pro 2.8.3 (Environmental Systems Research Institute, Redlands, CA, USA). Specifically, habitat suitability changes between scenarios were quantified using the spatial analyst and zonal statistics toolsets within the software. Differences in projected ranges were estimated as the net gain or loss of suitable habitat pixels, where positive values indicated range expansion (increased probability of occurrence in future climates) and negative values indicated range contraction (reduced probability of occurrence) (Hoveka et al., 2016).

3 Results

3.1 Phylogeny

The combined DNA matrix comprised five plastid regions (*rbcL, matK, rpl16, trnK* 3', and trnK 5'), totaling 4504 characters, of which 3262 were constant and 809 were parsimony-informative (Table 3). Among the plastid regions, *trnK* (5') contained the fewest parsimony-informative characters (69), followed by *rpl16* (104), *rbcL* (116), trnK (3') (165), and *matK* (355). Parsimony-uninformative characteristics were more abundant in *matK* (169) than in *trnK* (3') (95), *rpl16* (72), *rbcL* (55), and *trnK* (5') (42).

Using this dataset, a Maximum Parsimony phylogenetic tree was constructed, yielding a strong bootstrap support (91 BP) for the family Lemnaceae. Two major clades corresponded to the subfamilies Lemnoideae and Wolffioideae (Figure 3). Lemnoideae include four sections: Lemna, Alatae, Biformes, and Uninerves. Wolffioideae comprises six sections: Wolffia, Pseudorrhizae, Pigmentate, Wolffiela, Stipitatae, and Rotundae. The genus *Wolffiela* formed a highly supported clade (100 BP) containing Rotundae, Stipitatae, and *Wolffiela*, while the *Wolffia* clade (Wolffia, Pseudorrhizae, Pigmentate) showed 89 BP. *Spirodela polyrrhiza* and *Spirodela intermedia* were fully supported (100 BP) as outgroups (Figure 3).

The phylogenetic analysis provided the species-level resolution required to accurately assess the biogeographic status of duckweeds in South Africa. We mapped this status directly onto the phylogeny (Figure 3), which confirmed nine species as native. This included *Lemna aequinoctialis*, *Lemna minor*, *Lemna gibba*, and *Spirodela*

TABLE 3 Summary of DNA sequence characteristics for five plastid regions and the combined dataset used in the phylogenetic analysis of Lemnaceae.

Marker	No. of taxa	No. of included characters	No. of constant characters	No. of parsimony informative sites	No. of trees (Fitch)	No. of parsimony uninformative sites
*mat*K	38	1554	1030	355	880	169
*rpl*16	38	512	336	104	327	72
*rbc*L	38	1348	1177	116	319	55
*trn*K (3')	38	810	550	165	466	95
*trn*K (5')	38	280	169	69	205	42
Combined Plastids	38	4504	3262	809	2233	433

polyrrhiza in Lemnoideae, *Wolffiela hyalina*, *Wolffiela welwitschii*, *Wolffiela denticulata*, *Wolffia arrhizal* and *Landoltia punctata*. This analysis resolved previous taxonomic confusion, providing new evidence that *Lemna minor* and *Lemna gibba*, previously considered invasive, are in fact native. The remaining 29 species were non-native.

3.2 Current and future distribution of duckweed species

All variables showed a contribution greater than zero to the model. However, two variables (BIO1 and BIO7) were excluded from further modeling because they had zero permutation importance. The distribution of duckweed species (Table 2) was primarily influenced by BIO2 (Mean Diurnal Range; mean of monthly maximum–minimum temperature), BIO12 (Annual Precipitation), and BIO14 (Precipitation of the Driest Month). The current distribution of duckweed in South Africa is shown in Figure 4. It predominantly occurs along the eastern, southern, and southwestern coastal regions, including areas around Durban, Gqeberha, and Cape Town. Inland populations are more scattered, with significant presence near Johannesburg, Bloemfontein, and parts of the central plateau. The species is largely absent from arid regions such as the Karroo region.

Under the MIROC6 model (Figure 5), duckweed species in South Africa are projected to maintain extensive suitable habitat along the southern and eastern coasts across all scenarios. Under low-emission SSP1-2.6, the distribution is widespread and largely continuous, while intermediate SSP2-4.5 shows minor fragmentation in the interior. Higher emissions scenarios (SSP3-7.0 and SSP5-8.5) result in greater range contraction and fragmentation, particularly in northern and central regions, with coastal areas remaining the most stable habitats. These results indicate increasing vulnerability of inland populations under more severe climate change.

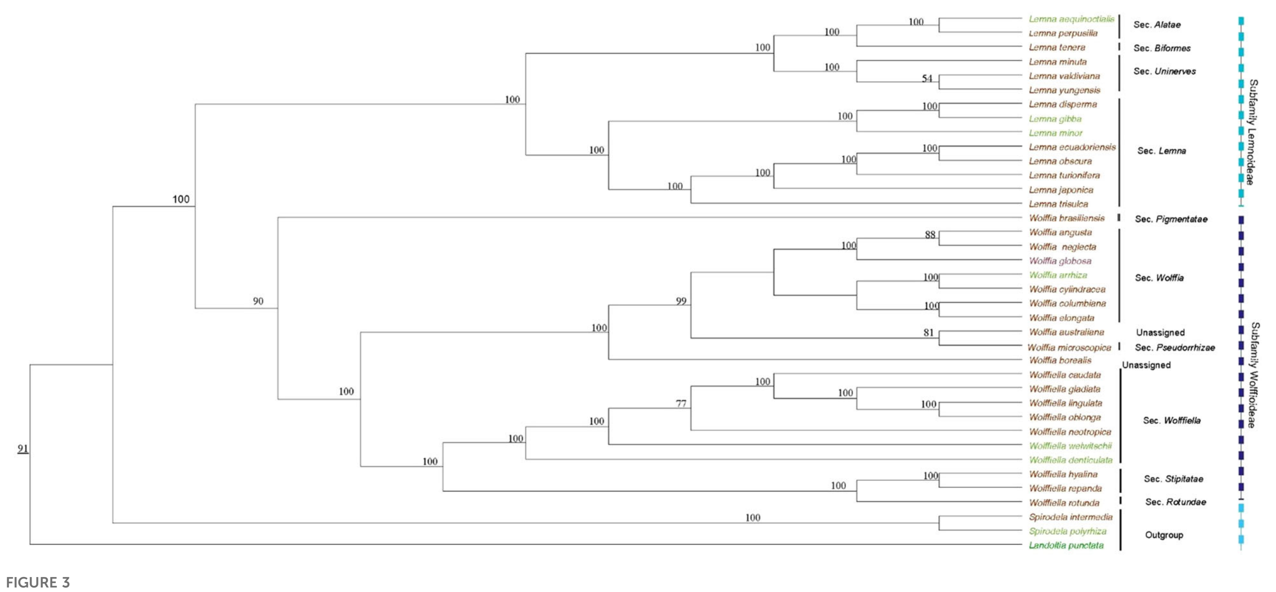

FIGURE 3
Maximum Parsimony (MP) phylogenetic tree of duckweed (Lemnaceae) species inferred from combined matK, rpl16, rbcL, trnK (3′), and trnK (5′) chloroplast regions. Bootstrap support values are shown above branches. Species are colour-coded by biogeographic status in South Africa, with native species shown in green and non-native species in red. Outgroup taxa are indicated.

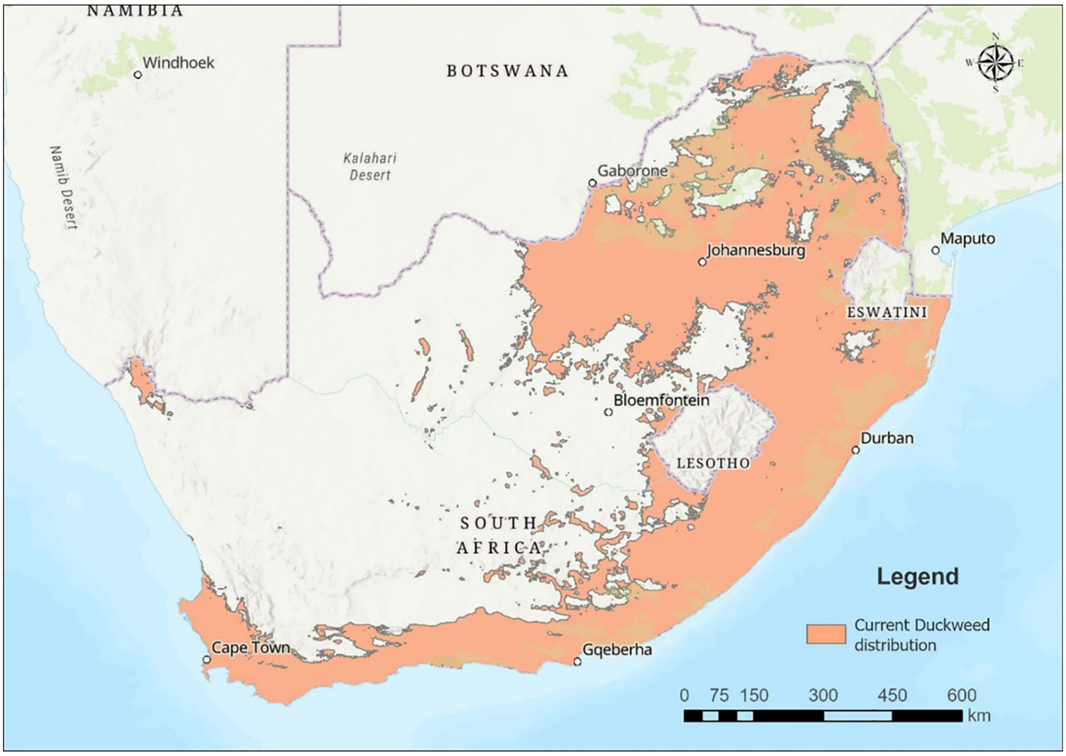

FIGURE 4
Current distribution of duckweed (Lemnaceae) species in South Africa.

Under the EC-Earth3 model (Figure 6), the projected distribution of the species in South Africa shows a clear decline with increasing emissions. Under SSP1-2.6, suitable habitat is widespread, while SSP2-4.5 shows moderate fragmentation. Higher-emission scenarios SSP3-7.0 and SSP5-8.5 result in pronounced habitat loss and fragmentation, with remaining suitable areas largely confined to the eastern and coastal regions, indicating strong climate-driven contraction.

According to the UKESM1-0-LL model (Figure 7), across all four SSP (a) SSP1-2.6, (b) SSP2-4.5, (c) SSP3-7.0, and (d) SSP5-8.5 scenarios the model consistently predicts a net contraction in total suitable area. Notable declines are projected for the eastern regions encompassing parts of KwaZulu-Natal, Mpumalanga, and the Free State.

In accordance to Table 4, projections based on MIROC6 indicate a consistent expansion of suitable area under all SSP scenarios, with increases ranging from +2.6% (SSP1-2.6) to +23.0% (SSP5-8.5). The largest gains are projected under higher-emissions scenarios (SSP2-4.5, SSP3-7.0, and SSP5-8.5), suggesting increased suitability under warmer future conditions. Similarly, EC-Earth3 projects moderate expansion across all scenarios, though increases are more constrained than those predicted by MIROC6. Projected gains range from +8.3% (SSP3-7.0) to +13.4% (SSP1-2.6), indicating relatively stable future suitability with limited sensitivity to emission intensity. In contrast, projections from UKESM1-0-LL consistently show a contraction of suitable area across all SSP scenarios. Reductions range from −8.7% (SSP1-2.6) to −11.1% (SSP2-4.5), suggesting that this model predicts decreased suitability under both low- and high-emissions futures.

3.3 Future of duckweed invasion in south african water bodies

Future projections indicate that several freshwater systems across South Africa are highly vulnerable to duckweed invasion, with notable spatial variation among the provinces (Table 5). Gauteng and North-West emerged as major hotspots, containing the highest number of dams and rivers predicted to fall within climatically suitable areas. In Gauteng, dams such as Roodeplaat, Rietvlei, Emmarentia, and Orlando, together with major rivers including Kliprivier, Blesbokspruit, and Pienaarsrivier, were identified as high-risk sites for infestation. Similarly, the North-West province showed extensive overlap between climatically suitable habitats and freshwater systems, with key dams (e.g., Hartbeespoort, Boskop, Molatedi) and numerous rivers (e.g., Hartsrivier, Groot-Maricorivier, Crocodile River) projected to be affected. Limpopo and Mpumalanga provinces also contained multiple vulnerable dams and rivers, particularly along the Olifants and Elands River systems, while the Free State was dominated by several medium-sized rivers such as the Wilgerivier, Renosterrivier, and Valsrivier, alongside the Vaal Dam on the provincial border. KwaZulu-Natal had fewer dams at risk but several rivers, including the Mfolozi, Hluhluwe, and Phongola, were identified as climatically suitable for future duckweed colonization. Collectively, these results suggest that densely dammed provinces with extensive river networks are particularly susceptible to future duckweed invasions, highlighting priority regions for monitoring and management interventions.

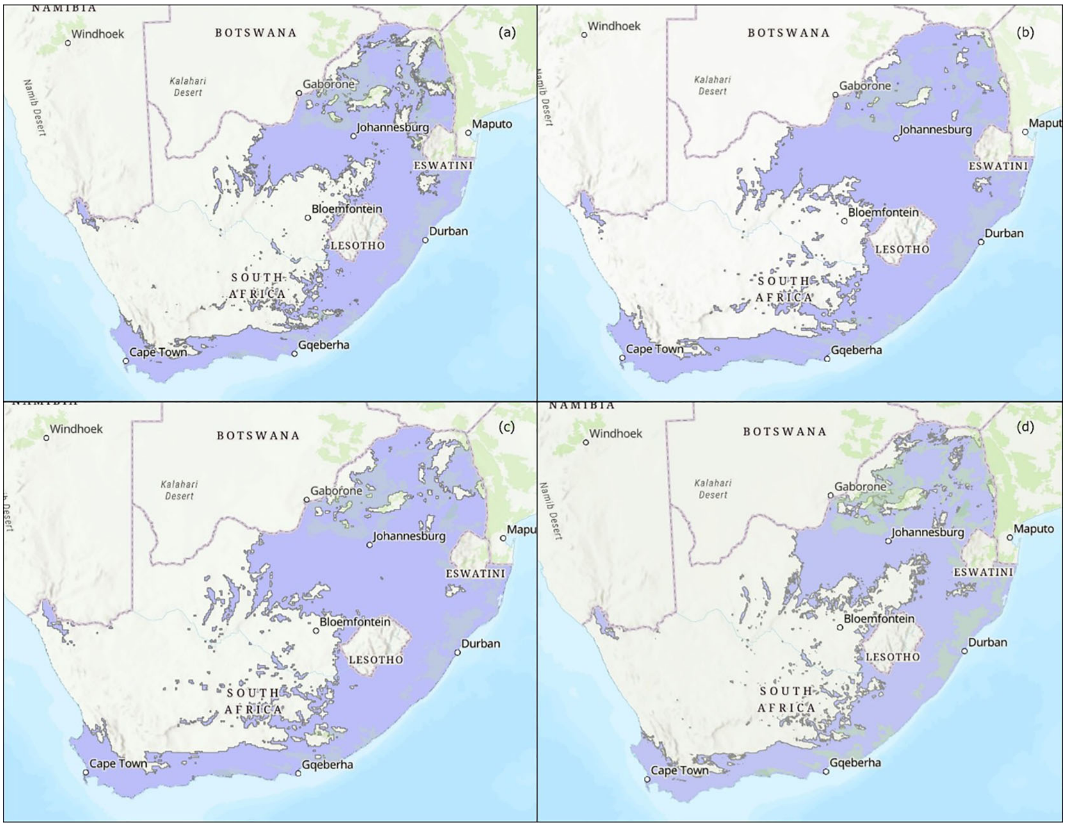

FIGURE 5
Future projections of climatically suitable habitat for duckweed in South Africa under the MIROC model for different SSP (Shared Socioeconomic Pathway) scenarios: **(a)** SSP1-2.6 **(b)** SSP2-4.5 **(c)** SSP3-7.0 and **(d)** SSP5-8.5.

These results highlight that phylogenetic identity (native vs. non-native) can inform predictions of the future spread of duckweed, providing a framework for prioritizing the monitoring and management of high-risk water bodies.

4 Discussion

This study bridges a critical gap by first resolving the taxonomic and biogeographic status of duckweeds in South Africa and then projecting their future habitat suitability under climate change. Having established that *Lemna minor* and *Lemna gibba* are native and delineated the status of 9 native and 29 non-native species, we provide a definitive baseline against which climate impacts can be assessed. The subsequent multi-model ensemble projections, however, reveal profound uncertainty in the future climatic suitability for these species, with the direction of change being influenced by the Global Climate (GC)Mselected.

4.1 Phylogeny

Duckweeds represent one of the most structurally reduced groups of angiosperms, and this reduction in morphological complexity makes species-level identification particularly challenging (Braglia et al., 2021). However, in the absence of clear diagnostic traits, reliance on molecular tools such as DNA sequencing has become essential for accurate species delimitation (Bog et al., 2019). However, earlier phylogenetic efforts were often constrained using a small number of markers, which limited the resolution of closely related taxa (Choi et al., 2019). The present study addressed these limitations by employing five plastid gene regions, thereby producing a more comprehensive and robust phylogeny of Lemnaceae. The phylogenetic reconstruction based on these markers corroborated earlier studies (Les et al., 2002; Tippery et al., 2015; Bog et al., 2019; Tippery and Les, 2020), consistently illustrating two distinct subfamilies of Lemnoideae and Wolffioideae. According to Bog et al. (2019), the Wolffioideae lineage comprises rootless taxa, whereas Lemnoideae includes species with variable numbers of roots. This study also reinforces the recognition of *Landoltia punctata* as a distinct genus, which is in line with previous findings (Les and Crawford, 1999). The phylogenetic separation of *Spirodela* and *Landoltia* from other duckweed taxa was further validated, underscoring the stability of these genera in molecular-based classifications.

Beyond phylogenetic tree topology, the results of the current study provide new insights into the biogeographic status of duckweed in South Africa. Earlier reports presented conflicting views on species origins, with some studies listing *Lemna minor* and *Lemna gibba* as non-native or invasive (Cholo and Foden, 2006;

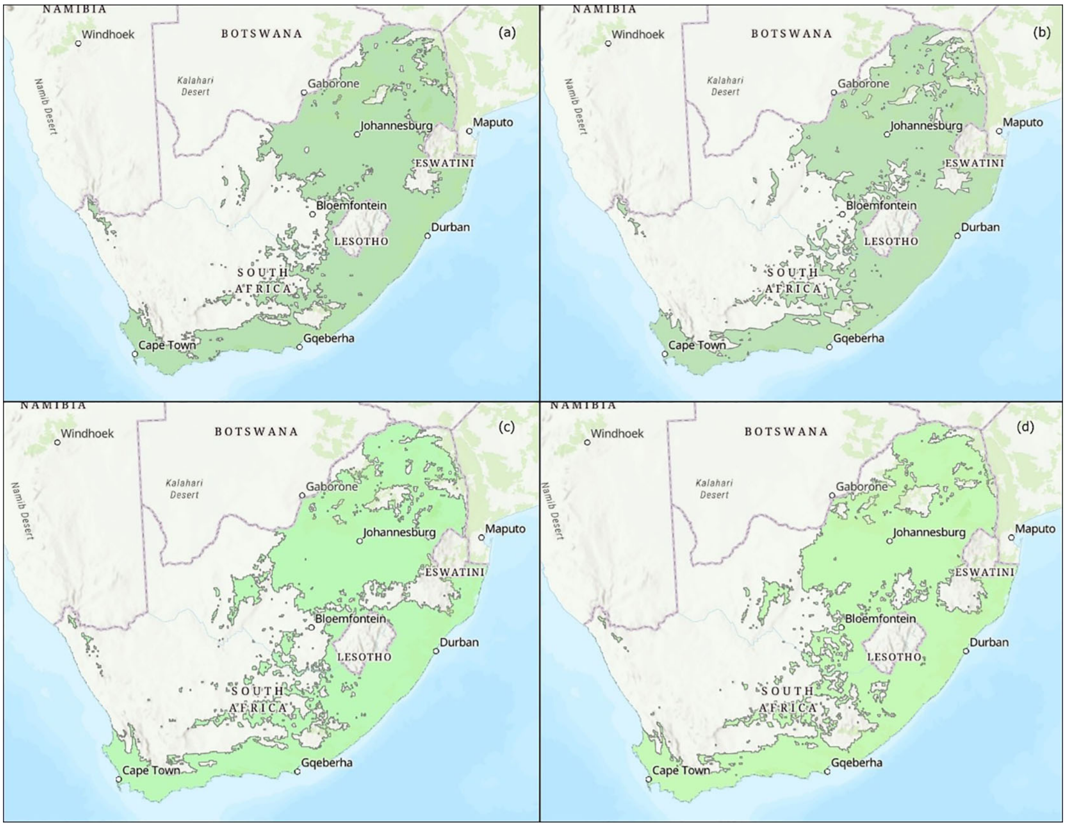

FIGURE 6
Future projections of climatically suitable habitat for duckweed in South Africa under the EC-Earth3 model for different SSP (Shared Socioeconomic Pathway) scenarios: **(a)** SSP1-2.6 **(b)** SSP2-4.5 **(c)** SSP3-7.0 and **(d)** SSP5-8.5.

ARC-PPRI, 2010; Mtshali et al., 2017). However, our findings indicate that both species are native to South Africa, aligning more closely with the earlier list of native species proposed by the Botanical Research Institute Pretoria (1980). Overall, the results demonstrated that of the 38 species assessed, 10 are native and 28 were non-native, refining earlier estimates (Germishuizen and Meyer, 2003). This clarification have significant implications for conservation policies, invasive species management, and ecological monitoring.

Despite these advances, several important challenges remain, first, resolving species complexes continues to be problematic due to the extreme morphological similarity among taxa, which complicates accurate delineation. Second, hybridization is known to occur frequently in duckweeds. This further obscures phylogenetic boundaries by introducing patterns of genetic introgression that can mislead tree reconstruction (Braglia et al., 2021). Future studies should integrate genome-wide data and population-level sampling to address these limitations and provide a more refined understanding of speciation, hybridization, and evolutionary history in Lemnaceae.

4.2 Climate change

Climate change has long been recognized as a major driver of the spread and persistence of aquatic non-native plants (Turbelin and Catford, 2021). In addition, human activities have significantly accelerated these changes, altering the ecological dynamics worldwide (Rai and Singh, 2020). For duckweed species, both dispersal ability and human-mediated introductions play critical roles in shaping their distribution in South Africa. Aquarium trade has emerged as a significant pathway for the introduction and spread of duckweed (Azan et al., 2015). As such, stronger monitoring and regulation of this activity should be prioritized, as it represents a key factor in promoting duckweed invasion across the country.

Climate change is a recognized catalyst for the spread and persistence of aquatic non-native plants, with human activities significantly accelerating these ecological shifts (Rai and Singh, 2020; Turbelin and Catford, 2021). For duckweeds in South Africa, the aquarium trade represents a critical human-mediated introduction pathway underscoring the need for stronger monitoring and regulation (Azan et al., 2015), Our species distribution models (SDMs) confirm that climate change strongly influences potential distributions, with spatially explicit outcomes.

While SDMs are valuable for anticipating invasion risks, key limitations must be acknowledged. First, models may underestimate expansion potential if species are not in climatic equilibrium with their current range (Václavík and Meentemeyer, 2012). Second, and critically, the absence of fine-scale aquatic variables, such as water flow, pH, and nutrient concentrations, which are not systematically

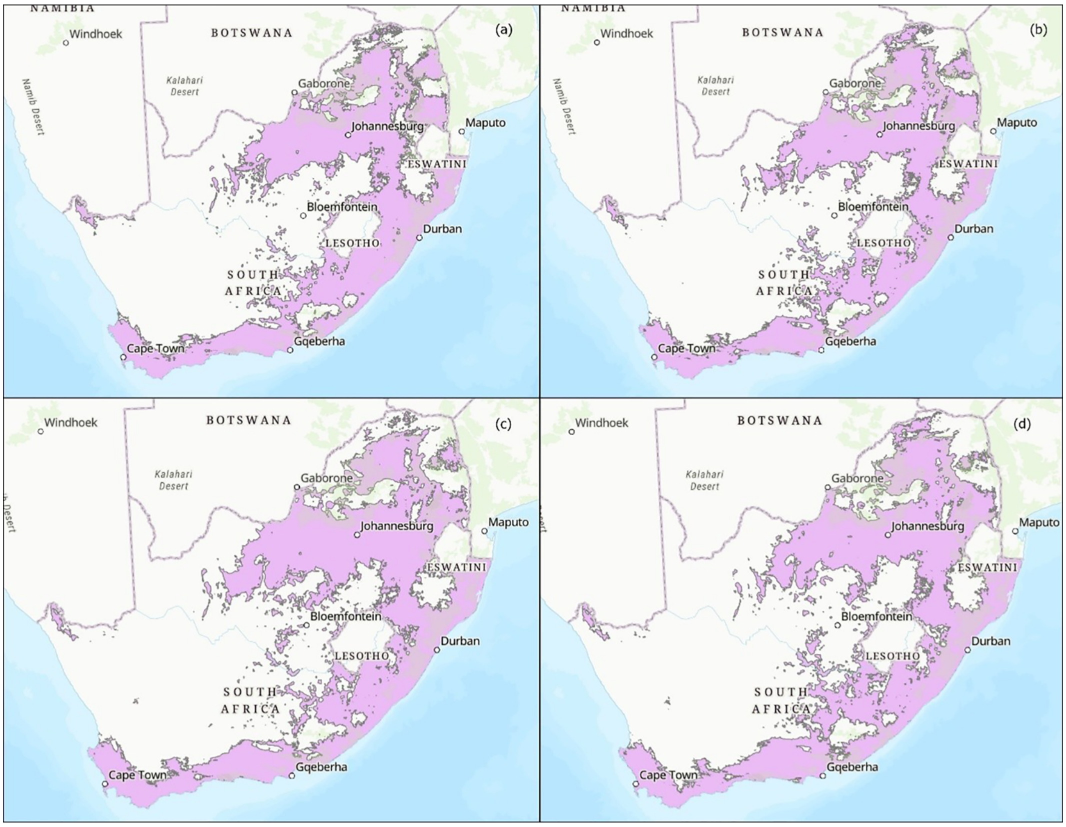

FIGURE 7
Future projections of climatically suitable habitat for duckweed in South Africa under the UKESM1-0-LL model for different SSP (Shared Socioeconomic Pathway) scenarios: **(a)** SSP1-2.6 **(b)** SSP2-4.5 **(c)** SSP3-7.0 and **(d)** SSP5-8.5.

TABLE 4 Projected changes in climatically suitable area (km²) for duckweed in South Africa under current conditions and future climate scenarios.

Model	Scenario	Future area (km²)	Δ Change from current (km²)	% Change
Current	-	550,898		-
MIROC6	SSP1-2.6	565,361	14,463	+2.6%
	SSP2-4.5	663,138	112,24	+20.4%
	SSP3-7.0	647,089	96,192	+17.5%
	SSP5-8.5	677,705	126,808	+23.0%
EC-Earth3	SSP1-2.6	624,724	73,826	+13.4%
	SSP2-4.5	611,163	60,265	+10.9%
	SSP3-7.0	596,851	45,953	+8.3%
	SSP5-8.5	603,245	52,347	+9.5%
UKESM1-0-LL	SSP1-2.6	502,818	-48,08	-8.7%
	SSP2-4.5	489,697	-61,2	-11.1%
	SSP3-7.0	498,642	-52,256	-9.5%
	SSP5-8.5	492,646	-58,252	-10.6%

TABLE 5 Freshwater systems projected to be affected by duckweed under future climate scenarios in South Africa.

Province	Dams	Rivers
Free State	Vaal (border of Gauteng and Free State), Saliba	Mopeli, Meulspruit, Moolmanspruit, Brandwaterrivier, Little Caledon River, Jordaanrivier, Asrivier, Liebenbergsvleirivier, Tierkloofrivier, Wilgerivier, Namahadi, Meulrivier, Dwaalspruit, Cornelisrivier, Holspruit, Spruittsonderdrif, Kommandospruit, Kliprivier, Wildemanspruit, Skoonspruit, Ventersspruit, Renosterrivier, Tweespruit, Valsrivier
Gauteng	Bon Accord, Roodeplaat, Rietvlei, Evaporation, Modderfontein (No. 1–4), Darrenwood, Emmarentia, Westdene, Cinderella, Monument, Eeufees, Princess, Fleurhof, New Canada, Orlando, Premiermyn	Rietspruit, Mooirivierloop, Kliprivier, Krokodilrivier, Steerpoortrivier, Blesbokspruit, Pienaarsrivier, Elandsrivier, Leeukloofspruit, Boekenhoutspruit, Osspruit
Limpopo	Donkerpoort, Matukwala, Phugwane, Mooigesig, Shangoni, Hoenderkop, Hudson Ntsanwisi, KaMakhaveni, Mintomeni	Pienaarsrivier, Nyl River, Tobiasspruit, Sterkrivier, Dwarsrivier, Sandspruit, Grootspruit, Mokolo, Poer se loop, Elandsrivier, Lepellane, Ngwaritsi, Mosesrivier, Nsama, Shingwedzi, Mutshindudi
Mpumalanga	Kruger, Robertson, Graham, Athlone, Pienaars, Doringpoort, Middelburg, Witbank, Clewer	Kameelrivier, Elandsrivier, Saalboomspruit, Wilgerivier, Swikerbosrantrivier, Watervalrivier, Klipspruit, Boesmanspruit, Vaalrivier, Langspruit, Kaalspruit, Blesbokspruit, Olifantsrivier, Klein-Olifantsrivier, Steelpoortrivier, Grootspruit, Selonsrivier
North-West	Taaibosspruit, Madikwane, Lehujwane, Kromellenboog, Marico-Bosveld, Molatedi, Linley's Poort, Swartruggens, Klein-Maricopoort, Klerkskraal, Boskop, Hartbeespoort	Droe Hartsrivier, Tlakgamenglaagte, Khudunkgwelaagte, Disipi, Mosita se Laagte, Modibeng, Setlagole, Mareetsane, Moloporivier, Hartsrivier, Klein-Hartsrivier, Jagspruit, Buisfonteinspruit, Kaalspruit, Taaibosspruit, Skoonspruit, Rietspruit, Mooirivierloop, Mooirivier, Sterkstroom, Crocodile River, Hexrivier, Leragane, Elandsrivier, Selonsrivier, Blakkloofspruit, Thulane, Groot-Maricorivier, Sandsloot, Doringrivier, Klein-Maricorivier, Ngotwane, Brakfonteinspruit, Klipspruit
KwaZulu-Natal	–	White Mfolozi, Mfolozi, Hluhluwe, Msunduzi, Mkuze, Nyawushane, Phongola, Ngwavuma

available for South Africa (Coetzee et al., 2009), presenting a significant constraint on predicting duckweed distributions. Despite this, our models provide a crucial early-warning system by identifying areas at highest risk. Notably, the projected range contractions align with a broader pattern observed in South African biota, including climate-induced mismatches in *Proteaceae* (Adedoja et al., 2024), contractions of indigenous medicinal plants (Tshabalala et al., 2022), and the potential for climate change to both reduce current invasions and create new invasion opportunities (Bezeng et al., 2017).

Our study bridges evolutionary history with future environmental change to shape duckweed management. The clarified biogeography confirming the native status of species like *L. minor* and *L. gibba*, provides the essential baseline against which climate impacts are assessed. The divergent climate projections from our multi-model ensemble (MIROC6 and EC-Earth3-Veg suggesting expansion, UKESM1-0-LL predicting contraction) create a spectrum of risk for both native and non-native taxa. Consequently, effective management requires an integrated perspective that considers evolutionary distinctiveness, current introduction pathways, and climate-driven distributional shifts. A precautionary approach is warranted: prioritizing *in situ* wetland protection for native species, enhancing surveillance in high-risk expansion zones, and regulating key introduction pathways like the aquarium trade.

The divergent projections can be attributed to how each GCM simulates the key climatic variables controlling duckweed ecology: primarily water availability and temperature. The expansion predicted by MIROC6, with its high climate sensitivity, likely stems from rising temperatures that enhance growth rates, reduce cold-season limitations, and increase year-round suitability of inland water bodies (Hoveka et al., 2016). These temperature-driven gains are likely to outweigh regional variability in rainfall, particularly in nutrient-rich and human-modified aquatic systems that facilitate rapid colonisation and persistence. EC-Earth3-Veg's integrated vegetation feedbacks may simulate altered hydrology or increased nutrient runoff, enhancing habitat suitability (Gu et al., 2024). Conversely, UKESM1-0-LL, with its comprehensive aerosol modeling and very high sensitivity, likely projects more severe regional drying and elevated evaporation rates, pushing conditions beyond the hydrologic thresholds required for duckweed persistence. This mechanism mirrors studies forecasting habitat contraction for other aquatic and arid-zone species due to intensified drought stress (Abubakar et al., 2024). Crucially, these model-specific climatic pathways apply equally to native and non-native species, meaning the future composition of duckweed communities may depend on which GCM's regional climate projection proves most accurate model.

Our results highlight how evolutionary history and environmental change interact to shape duckweed diversity in South Africa. Although phylogenetic analyses clarify the distinct clades and origins of native versus non-native taxa, climate projections demonstrate how ongoing environmental shifts may reinforce or challenge these biogeographic boundaries. Thus, the effective management of duckweeds requires an integrated perspective that considers both evolutionary distinctiveness and climate-driven changes in distribution.

4.3 Management implications

The combined insights from the phylogenetic and climate modeling components of this study have direct implications for the management of duckweed species in South Africa. Phylogenetic analysis clarified evolutionary relationships within Lemnaceae and confirmed that both native and non-native lineages occur in the region. Recognizing which species are native or invasive is critical for management decisions, as conservation strategies must aim to protect native biodiversity while preventing the establishment and spread of invasive taxa.

Climate projections further revealed that the distribution of duckweed species is likely to be altered under future scenarios, with some species contracting while others expand. Of particular concern is *Lemna aequinoctialis*, which showed potential for range expansion under multiple climate change scenarios, highlighting the need for early detection and monitoring in provinces such as Mpumalanga and Limpopo. Conversely, predicted contractions in KwaZulu-Natal and Eastern Cape suggest that native duckweed populations in these regions may be at risk, warranting targeted conservation interventions.

From a management perspective, several priorities emerge,

i. Surveillance and monitoring: Areas identified as at risk of duckweed expansion, particularly in inland provinces, should be prioritized for long-term monitoring programs. This is especially critical given the potential lag between climatic suitability and realized distribution due to dispersal and human-mediated introductions.
ii. Regulation of introduction pathways: The role of the aquarium trade in facilitating introductions (Azan et al., 2015) underscores the urgent need for tighter regulations and enforcement. Public awareness campaigns could further discourage the intentional release of duckweeds into natural water bodies.
iii. Integration of water-quality variables: Although not available for this study, the incorporation of aquatic-specific variables (e.g., flow rate, nutrient load and pH) in future models would substantially improve management planning by linking climatic suitability with habitat quality.
iv. Conservation of native species: Management plans should avoid the blanket removal of duckweeds, as several taxa have been confirmed to be native and form part of South Africa's natural aquatic ecosystems. Conservation strategies should focus on reducing the spread of invasive species, while maintaining the ecological roles of native duckweeds.
v. Adaptive management under climate change: Given that climate projections show both expansions and contractions, management must remain adaptive. This includes reassessing risk assessments and updating priority areas as new climate and ecological data become available.

Overall, these findings emphasize the importance of a dual approach: conserving phylogenetically and ecologically significant native species, while proactively mitigating the spread of invasive duckweeds under a changing climate. Such integrated strategies will not only protect aquatic biodiversity but also reduce the ecological and economic costs associated with invasive species management.

5 Conclusion

This study provides an integrated assessment of duckweed species in South Africa by combining phylogenetic analysis and species distribution modeling. Five plastid gene regions revealed two major subfamilies, with nine native and 29 non-native species. Climate projections indicate contraction in coastal provinces and potential expansion in inland areas such as Mpumalanga, Limpopo, North-West, and Gauteng.

These findings highlight the importance of monitoring at-risk regions, regulating introductory pathways, and protecting native species. Despite knowledge gaps-such as species complexes, hybridization, and the influence of water-specific variables, this study provides a strong foundation for managing duckweed under changing climatic conditions.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: NCBI GenBank. See Supplementary Table 1 for a list of accessions numbers.

Author contributions

UHN: Writing – original draft, Formal analysis, Visualization, Methodology, Investigation. TT: Writing – original draft, Visualization, Methodology, Investigation. LTM: Methodology, Writing – review & editing, Validation. BSB: Validation, Writing – review & editing.

Funding

The author(s) declared that financial support was received for this work and/or its publication. The authors acknowledge University of South Africa (Women in Research) for financial support.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The Handling Editor EC declared a past authorship with the author LM.

Generative AI statement

The author(s) declared that generative AI was used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1715912/full#supplementary-material.

SUPPLEMENTARY TABLE S1
List of accession and voucher numbers.

SUPPLEMENTARY TABLE S2
Duckweed molecular matrix dataset

References

Abubakar, I., Pantović, J. P., Šinžar-Sekulić, J. B., and Sabovljević, M. S. (2024). Modeling the distribution of the rare and red-listed halophytic moss species entosthodon hungaricus under various climate change scenarios in Serbia. *Plants*. 13, 3347. doi: 10.3390/plants13233347

Adedoja, O. A., Dormann, C. F., Coetzee, A., and Geerts, S. (2024). Moving with your mutualist: Predicted climate-induced mismatch between Proteaceae species and their avian pollinators. *J. Biogeography*. 51, 992–1003. doi: 10.1111/jbi.14804

Ahmed, A. S., Rahman, M. M., Hasan, M. N., and Hossain, M. (2022). Uncovering the hidden gems: A review of freshwater biodiversity in Bangladesh.

ARC-Plant Protection Research Institute, Agricultural Research Council (2010). *ARC-Plant Protection Research Institute, Focus on invasive aquatic plants* (Pretoria: South African Plant Invaders Atlas, ARC-Plant Protection Research Institute, Agricultural Research Council), 17, 1–17, 6.

Azan, S., Bardecki, M., and Laursen, A. (2015). Invasive aquatic plants in the aquarium and ornamental pond industries: A risk assessment for southern O ntario (C anada). *Weed Res.* 55, 249–259. doi: 10.1111/wre.12135

Bănăduc, D., Barinova, S., Cianfaglione, K., and Curtean-Bănăduc, A. (2023). 'Editorial: Multiple freshwater stressors—key drivers for the future of freshwater environments', *Front. Environ. Sci.* 11, 1143706. doi: 10.3389/fenvs.2023.1143706

Benavides Rios, E., Sadler, J., Graham, L., and Matthews, T. J. (2024). 'Species distribution models and island biogeography: challenges and prospects', *Glob. Ecol. Conserv.* 51, e02943. doi: 10.1016/j.gecco.2024.e02943

Bezeng, B. S., Morales-Castilla, I., van der Bank, M., Yessoufou, K., Daru, B. H., and Davies, T. J. (2017). Climate change may reduce the spread of non-native species. *Ecosphere*. 8, e01694. doi: 10.1002/ecs2.1694

Bog, M., Appenroth, K.-J., and Sree, K. S. (2019). Duckweed (Lemnaceae): its molecular taxonomy. *Front. Sustain. Food Syst.* 3, 117. doi: 10.3389/fsufs.2019.00117

Botanical Research Institute Pretoria (1980). *Duckweed/Damslyk (*Lemna gibba *L.) Family* (Pretoria: Botanical Research Institute, South Africa).

Braglia, L., Lauria, M., Appenroth, K. J., Bog, M., Breviario, D., Grasso, A., et al. (2021). Duckweed species genotyping and interspecific hybrid discovery by tubulin-based polymorphism fingerprinting. *Front. Plant Sci.* 12, 625670. doi: 10.3389/fpls.2021.625670

Carosi, A., Lorenzoni, F., and Lorenzoni, M. (2023). 'Synergistic effects of climate change and alien fish invasions in freshwater ecosystems: *A review', Fishes*. 8, 486. doi: 10.3390/fishes8100486

Ceschin, S., Abati, S., Traversetti, L., Spani, F., Del Grosso, F., and Scalici, M. (2019). Effects of the invasive duckweed Lemna minuta on aquatic animals: evidence from an indoor experiment. *Plant Biosystems-An Int. J. Dealing all Aspects Plant Biol.* 153, 749–755. doi: 10.1080/11263504.2018.1549605

Choi, B., Crisp, M. D., Cook, L. G., Meusemann, K., Edwards, R. D., Toon, A., et al. (2019). Identifying genetic markers for a range of phylogenetic utility–From species to family level. *PLoS One* 14, e0218995. doi: 10.1371/journal.pone.0218995

Cholo, F., and Foden, W. (2006). *Lemna gibba L. National Assessment: Red List of South African Plants version*. Available online at: http://redlist.sanbi.org/species.php?species=3874-2 (Accessed March 18, 2024).

Coetzee, J. A., Hill, M. P., and Schlange, D. (2009). Potential spread of the invasive plant Hydrilla verticillata in South Africa based on anthropogenic spread and climate suitability. *Biol. Invasions*. 11, 801–812. doi: 10.1007/s10530-008-9294-2

Dijkstra, K. D. B., Monaghan, M. T., and Pauls, S. U. (2014). 'Freshwater biodiversity and aquatic insect diversification', *Annu. Rev. Entomol.* 59, 143–163. doi: 10.1146/annurev-ento-011613-161958

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*. 36, 27–46. doi: 10.1111/j.1600-0587.2012.07348.x

Edelman, M., Colt, M., and Moraes, C. M. (2020). 'Duckweed: Tiny plants with enormous potential for agriculture and environment', *Plant Science*. 295, 110215. doi: 10.1016/j.plantsci.2020.110215

Escobar, L. E., Qiao, H., Cabello, J., and Peterson, A. T. (2018). 'Ecological niche modeling re-examined: a case study with the Darwin's fox', *Ecol. Evol.* 8, 4757–4770. doi: 10.1002/ece3.4014

Döscher, R., Acosta, M., Alessandri, A., Anthoni, P., Arsouze, T., Bergman, T., et al. (2022). The EC-Earth3 earth system model for the coupled model intercomparison project 6. *Geosci Model. Dev.* 15, 2973–3020. doi: 10.5194/gmd-15-2973-2022

Fick, S. E., and Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. climatology*. 37, 4302–4315. doi: 10.1002/joc.5086

Friedjung Yosef, A., Ghazaryan, L., Klamann, L., Kaufman, K. S., Baubin, C., Poodiack, B., et al. (2022). Diversity and differentiation of duckweed species from Israel. *Plants*. 11, 3326. doi: 10.3390/plants11233326

Germishuizen, G., and Meyer, N. (2003). *Plants of southern Africa: an annotated checklist* (Pretoria: National Botanical Institute).

Graham, M. H. (2003). Confronting multicollinearity in ecological multiple regression. *Ecology*. 84, 2809–2815. doi: 10.1890/02-3114

Gu, H., Ke, Y., Bai, Z., Ma, D., Wu, Q., Sun, J., et al. (2024). Improving hydrological simulations with a dynamic vegetation parameter framework. *Water* 16, 3335. doi: 10.3390/w16223335

Hill, M. P., Coetzee, J. A., Martin, G. D., Smith, R., and Strange, E. F. (2020). "Invasive alien aquatic plants in South African freshwater ecosystems," in *Biological Invasions in South Africa* (Springer International Publishing, Cham), 97–114.

Hoveka, L., Bezeng, B., Yessoufou, K., Boatwright, J., and van der Bank, M. (2016). Effects of climate change on the future distributions of the top five freshwater invasive plants in South Africa. *South Afr. J. Bot.* 102, 33–38. doi: 10.1016/j.sajb.2015.07.017

Konwar, P., Das, B., Saikia, J., Borah, T., Washmin, N., Siga, A., et al. (2023). Identifying conservation priority areas and predicting the climate change impact on the future habitats of endangered Nepenthes khasiana Hook. f. utilizing ecological niche modeling. *J. Nat. Conserv.* 74, 126436. doi: 10.1016/j.jnc.2023.126436

Les, D. H., and Crawford, D. J. (1999). *Landoltia (Lemnaceae), a new genus of duckweeds* (St. Louis, MO: Novon), 530–533.

Les, D. H., Crawford D.J., E. L., Gabel, J. D., and Kimball, R. T. (2002). Phylogeny and systematics of Lemnaceae, the duckweed family. *Systematic Bot.* 27, 221–240. doi: 10.1043/0363-6445-27.2.221

Liao, Y., Lei, Y., Ren, Z., Chen, H., and Li, D. (2017). Predicting the potential risk area of illegal vaccine trade in China. *Sci. Rep.* 7, 3883. doi: 10.1038/s41598-017-03512-3

Lu, W. X., and Rao, G. Y. (2024) 'Incorporating eco-evolutionary data into species distribution models to predict range shifts under climate change', *Science of the Total Environment*, 912, 169501. doi: 10.1016/j.scitotenv.2023.169501

Mahmoud, A. R., Farahat, E. A., and Hassan and Halmy, L. M. M. W. A. (2025). 'Predicting the future impact of climate change on the distribution of species in Egypt's Mediterranean ecosystems', *BMC Plant Biology*. 25, 644. doi: 10.1186/s12870-025-06630-7

Martin, G. D., and Coetzee, J. A. (2011). Pet stores, aquarists and the internet trade as modes of introduction and spread of invasive macrophytes in South Africa. *Water SA*. 37, 371–380. doi: 10.4314/wsa.v37i3.68488

Meinshausen, M., Nicholls, Z. R., Lewis, J., Gidden, M. J., Vogel, E., Freund, M., et al. (2020). The shared socio-economic pathway (SSP) greenhouse gas concentrations and their extensions to 2500. *Geoscientific Model. Dev.* 13, 3571–3605. doi: 10.5194/gmd-13-3571-2020

Mtshali, H., Cholo, F., and Foden, W. (2017). *Lemna minor L. National Assessment: Red List of South African Plants*. Available online at: http://redlist.sanbi.org/species.php?species=3874-3 (Accessed January 27, 2025).

Peterson, A. T., Soberon, J., Pearson, R. G., Anderson, R. P., Martinez-Meyer, E., Nakamura, M., et al. (2011). *Ecological Niches and Geographic Distributions*. (Princeton, NJ: Princeton University Press).

Phillips, S. J., Anderson, R. P., and Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259. doi: 10.1016/j.ecolmodel.2005.03.026

Phillips, S. J., and Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*. 31, 161–175. doi: 10.1111/j.0906-7590.2008.5203.x

Phillips, S. J., Dudík, M., and Schapire, R. E. (2009). 'Maximum entropy modeling of species geographic distributions', *Ecol. Model*. 190, 231–259. doi: 10.1016/j.ecolmodel.2005.03.026

Phillips, S. J., Dudík, M., and Schapire, R. E. (2017). Opening the black box: an open-source release of Maxent. *Ecography*. 40, 887–893. doi: 10.1111/ecog.03049

POWO (2025). *Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew*. Available online at: http://www.plantsoftheworldonline.org/ (Accessed November 11, 2025).

Qi, S., Wang, J., Zhang, Y., Naz, M., Afzal, M. R., Du, D., et al. (2023). Omics approaches in invasion biology: understanding mechanisms and impacts on ecological health. *Plants*. 12, 1860. doi: 10.3390/plants12091860

Rai, P. K., and Singh, J. (2020). Invasive alien plant species: Their impact on environment, ecosystem services and human health. *Ecol. Indic*. 111, 106020. doi: 10.1016/j.ecolind.2019.106020

Rambaut, A. (2018). *Figtree ver 1.4. 4* (Edinburgh: Institute of evolutionary biology. University of Edinburgh).

Ronquist, F., and Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*. 19, 1572–1574. doi: 10.1093/bioinformatics/btg180

Sellar, A. A., Jones, C. G., Mulcahy, J. P., Tang, Y., Yool, A., Wiltshire, A., et al. (2019). UKESM1: description and evaluation of the UK earth system model. *J. Adv. Modeling Earth Syst.* 11, 4513–4558. doi: 10.1029/2019MS001739

Senayai, A., Harnvanichvech, Y., Vajrodaya, S., Oyama, T., and Kraichak, E. (2025). Genetic and Morphological Variation Among Populations of Duckweed Species in Thailand. *Plants*. 14, 2030. doi: 10.3390/plants14132030

Swofford, D. L. (2002). *PAUP*: Phylogenetic Analysis Using Parsimony (* and other methods)[CD-ROM]. Version 4.0 b10. Evolution*. doi: 10.1111/j.0014-3820.2002.tb00191.x

Tang, J., Song, P., Hu, X., Chen, C., Wei, B., and Zhao, S. (2023). Coupled effects of land use and climate change on water supply in SSP–RCP scenarios: A case study of the Ganjiang river Basin, China. *Ecol. Indic*. 154, 110745. doi: 10.1016/j.ecolind.2023.110745

Tatebe, H., Ogura, T., Nitta, T., Komuro, Y., Ogochi, K., Takemura, T., et al. (2019). Description and basic evaluation of simulated mean state, internal variability, and climate sensitivity in MIROC6. *Geoscientific Model. Dev.* 12, 2727–2765. doi: 10.5194/gmd-12-2727-2019

Tippery, N. P., and Les, D. H. (2020). "Tiny plants with enormous potential: phylogeny and evolution of duckweeds," in *The duckweed genomes*. (Cham: Springer), 19–38.

Tippery, N. P., Les, D. H., Appenroth, K. J., Sree, K. S., Crawford, D. J., and Bog, M. (2021). Lemnaceae and Orontiaceae are phylogenetically and morphologically distinct from Araceae. *Plants*. 10, 2639. doi: 10.3390/plants10122639

Tippery, N., Les, D., and Crawford, D. (2015). Evaluation of phylogenetic relationships in L emnaceae using nuclear ribosomal data. *Plant Biol.* 17, 50–58. doi: 10.1111/plb.12203

Tshabalala, T., Mutanga, O., and Abdel-Rahman, E. M. (2022). Predicting the geographical distribution shift of medicinal plants in South Africa due to climate change. *Conservation*. 2, 694–708. doi: 10.3390/conservation2040045

Turbelin, A., and Catford, J. A. (2021). "Invasive plants and climate change," in *Climate change* (Amsterdam: Elsevier), 515–539.

Václavík, T., and Meentemeyer, R. K. (2012). Equilibrium or not? Modeling potential distribution of invasive species in different stages of invasion. *Diversity Distributions*. 18, 73–83. doi: 10.1111/j.1472-4642.2011.00854.x

Van Vuuren, D. P., Stehfest, E., Gernaat, D. E., Doelman, J. C., Van den Berg, M., Harmsen, M., et al. (2017). Energy, land-use and greenhouse gas emissions trajectories under a green growth paradigm. *Global Environ. Change*. 42, 237–250. doi: 10.1016/j.gloenvcha.2016.05.008

Wang, W., Haberer, G., Gundlach, H., Gläßer, C., Nussbaumer, T., Luo, M., et al. (2014). The Spirodela polyrhiza genome reveals insights into its neotenous reduction fast growth and aquatic lifestyle. *Nat. Commun.* 5, 3311. doi: 10.1038/ncomms4311

Weiskopf, S. R., Rubenstein, M. A., Crozier, L. G., Gaichas, S., Griffis, R., Halofsky, J. E., et al. (2020). Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Scie. Total Environ*. 733, 137782. doi: 10.1016/j.scitotenv.2020.137782

Zeng, Y., Low, B. W., and Yeo, D. C. (2016). Novel methods to select environmental variables in MaxEnt: A case study using invasive crayfish. *Ecol. Model.* 341, 5–13. doi: 10.1016/j.ecolmodel.2016.09.019

Zhou, Y., Stepanenko, A., Kishchenko, O., Xu, J., and Borisjuk, N. (2023). Duckweeds for phytoremediation of polluted water. *Plants* 12, 589. doi: 10.3390/plants12030589

Ziegler, P., Appenroth, K. J., and Sree, K. S. (2023) 'Survival strategies of duckweeds, the world's smallest angiosperms', *Plants*. 12, 2215. doi: 10.3390/plants12112215