




Assessing Present and Future Potential Distributions of *Sagittaria macrophylla* Zucc. and *Sagittaria latifolia* Willd. in Mexico under Various Climate Models and Timeframes

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Abstract

Anthropogenic climate change significantly impacts ecosystem health, biodiversity, and the life cycle and distribution of aquatic macrophytes. Mexican aquatic habitats for macrophytes are particularly vulnerable, with their degradation posing severe ecological risks for freshwater, wetland, and terrestrial ecosystems. This study analyzed the current and future distributions of *Sagittaria latifolia* and *S. macrophylla*, two crucial aquatic plant species in Mexico. Species distribution models (SDM) were used, incorporating bioclimatic and topographic variables, with projections for 2041–2060 and 2061–2080 using three Global Circulation Models. Niche overlap was also assessed. The Trans-Mexican Volcanic Belt emerged as a significant region for both species. We observed substantial variability among climate models. For *S. latifolia*, gains ranged from 1.708% (CNRM-CM6-1 model) to 74.806% (HadGEM3-GC31-LL model) for 2041–2060, while the highest loss was 44.11% (MPI-ESM1-2-HR model). Similarly, *S. macrophylla* showed gains up to 73.591% (MPI-ESM1-2-HR) and losses up to 19.734% (CNRM-CM6-1). These results highlight species-specific responses to future climate scenarios. Niche overlap analyses revealed that both species currently share up to 41% of their niches, with this overlap likely to continue in the future. This study provides insights into the potential impacts of climate change on species distributions, informing conservation and management strategies. Given *S. latifolia*'s native status and *S. macrophylla*'s endemic and threatened nature, understanding their distribution dynamics is crucial for conservation efforts. This research underscores the need to address climatic threats to ensure the survival of these key species and maintain the health of Mexican aquatic ecosystems.

Keywords Aquatic Flora · Climate Change · Environmental Niche Modeling · Trans-Mexican Volcanic Belt · Wetlands

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Resumen

El cambio climático antropogénico impacta significativamente la salud de los ecosistemas, la biodiversidad y el ciclo de vida y distribución de las macrófitas acuáticas. Los hábitats acuáticos mexicanos para macrófitas son particularmente vulnerables, y su degradación plantea graves riesgos ecológicos para los ecosistemas de agua dulce, humedales y terrestres. Este estudio analizó las distribuciones actuales y futuras de *Sagittaria latifolia* y *S. macrophylla*, dos especies de plantas acuáticas cruciales en México. Se utilizaron modelos de distribución de especies (SDM), incorporando variables bioclimáticas y topográficas, con proyecciones para 2041-2060 y 2061-2080 utilizando tres Modelos de Circulación Global. También se evaluó la superposición de nichos. El Eje Neovolcánico Transversal surgió como una región significativa para ambas especies. Observamos una variabilidad sustancial entre los modelos climáticos. Para *S. latifolia*, las ganancias oscilaron entre 1.708% (modelo CNRM-CM6-1) y 74.806% (modelo HadGEM3-GC31-LL) para 2041-2060, mientras que la mayor pérdida fue del 44.11% (modelo MPI-ESM1-2-HR). De manera similar, *S. macrophylla* mostró ganancias de hasta 73.591% (MPI-ESM1-2-HR) y pérdidas de hasta 19.734% (CNRM-CM6-1). Estos resultados destacan respuestas específicas de las especies a escenarios climáticos futuros. Los análisis de superposición de nichos revelaron que ambas especies actualmente comparten hasta un 41% de sus nichos, con esta superposición probablemente continuando en el futuro. Este estudio proporciona información sobre los impactos potenciales del cambio climático en las distribuciones de especies, informando estrategias de conservación y manejo. Dada la condición nativa de *S. latifolia* y la naturaleza endémica y amenazada de *S. macrophylla*, comprender sus dinámicas de distribución es crucial para los esfuerzos de conservación. Esta investigación subraya la necesidad de abordar las amenazas climáticas para asegurar la supervivencia de estas especies clave y mantener la salud de los ecosistemas acuáticos mexicanos.

Palabras clave Flora Acuática · Cambio Climático · Modelado de Nicho Ambiental · Eje Neovolcánico Transversal · Humedales

Introduction

Aquatic macrophytes provide multiple ecosystem services including water filtration, disease control, nutrient cycling, habitat provision, food and fiber production, biochemicals, natural medicines, and cultural benefits (Thomaz 2023). These services are most prominent in wetland ecosystems, where aquatic macrophytes contribute significantly to nutrient recycling, biogeochemical processes, biomass production, water resource management, carbon sequestration, environmental remediation, and bioenergy production (Lot and Novelo 2004; Hossain et al. 2017; Thomaz 2023). Globally, aquatic macrophytes have narrow distributions, with the Neotropical region being one of the areas with the highest diversity (Chambers et al. 2008, Murphy et al. 2019). In México, approximately 1,000 aquatic and submerged plant species exist (Rzedowski 1991), with variations in counts reported by different sources over the years. Lot et al. (1993) mentioned 747 hydrophytes, while Mora-Olivo et al. (2015) documented 1,344 species constituting the wetland flora across the country. Aquatic flora thrives in permanent water bodies such as lakes, dams, and rivers, but temporary wetlands like puddles also harbor rich biodiversity, particularly at the regional level (Mora-Olivo et al. 2013). While some hydrophytes have expansive, cosmopolitan distributions, others exhibit narrow ranges, are endemic, and are often confined to specific water bodies (Rzedowski 2006).

The genus *Sagittaria* (Alismataceae), includes 25 aquatic species distributed from Canada to southern Argentina and

Chile (Zepeda and Lot 2005). *Sagittaria macrophylla* Zucc. and *S. latifolia* Willd. are emergent rooted hydrophytes commonly found in shallow water bodies with minimal or no current (Bonilla-Barbosa 1992). Traditional use of both species, suggests they could be alternatives in human and animal diets (Zepeda and Lot 1999; Colón-Quezada 2009). *S. macrophylla*, endemic to Mexico, is concentrated in the Lerma River Basin and Valley of Mexico and currently is listed as Endangered according with Mexican regulations NOM-059-SEMARNAT-2019, while is not specifically listed as a protected species under international conventions or treaties. Factors contributing to its decline include population growth, habitat loss, and overexploitation. The tubers of *S. macrophylla*, have economic importance in the Lerma River region (Zepeda and Lot 2005). In contrast, *S. latifolia* boasts the widest distribution within the genus, ranging from Canada to South America and the Antilles, the overall distribution of the species seems unlikely to be reduced, despite the reduction in some areas, therefore IUCN considers it to be of Least Concern (Maiz-Tome 2016). In Mexico, the species occurs in 11 states, notably Lakes Chalco and Lerma in the State of Mexico (Zepeda and Lot 2005), but its presence in certain areas has decreased due to factors such as urban expansion, water desiccation, and pollution (Zepeda and Lot 2005).

Climate has been the primary driver of the current distribution of endemic freshwater macrophytes (Alahuhta et al. 2011; Dhir 2015; Knouft and Ficklin 2017; Viana 2017; Murphy et al. 2019), the impact of past climate change

caused expansions and contractions in the distribution areas of several endemic species (Murphy et al. 2019). Ongoing climate change worldwide influences distribution and abundance of species (Gutiérrez and Trejo 2014; Maciel-Mata et al. 2015). In aquatic habitats anthropogenic activities and climate change, induces environmental impacts such as accelerated eutrophication, changes in nutrient cycling, algal blooms, pollution, habitat fragmentation and extreme hydrological events (such as droughts and floods). These factors can have significant consequences for the health of aquatic ecosystems and their biodiversity and can impact the life cycle and distribution of macrophytic plants (Yuan et al. 2024). Given that projections suggest the disappearance of half of the planet's species in the coming decades, conservation efforts are imperative, especially amid habitat destruction and other anthropogenic factors (Mora-Olivo et al. 2013). The challenges that aquatic plants face regarding habitat suitability and distribution changes due to global change disturbances remain unclear. Our understanding of Mexico's aquatic vegetation has been incomplete, with wetland loss and human activities posing significant threats to the species richness (Mora-Olivo et al. 2013; Rzedowski 1991).

Understanding how the changing climatic conditions affecting aquatic plants distribution is crucial for enhancing conservation efforts and expanding our current knowledge of their impacts on aquatic plant species. To achieve these goals, this study utilized Species Distribution Models (SDM) to identify the current and future potential distributions of two *Sagittaria* species. This study hypothesizes that the climate change will reduce suitable habitats for these species in the future. In this study we aim to identify crucial bioclimatic and topographic variables that influence the current distribution of *S. macrophylla* and *S. latifolia* and predict how it might change under future climatic conditions. Furthermore, estimate the extent of environmental niche overlap and similarity among the two *Sagittaria* species, and the potential expansion or reduction in distribution of both species. By investigating these questions, this study aims to contribute to a better understanding of the factors influencing the distribution and environmental requirements of *Sagittaria* species and to provide insights into the potential impacts of future environmental changes on their survival and persistence.

Materials and Methods

Study Area

We determined the study area for SDM and established a calibration space for the models, referred to as M in the BAM diagram, which represents the accessible geographic

area for the species (Soberón and Peterson 2005, Franklin 2023). *Sagittaria* species was examined within distinct geographic areas to ensure the inclusion of suitable regions while avoiding biases related to uninhabited areas (Anderson 2015; Sillero and Barbosa 2021). To delineate the study areas, the boundaries of Mexico's physiographic provinces, available on the INEGI portal, were utilized. Using the ArcToolbox tool of ArcMap version 10.5, the desired areas were obtained and subsequently employed to delimit the climatic layers with R software (R Core Team 2023). For *S. latifolia*, the study area encompassed the provinces of Sonora, Sierra Madre Occidental, Tamaulipeca, the Costa of the Pacific, Southern Altiplano, Sierra Madre Oriental, the Gulf of Mexico, Yucatán, Peten, the Trans-Mexican Volcanic Belt, the Balsas Depression, Oaxaca, Sierra Madre del Sur, the Los Altos de Chiapas, and Soconusco. Since the study area should encompass relevant and accessible areas for the species (M), provinces corresponding to arid regions, where the species is unlikely to be found (Rzedowski and Rzedowski 2005; Rzedowski 2006), and inaccessible via dispersal, due to the temporal nature of water bodies (Murphy et al. 2019), were excluded from the analysis (Merow et al. 2013). For *S. macrophylla*, which is an endemic species, the study area included the provinces of Sierra Madre Occidental, Altiplano Sur, the Trans-Mexican Volcanic Belt, the Balsas Depression, and Sierra Madre del Sur. This choice was based on records confirming the species' distribution in the Lerma River Basin and Valley of Mexico (Rzedowski and Rzedowski 2005; Zepeda and Lot 2005).

Species Occurrence and Environmental Variables

Species occurrence records, along with geographical coordinates, were sourced from online databases, including the Global Biodiversity Information Facility (GBIF), iNaturalist, and field records provided by the Aquatic Plant Laboratory at the Faculty of Sciences, UAEMéx. To ensure robust analysis, only records spanning from 1990 to 2022 were considered; these records were aligned with the recommended reference period of 20 to 30 years but were adjustable based on research needs (Instituto Nacional de Ecología y Cambio Climático (INECC), 2022). Occurrence data cleaning was performed with the ntbox package (Osorio-Olvera et al. 2020) in R as follows: 1) occurrence data were previsualized to remove erroneous records or records out of the potential geographic range, 2) duplicate records were eliminated, and 3) to avoid pseudoreplication, the species distribution data were subsampled considering only records that were spaced at least 1 km apart, as this method has been shown to substantially reduce the degree of model overfitting (Seguardo et al. 2009; Boria et al. 2014). After data cleaning, 102 records were used for *S. latifolia* and 40 for *S. macrophylla*. Finally, the

accessible areas considered for each species were the biogeographic regions with records of the species or records close to their borders (Fig. 1).

Bioclimatic variables were obtained from WorldClim version 2.1 (Fick and Hijmans 2017) with a resolution of 1 km². Topographic variables (Fick and Hijmans 2017), such as elevation, slope, and aspect (slope and aspect), were extracted from Digital Elevation Models using ArcMap 10.5. All layers were processed in raster format with a 1 km resolution using the packages raster (Hijmans 2023) and rgdal (Bivand et al. 2023) for R software (version 4.2.3; R Core Team 2023). After a literature review and Pearson's correlation analysis was carried out with the ENMTools (Warren et al. 2010; Warren and Dinnage 2023) and usdm (Naimi et al. 2014) packages for R software, highly correlated variables were discarded ($r^2 > 0.7$, Dorman et al. 2013). Out of the 22 climatic and topographic variables obtained from the WorldClim platform, 11 were selected for further analysis due to their lack of correlation (Table 1). These variables include slope, annual mean diurnal range (Bio2), isothermality (Bio3), precipitation seasonality (Bio15), and precipitation of the warmest quarter (Bio18), which exhibited the lowest variance inflation factor (VIF) values, indicating minimal multicollinearity. Elevation was included in the analysis due to its relevance to the species' specific distribution range. The Pearson correlation heatmap (Fig. 1) illustrates the correlation values for all 22 variables. Despite recommendations to exclude certain bioclimatic layers due to potential spatial anomalies (Escobar and Craft 2016), we retained layers 8, 9, 18, and 19 within the 19 bioclimatic layers of WorldClim. Our analysis revealed moderate correlation

Table 1 Bioclimatic variables selected through variance inflation factor (VIF)

Bioclimatic variables	Abbreviation	VIF
Mean Diurnal Range (Mean of monthly (max temp—min temp))	Bio2	2.593
Isothermality (BIO2/BIO7) (×100)	Bio3	2.416
Mean Temperature of Wettest Quarter	Bio8	5.689
Mean Temperature of Driest Quarter	Bio9	6.131
Precipitation of Wettest Month	Bio13	6.776
Precipitation of Driest Month	Bio14	7.846
Precipitation Seasonality (Coefficient of Variation)	Bio15	3.93
Precipitation of Warmest Quarter	Bio18	3.539
Precipitation of Coldest Quarter	Bio19	5.896
Aspect		1.03
Slope		1.3

values (3.539 to 6.131), as demonstrated by the VIF and Pearson correlation coefficient results (Fig. 2).

Environmental Niche Modeling

Modeling of the environmental niche was carried out using the maximum entropy algorithm applied with Maxent 3.3.3 software (Phillips et al. 2006), with species-specific fits selected using the ENMeval 2.0 R package (Kass et al. 2023). The spatial distribution of a species can be modeled in MaxEnt uses correlative algorithms and occurrences of a given species in relation to various bioclimatic variables (Elith et al. 2011) and produces a suitability map showing

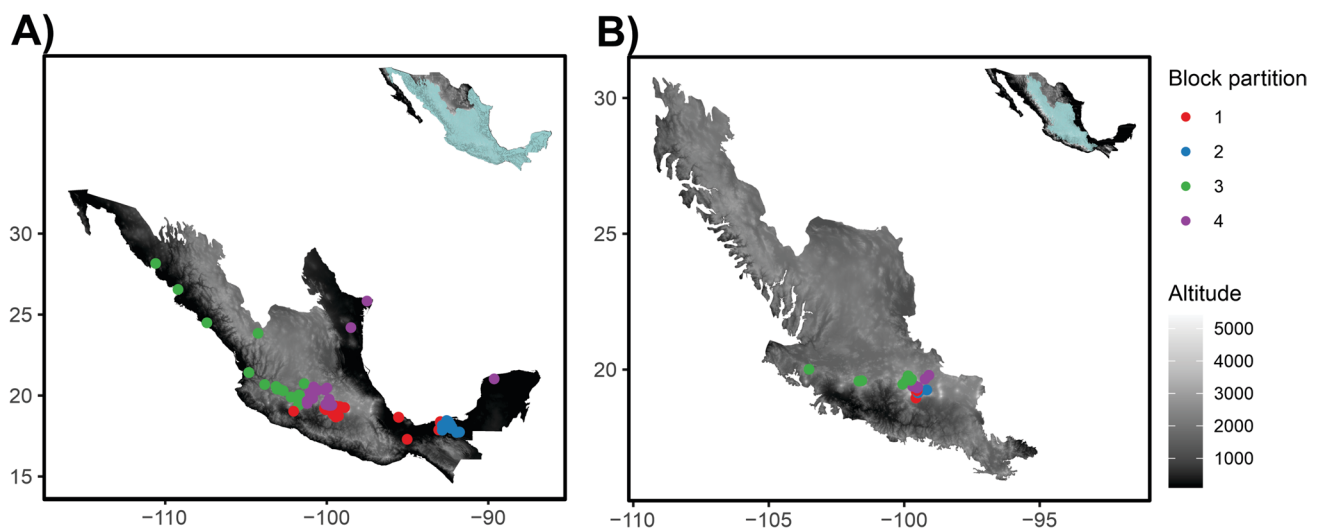


Fig. 1 A) Occurrence records of *Sagittaria latifolia* with the Block method partition. B) Occurrence records of *Sagittaria macrophylla* with the Block method partition. In both images, the region represent-

ing the used M is highlighted in blue, overlaid on a map of Mexico featuring the country's elevation gradient in the background. The M used with the elevation layer is shown in gray

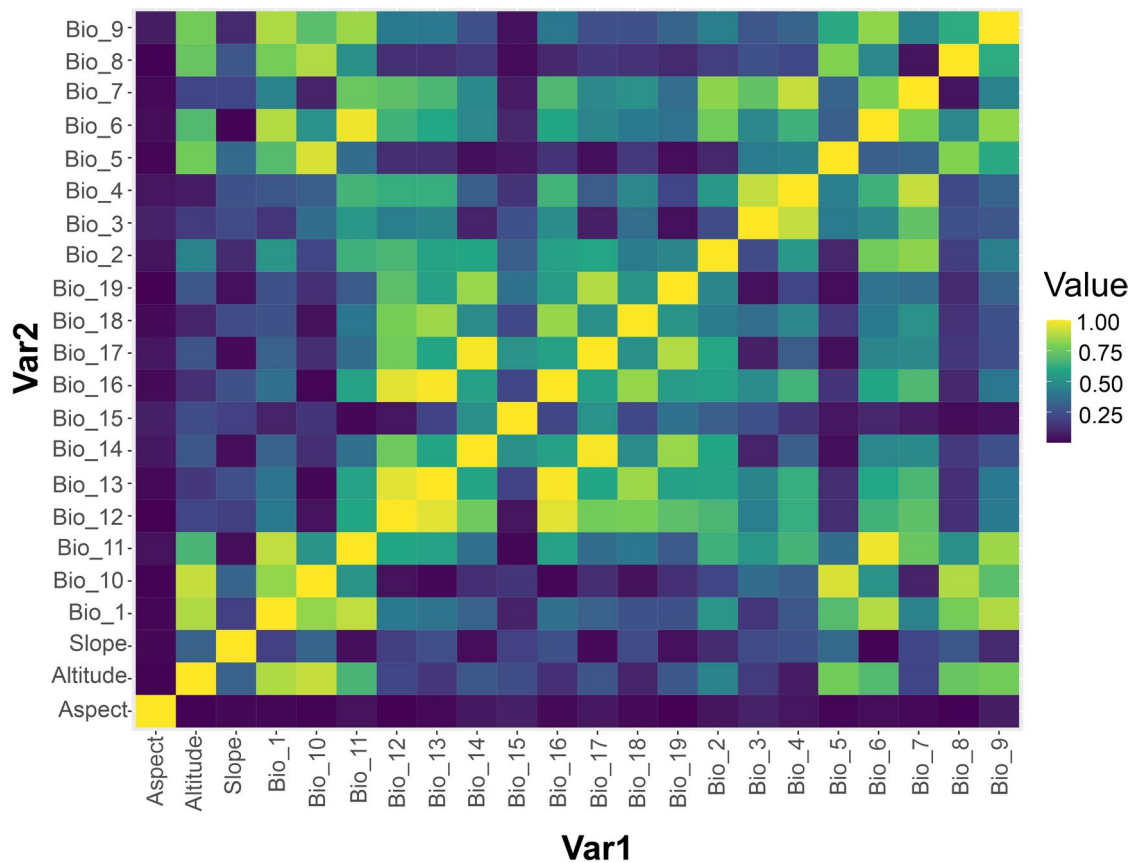


Fig. 2 Pearson diagram. The correlations between bioclimatic and topographic variables are shown. Values ranging from 0–1 are associated with corresponding colors, where purple indicates uncorrelated variables and yellow indicates variables with high correlation values

probability of presence. Several Maxent models were calculated using different combinations of parameters to select the fits that optimized the trade-off between goodness-of-fit and overfitting. ENMeval was configured to test 1- and 2-step regularization values, as well as the following feature classes: linear (L), quadratic (Q), product (P), threshold (T), and hinge (H), with the following combinations: L, H, LQ, LQP, LQH, LQHP, and LQHPT. In the ENMeval workflow, 100,000 random points were generated as background points. To avoid nonindependence between training and testing data, we implemented the ENMeval ‘block’ approach, which partitions occurrences according to their longitude and latitude, as recommended by Radosavljevic and Anderson (2014). The result is four nonoverlapping geographical intervals of equal numbers of occurrences, corresponding to each corner of the geographical space (Fourcade et al. 2018). In this approach, the background points were also split following the same spatial partitions. Then, in each modeling step, the model was trained without background points located in the same area as the test points. Therefore, the block method provides the best spatial independence between the training and testing datasets that can be obtained from partitioning a single dataset (Fourcade et al. 2018).

Consequently, this method quantifies the ability of models to extrapolate their predictions into new areas (Fourcade et al. 2018). For model selection, the Akaike information criterion corrected for small sample sizes (AICc) was used (Burnham and Anderson 2002). To assess the overall model accuracy in both the Maxent and ensemble models, area under the curve (AUC) scores from the receiver operating characteristic (ROC) plot were used first (Metz 1978; Phillips et al. 2006), followed by the transformation of the AUC into partial-receiver operating characteristic (PROC) curve plots (Partial-ROC; Peterson et al. 2008). For this purpose, the ntbox package in R was used.

To generate potential distribution maps, we procured bioclimatic data spanning the period from 1970 to 2000 (version released in January 2020). Utilizing these datasets, we conducted projections to delineate the present distribution of the species. Additionally, bioclimatic variables were extracted from general circulation models (GCMs) for the future timeframes 2041–2060 and 2061–2080. These projections were based on the shared socioeconomic pathways (SSP) 5–8.5 climate change scenario (Fossil fueled development), which represents the most extreme conditions with high greenhouse gas emissions and intensive use of fossil

fuels (O'Neill et al. 2017), and was derived from the WorldClim reduced CMIP6 (Coupled Model Intercomparison Project Phase 6) dataset. The future bioclimatic variables were sourced from three GCM models: CNRM-CM6-1 and HadGEM3-GC31-LL, and MPI-ESM1-2-HR. These scenarios were specifically chosen due to their demonstrated efficacy in capturing the regional climate patterns of Mexico (Instituto Nacional de Ecología y Cambio Climático (INECC), 2022).

After modelling processing, continuous maps were reclassified to binary using 80% and the 10th percentile training presence threshold, which sets the threshold as the value that excludes 10% of the localities that have the lowest predicted values (Radosavljevic and Anderson 2014). These binary maps were used to assess the change in the potential distribution of each species in terms of gains or losses of climatic suitability under climate change scenarios according to Phillips and Dudík (2008).

Niche Overlap

To calculate niche overlap and determine if environmental areas for *Sagittaria* species are equivalent, the bioclimatic variables used in the modeling were reduced using principal component analysis (PCA). We defined the environmental space by utilizing the first two PCA axes. Species presence records were then plotted within this environmental space using a Kernel density function, which accounts for potential sampling bias (Broennimann et al. 2012). The overlap between niches was calculated using Schoener's D and Hellinger's I metrics (Schoener 1970; Warren et al. 2008; Rödder and Engler 2011) and Spearman's rank correlation coefficient. Although D and I are commonly used in the SDM literature, they may tend to overestimate the similarity between SDM when many grid cells have similar values; for example, when two species prefer different habitats, the region contains a large number of habitats that are not suitable for both (Warren et al. 2021). We used these same metrics in the n-dimensional space of all combinations of environmental variables rather than restricting the model's similarity measures to those sets of conditions that appeared in the training region. To do this, samples of latin hypercubes are repeatedly drawn from the space of all possible combinations of environmental variables given the minimum and maximum of each variable within the training region, and samples are drawn until subsequent iterations differ by less than a specified tolerance value. Lower tolerance values result in more accurate estimates of overlap. Similarly, to assess whether the geographic regions occupied by both *Sagittaria* species are more environmentally different than expected by chance, we conducted a niche identity analysis or equivalence between species under the null hypothesis that the occurrences of two species in the environment are

effectively random and drawn from the same underlying distribution. Additionally, we conducted background or similarity testing to compare the ENMs of two species, assuming the expected overlap by chance if one or both species were effectively choosing habitat at random within their broad geographic range. For both tests, null distributions for the similarity metrics I and D are generated by calculating the niche overlap in each of the 100 random replicates. The null hypothesis, of no environmental transition, is rejected when the observed value of I or D is less than 95% of the values of the null distribution (Warren et al. 2021). These analyses were carried out with the package ENMTools (Warren et al. 2021) in R software.

Results

Ecological Niche Modeling: *Sagittaria latifolia*

According to the ENMeval analysis for *S. latifolia*, the LQP combination with a regularization multiplier of 2 was the optimal model for the present scenario. For the period 2041–2060, the CNRM-CM6-1 model favored the LQP combination with a regularization multiplier value of 2, while HadGEM3-GC31-LL favored the LQ combination with a regularization multiplier value of 1. Conversely, MPI-ESM1-2-HR showed the best performance with the LQHPT combination and a regularization multiplier value of 2. Looking ahead to the period 2061–2080, the LQHPT combination with a regularization multiplier value of 2 proved to be the most effective across all three climate change models. The Maxent models run in the ENMeval dataset, both for the present and future scenarios, exhibited superior performance beyond random chance, as evidenced by the AUC values ranging from 0.913 to 0.956 and significant partial-ROC bootstrap tests, with AUC ratios ranging from 1.83 to 1.915 (Table 2).

Ecological Niche Modeling: *Sagittaria macrophylla*

Our models exhibited better-than-expected performance, with AUC values ranging from 0.913 to 0.978 and p

Table 2 Predictive performance of ENMeval distribution models, present and future, developed for *Sagittaria latifolia*

	2041–2060		2061–280	
	ROC	Partial-ROC	ROC	Partial-ROC
2020	0.935	1.873		
CNRM-CM6-1	0.940	1.883	0.954	1.909
HadGEM3-GC31-LL	0.913	1.830	0.951	1.905
MPI-ESM1-2-HR	0.952	1.906	0.956	1.915

values < 0.001. For *S. macrophylla*, the ENMeval analysis revealed that the LQ combination with a regularization multiplier value of 1 performed best in the present scenario. Similarly, for the period 2041–2060, both CNRM-CM6-1 and MPI-ESM1-2-HR favored the LQ combination with a regularization multiplier value of 1, while HadGEM3-GC31-LL showed a preference for the LQP combination with a regularization multiplier value of 2. Transitioning to the period 2061–2080, the LQ combination with a regularization multiplier value of 1 emerged as the optimal choice across all three climate change models. Like those for *S. latifolia*, the Maxent models for *S. macrophylla* exhibited exceptional performance, surpassing random chance expectations, with AUC values ranging from 0.969 to 0.978 and significant partial-ROC bootstrap tests, yielding AUC values between 1.932 and 1.953 (Table 3).

Percentage Contribution of the Variables

The jackknife test analysis showed the bioclimatic and topographic variables influencing the suitable geographic area of both *Sagittaria* species. For *Sagittaria latifolia*, elevation (18.2%), average temperature of the wettest quarter (Bio8;

17.3%), and slope (14.5%) were among the most significant variables. Elevation was positively correlated with presence, with probabilities ranging from 10 to 45% below 1500 m and 50% to 95% above 2000 m. Conversely, higher temperatures during the wettest quarter and steeper slopes decreased the probability of presence. Precipitation variables, such as the precipitation of the coldest quarter and rainiest month, had varying impacts across climatic changes scenarios, with optimal ranges favoring presence, while extreme values reduced the probabilities of occurrence. For *S. macrophylla*, the most influential variables were the average temperature in the wettest month (Bio8; 39.4%), the slope (22.8%), and the precipitation in the wettest month (Bio13; 13.8%). Lower temperatures during the wettest quarter and steeper slopes were negatively correlated with presence, while precipitation variables had varying impacts. Higher precipitation levels in the wettest month were favorable for presence, whereas extreme values in the coldest month had negative effects. Isothermality positively influenced the presence of CBZ within specific temperature ranges. Overall, variables such as elevation, slope, and precipitation had significant contributions to the presence of both species, albeit with different magnitudes of influence.

Potential Distribution Maps

Sagittaria latifolia exhibited a high probability of being present in the Trans-Mexican Volcanic Belt province, which extends to the Gulf of Mexico and the Sonoran Province near the Baja California limits. However, lower probabilities were observed in the Sierra Madre del Sur and Peten provinces. Notably, projections with the HadGEM3-GC31-LL climate model for the 2041–2060 period indicated an increased probability of distribution in the Sierra Madre Occidental

Table 3 Predictive performance of ENMeval distribution models, present and future, developed for *Sagittaria macrophylla*

	2041–2060		2061–280	
	ROC	Partial-ROC	ROC	Partial-ROC
2020	0.976	1.951		
CNRM-CM6-1	0.978	1.953	0.976	1.951
HadGEM3-GC31-LL	0.976	1.950	0.972	1.932
MPI-ESM1-2-HR	0.975	1.947	0.969	1.938

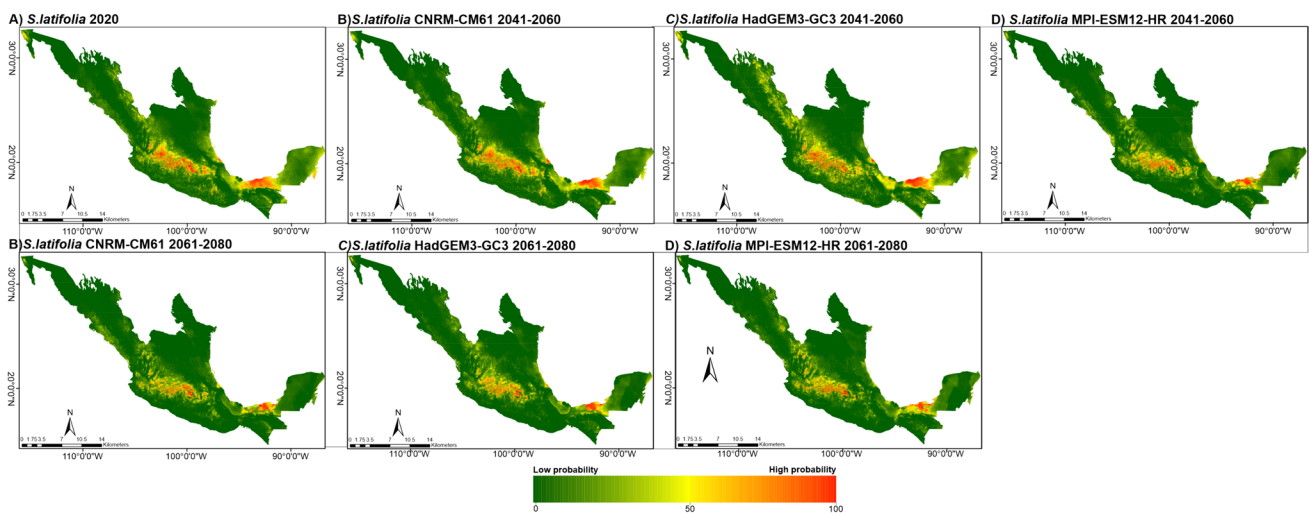


Fig. 3 Present potential and Future Distribution Maps of *Sagittaria latifolia*

Province (Fig. 3). Similarly, *Sagittaria macrophylla* exhibited a high probability of being present within the Trans-Mexican Volcanic Belt, bordering Oaxaca Province. Conversely, lower probabilities were observed in the Sierra Madre Occidental, Southern Altiplano, Balsas Depression, and Sierra Madre del Sur. The CNRM-CM6-1 climate model for the 2041–2060 period indicated a reduced probability of distribution (Fig. 4). Both *S. latifolia* and *S. macrophylla* predominantly occupied the Trans-Mexican Volcanic Belt region, highlighting their significance as favorable habitats for these hydrophytes (Fig. 4).

Areas of Suitability

Sagittaria latifolia exhibited a broader potential distribution area than *Sagittaria macrophylla*. However, there was notable variability among the different climate models considered for future periods. For the 2041–2060 period, significant differences were observed between the climate models in terms of gains and losses (Table 4). With the CNRM-CM6-1 model, *S. latifolia* showed a gain of 1.708%, while the HadGEM3-GC31-LL model indicated a substantial gain of 74.806%. Conversely, the MPI-ESM1-2-HR model revealed a loss of future potential area of 5.925% for *S. latifolia*. For *S. macrophylla*, losses were observed with the CNRM-CM6-1 model (19.734%), while gains were observed with the MPI-ESM1-2-HR (73.591%) and HadGEM3-GC31-LL (22.059%) models. Notably, both species exhibited considerable gains according to the HadGEM3-GC31-LL model. For the 2061–2080 period, discrepancies among the climate models persisted (Table 5). *S. latifolia* experienced losses in

all three models, with the MPI-ESM1-2-HR model showing the highest loss percentage (44.11%). Conversely, *S. macrophylla* demonstrated gains in the HadGEM3-GC31-LL (0.775%) and MPI-ESM1-2-HR (27.862%) models but experienced a loss in the CNRM-CM6-1 model (8.236%). Furthermore, both species showed losses in the CNRM-CM6-1 and HadGEM3-GC31-LL models. Considering both future periods with a probability of training presence at the 10th percentile, *S. latifolia* exhibited the highest percentage gain (74.806%) for the 2041–2060 period and the highest percentage loss (44.11%) for the 2061–2080 period. In contrast, *S. macrophylla* showed the lowest percentage loss (0.775%) for the 2061–2080 period. For both future periods with a probability of occurrence of 80%, *S. macrophylla* demonstrated the highest percentage gain (15.599%) and the lowest percentage loss (0.831%), while *S. latifolia* showed the highest percentage loss (26.61%), indicating differing responses to future climate scenarios.

Niche Overlap

The environmental niches of *S. latifolia* and *S. macrophylla* exhibited a statistically similar overlap of up to 41%, as indicated by Hellinger's I metric. However, Schoener's D metric suggested lower overlap values, potentially indicating nonoverlapping niches. The niche expansion values across the present and future periods suggest stability rather than expansion for both species (Table 6). Considering the env values D and I, both species share a similar environmental niche, with the lowest overlap observed in the future period of 2041–2060 with the CNRM-CM6-1 climate model. Env.

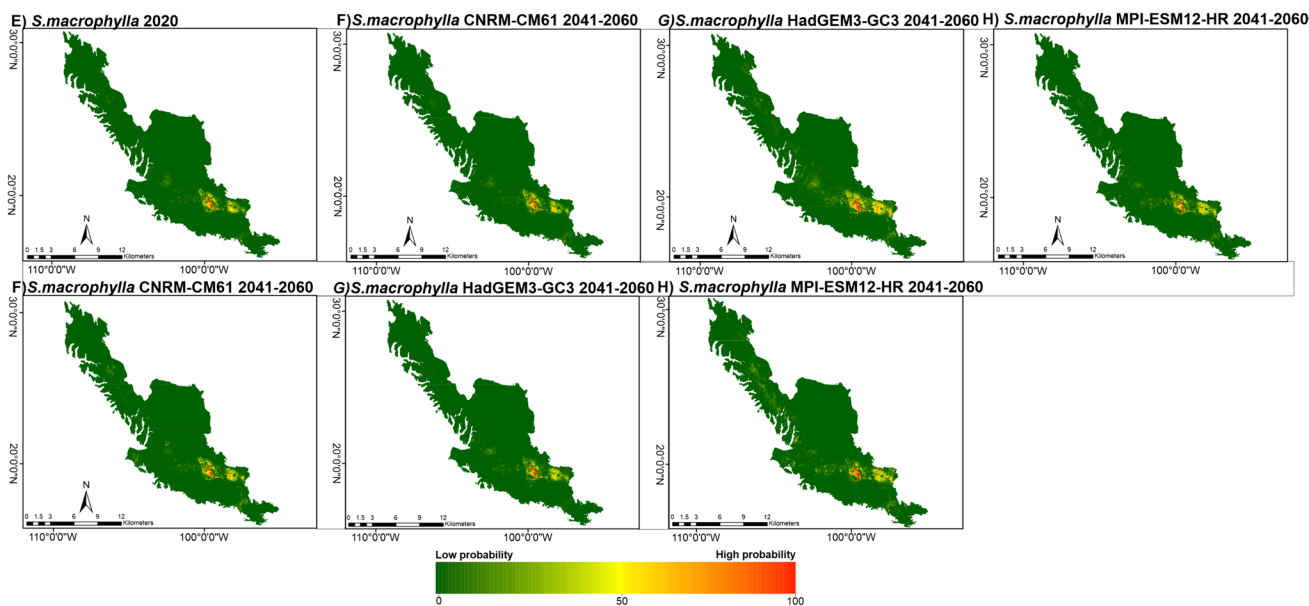


Fig. 4 Present potential and Future Distribution Maps of *Sagittaria macrophylla*

Table 4 Present (2020) suitability area (km²) and for the future period of 2041–2060, percentage of area loss for *Sagittaria latifolia* and *Sagittaria macrophylla* with three climate models (CNRM-CM6-1, HadGEM3-GC31-LL, MPI-ESM1-2-HR)

	10th percentile training presence													
	2041–2060			80%										
	2020 (Km ²)	CNRM-CM6-1 (Km ²)	Loss %	HadGEM3-GC31-LL (Km ²)	Loss %	MPI-ESM1-2-HR (Km ²)	Loss %	HadGEM3-GC31-LL (Km ²)	Loss %	MPI-ESM1-2-HR (Km ²)	Loss %			
<i>S. latifolia</i>	270,632.3	275,254.8	-1.708	473,083.5	-74.806	254,596.5	5.925	7417.041	7039.667	5.087	8546.183	-15.223	5895.846	20.509
<i>S. macrophylla</i>	23,867.13	19,157.26	19.734	41,431.35	-73.591	29,131.9	-22.059	679.177	710.599	-4.626	768.829	-13.2	688.961	-1.440

Table 5 Present (2020) suitability area (km²) and for the future period of 2061–2080, percentage of area loss for *Sagittaria latifolia* and *Sagittaria macrophylla* with three climate models (CNRM-CM6-1, HadGEM3-GC31-LL, MPI-ESM1-2-HR)

	10th percentile training presence													
	2061–2080			80%										
	2020 (Km ²)	CNRM-CM6-1 (Km ²)	Loss %	HadGEM3-GC31-LL (Km ²)	Loss %	MPI-ESM1-2-HR (Km ²)	Loss %	HadGEM3-GC31-LL (Km ²)	Loss %	MPI-ESM1-2-HR (Km ²)	Loss %			
<i>S. latifolia</i>	270,632.3	177,159	34.538	209,886.6	22.445	151,254.8	44.11	7417.041	5718.843	22.895	5443.091	26.613	6697.353	9.703
<i>S. macrophylla</i>	23,867.13	21,901.37	8.236	24,052.18	-0.775	30,517.13	-27.862	679.1766	673.5303	0.831	646.978	4.741	785.123	-15.599

Table 6 Niche overlap between *Sagittaria latifolia* and *Sagittaria macrophylla* in present and future potential distribution. Values in bold are statistically significant values (* indicates p -value < 0.05)

	2020	CNRM-CM6-1		HadGEM3-GC31-LL		MPI-ESM1-2-HR	
		2041–2060	2061–2080	2041–2060	2061–2080	2041–2060	2061–2080
env.D	0.432	0.216	0.263	0.237	0.250	0.508	0.276
env.I	0.570	0.354	0.378	0.283	0.403	0.554	0.430
env.cor	0.263	0.027	-0.023	0.216	0.131	0.487	0.186
D	0.185*	0.193*	0.201*	0.191*	0.172*	0.178*	0.164*
I	0.410*	0.420*	0.428*	0.413*	0.391*	0.402*	0.382*
expansion	0.001	0.001*	0.000*	0.001*	0.001*	0.001*	0.001
stability	0.999*	0.999*	1.000*	0.999*	0.999*	0.999*	0.999*
unfilling	0.558	0.559	0.567	0.535	0.545	0.558	0.545

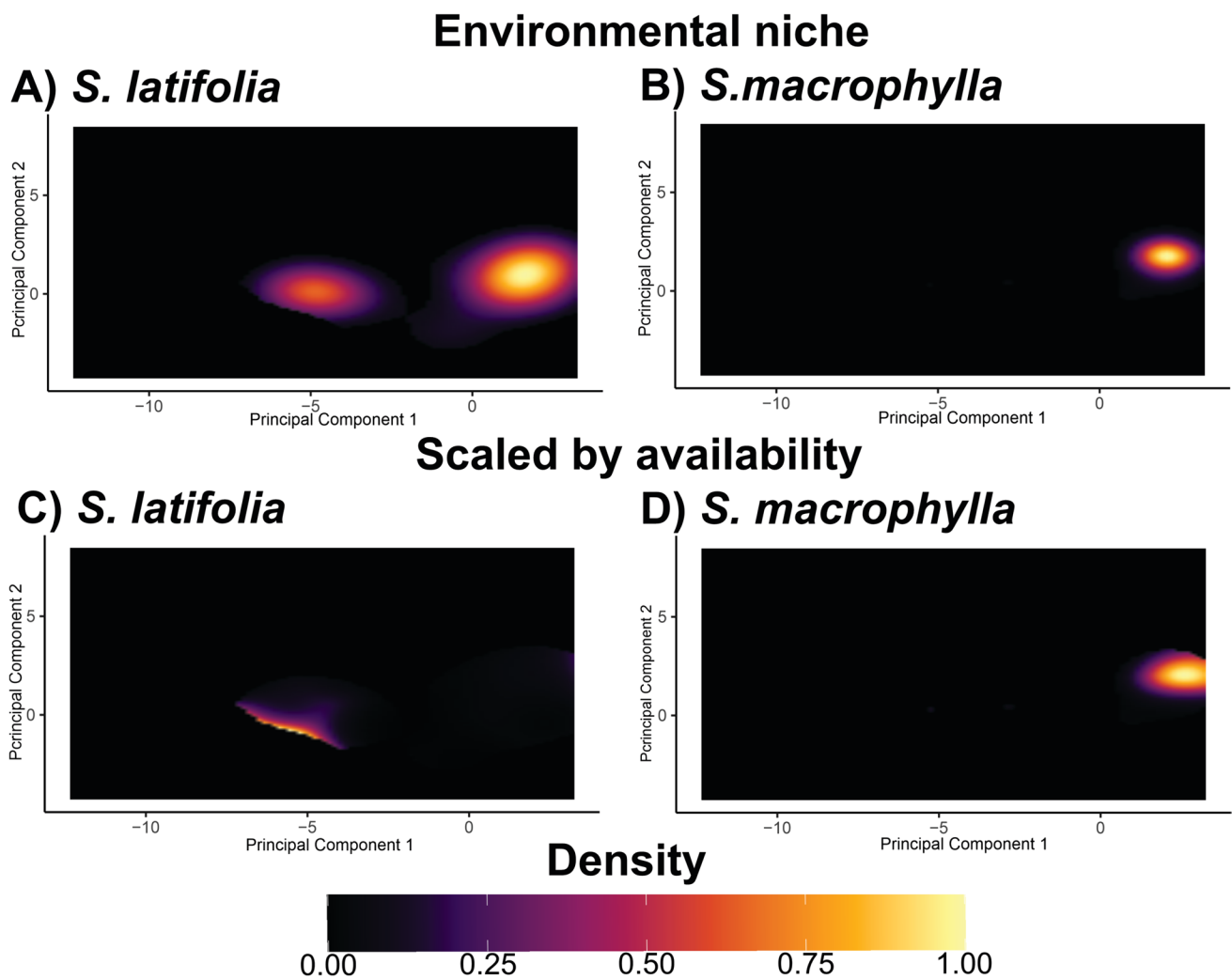


Fig. 5 Environmental niche overlap between *Sagittaria latifolia* and *Sagittaria macrophylla* **A)** Environmental niche of *S. latifolia*. **B)** Environmental niche of *S. macrophylla*. **C)** Potential expansion or

colonization niche of *S. latifolia*. **D)** Potential expansion or colonization niche of *S. macrophylla*

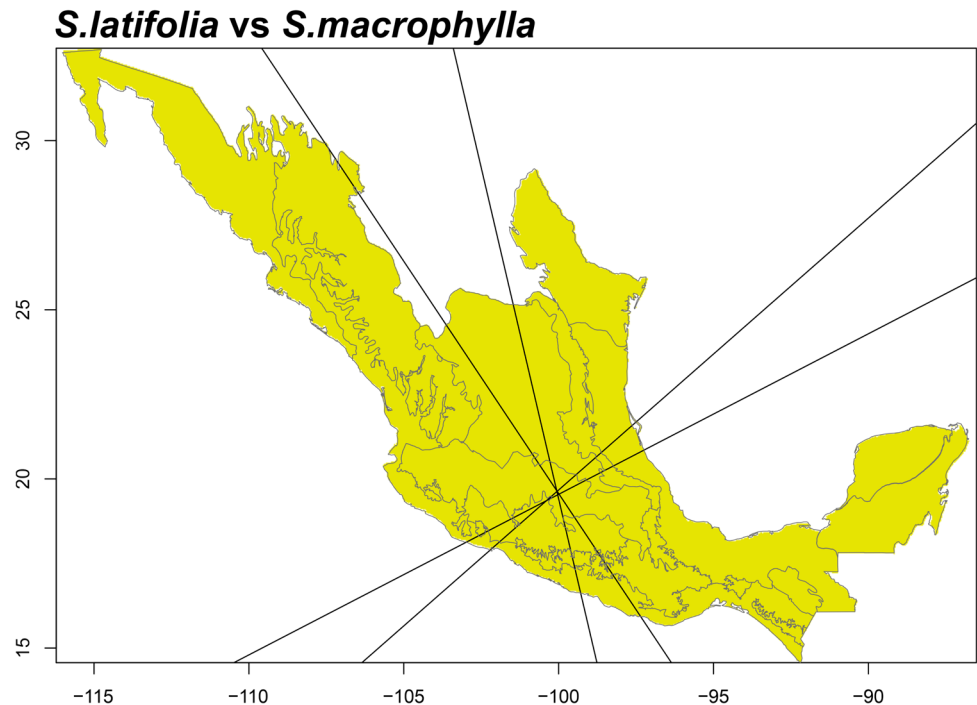
cor values ranging from -0.023 to 0.487 indicate a low level of niche overlap (Table 6). Additionally, compared with *S. macrophylla*, *S. latifolia* has a broader environmental niche and greater potential for expansion, particularly as

evidenced by density values exceeding 0.5 (Fig. 5). The results of the linear, Blob, and ribbon range break tests did not yield statistically significant findings ($p < 0.2$). Nevertheless, the values of I, env. D, and env. I further underscore

Table 7 Linear, blob, and ribbon range break tests as developed in Glor and Warren 2011, between *Sagittaria* species in environmental space

	2020	CNRM-CM6-1		HadGEM3-GC31-LL		MPI-ESM1-2-HR	
		2041–2060	2061–2080	2041–2060	2061–2080	2041–2060	2061–2080
env.D	0.463	0.345	0.342	0.377	0.431	0.420	0.334
env.I	0.657	0.521	0.517	0.574	0.649	0.607	0.542
env.cor	0.332	0.147	0.091	0.396	0.540	0.252	0.200
D	0.351	0.284	0.401	0.308	0.323	0.342	0.279
I	0.607	0.525	0.643	0.512	0.546	0.581	0.541
rank.cor	0.170	0.084	0.231	0.001	0.001	0.108	-0.009

Fig. 6 Break test of the ribbon range between *Sagittaria latifolia* and *Sagittaria macrophylla*. The MDS was designed to test whether the ranges of two species were divided by a region that was relatively unsuitable for one or both species



the similarity between the environmental niches of the two species (Table 7). Moreover, the Ribbon range break test analysis suggested that the center of the Trans-Mexican Volcanic Belt Province, characterized by distinct climatic and topographic features, serves as the range break area between *S. latifolia* and *S. macrophylla* (Fig. 6).

Discussion

Our study provides a detailed overview of the present and future potential distributions of two hydrophyte species in Mexico, based on bioclimatic and topographic variables. The species distribution models (SDMs) indicate that suitable climatic conditions for both species are primarily found in the Trans-Mexican Volcanic Belt. However, *S. latifolia* exhibits a larger area of climatic suitability, also encompassing the Coastal Plain of Mexico. The assessment of potential distributions and suitability areas for

Sagittaria species in Mexico reveals their vulnerability to climate change, since projections generated by the three GCMs indicate notable shifts in the distributions of *S. latifolia* and *S. macrophylla* in all the periods analyzed. Additionally, future predictions indicate that the niche overlap will remain stable for both species in the regions and persist in 40% of their distribution.

Our results show, that climatic and topographic factors influenced the distributions of *S. latifolia* and *S. macrophylla*. Increases in the average temperature of the wettest quarter and slope negatively impact species presence, suggesting susceptibility to drastic changes in these variables. High temperatures (> 35 °C) during the wettest quarter can hinder growth and development, affecting essential processes such as photosynthesis, respiration, and water relations, with varying effects depending on species tolerance capacities (Sculthorpe 1967; Jarma et al. 2012; Sadava et al. 2009; Lind et al. 2022). The analysis showed that slope

negatively influences both *S. latifolia* and *S. macrophylla*, likely due to its impact on water levels and soil movement. An increased slope inclination hampers water flow and soil moisture retention, reducing the likelihood of plant presence in such locations (Hincapié and Tobón 2012). Given that *S. latifolia* is a native species with a broader distribution than other *Sagittaria* species (Zepeda and Lot 2005), bioclimatic factors such as precipitation and precipitation seasonality increase its probability of occurrence, especially when precipitation levels reach 350 mm. Adequate precipitation likely ensures stable water bodies with sufficient water availability for *S. latifolia* development and aids in its reproduction, both sexually and asexually (Zepeda-Gómez 2001; Terneus et al. 2019). Moreover, precipitation during the coldest quarter supports species distribution, potentially because *S. latifolia* completes its life cycle during winter, matures tubers and releases seeds for propagation (Zepeda-Gómez 2001). The increase in precipitation during the coldest months likely fosters an environment ideal for perennialization and seed maturation, facilitated by cold stratification during the winter season (Zepeda-Gómez 2001). Aquatic plants exhibit diverse altitudinal ranges, the distribution of which is often limited within this range (Sculthorpe 1967; Murphy et al. 2019). While *S. latifolia* has been observed from 0 to 2600 m above sea level, the probability of its presence notably increases between 2000 and 4000 m above sea level, despite not being observed beyond 2600 m (Zepeda-Gómez 2001; Miranda 2014). Conversely, the average temperature of the driest quarter negatively affects *S. latifolia*, as water availability diminishes during this period, exacerbated by increased temperatures leading to evaporation losses (Sculthorpe 1967; Esparza 2014; Arenas 2021). *Sagittaria macrophylla*, an endemic species (Sculthorpe 1967), is adversely affected by high precipitation during both the rainiest and coldest months, particularly in the Valley area in Toluca where low winter precipitation prevails (Morales et al. 2007; Climate-Data 2023). Conversely, isothermality positively influences its distribution, although the areas where the species thrives typically lack isothermal climates, suggesting that microclimate factors limit GIS-applied variables (O'Donnell and Ignizio 2012; Barnes et al. 1998; Zepeda-Gómez 2001).

Regions such as the Trans-Mexican Volcanic Belt, Gulf of Mexico, and Sonoran Province have historically exhibited a high probability of *S. latifolia* presence, characterized by temperate and warm subhumid climates (INEGI 2021), providing favorable conditions for their development and distribution. However, projections for *S. latifolia* under the HadGEM3-GC31-LL model for the period 2041–2060 indicate a potential increase of up to 74.8% in the distribution area. It is worth noting that these projections may not fully account for recent climatic trends, such as a reported precipitation deficit of 15.8% in 2023, leading to increased droughts and reduced water availability in wetlands and

rivers (Comisión Nacional del Agua (CONAGUA), 2023). Additionally, losses of 5.9% to 44.1% were observed across all the models for the 2061–2080 future scenario, challenging the hypothesis of an expansion in *S. latifolia*'s distribution due to its limited tolerance to extreme precipitation and temperature conditions (Sculthorpe 1967; Jarma et al. 2012; Sadava et al. 2009). Similarly, *Sagittaria macrophylla* exhibited gains ranging from 0.7% to 73.5% under the HadGEM3-GC31-LL and MPI-ESM1-2-HR models for the periods 2041–2060 and 2061–2080, suggesting potential expansion in distribution. However, projections also highlight the risk of reduced rainfall and increased droughts in central Mexico, potentially limiting species development due to decreased water availability (Comisión Nacional del Agua (CONAGUA), 2023). Losses of up to 19.7% were observed with the CNRM-CM6-1 model, indicating a reduced distribution area for this endemic species than previously reported (Sculthorpe 1967; Rzedowski 1991, 2006). Despite the potential contribution of isothermality to the *S. macrophylla* distribution, microclimate factors not considered in climate models may influence interpretation. Despite the statistical performance of our models based on assessment metrics such as partial ROC and AUC (Soberón and Peterson 2005; Boria et al. 2014). Uncertainties persist about future events and the full extent of species niches; this highlights the importance of understanding possible alternative scenarios under drastic human activities and ongoing climate change (Brown 2003; Mateo et al. 2011). Moreover, the three models utilized in this study are part of a larger group of forty GCMs previously assessed by Kamworapan and Surussavadee (2019). They highlighted the CNRM-CM5-2 model as the top performer among the 40 GCMs; this model belongs to the CIMP5 group, a version of WorldClim preceding the one employed in this research. While the models exhibited varying levels of performance, they continue to furnish crucial climate information (Radosavljevic and Anderson 2014; Sunny et al. 2023; Rubio-Blanco et al. 2024).

Niche Overlap

The results indicate that *S. latifolia* and *S. macrophylla* currently exhibit niche overlaps of up to 41%, with future predictions suggesting that this overlap will remain between 38 and 42%. Niche coexistence does not invariably denote competitive interaction; species can coexist through stable segregation, sharing available resources (Smith and Smith 2007). This stability implies that the niches of both species are not expanding but remain stable. The Trans-Mexican Volcanic Belt Province is renowned for its environmental heterogeneity and is recognized as a center of diversification, endemism, and biogeographic transition. It hosts approximately 7,000 species of vascular plants distributed across the Trans-Mexican Volcanic Belt. Confirming the presence

of both *S. latifolia* and *S. macrophylla* in the same area is crucial for supporting other species and providing food and shelter for local fauna (Gámez et al. 2012; Rzedowski 2020; Zepeda-Gómez 2001; Rzedowski 2005). According to the results of the linear, Blob, and ribbon break tests, although they suggest niche overlap and a range break point in the center of the Trans-Mexican Volcanic Belt province, where species are absent, these observations lack statistical significance ($p < 0.2$). However, these findings provide preliminary evidence of niche overlap between *S. latifolia* and *S. macrophylla*, corroborated by the Hellinger metric results (Fig. 5; Table 7).

Conclusions

Our study provides insights into the distribution of understudied aquatic macrophyte species, examining their relationship with various bioclimatic and topographic variables. Additionally, we explore potential shifts in their climatic suitability areas under different climate change scenarios. In this work, potential distribution models emphasize the biological significance of the Trans-Mexican Volcanic Belt Province, given the presence of essential aquatic plants in freshwater ecosystems. Our findings reveal that *Sagittaria latifolia* benefits from increased and stable precipitation, especially during colder months. Conversely, *S. macrophylla* thrives under stable temperature conditions. However, both species face challenges with high temperatures during wet periods, as well steep slopes, and reduced water availability during dry periods. Notably, excessive precipitation during the rainiest and coldest months negatively impacts *S. macrophylla*.

Contrary to our initial expectations, the general circulation models (GCMs) used in our study do not provide clear evidence of species range reductions. Instead, we observe large changes with varying percentages of loss and gain across the distribution models for both species. This diversity in GCM responses underscores the complexity of Earth's climate system, influenced by numerical methods and parameterizations. These variations lead to divergent responses reflected in our species distribution models. Nevertheless, the varying percentages of change are compensated by the statistical performance of our SDMs. Our models accurately characterize the potential habitats for *Sagittaria* species within the study area using the chosen predictors. This information is valuable for assessing habitat suitability and susceptibility under climate change scenarios. Understanding these dynamics is crucial for maintaining ecosystem functioning and developing effective management and conservation strategies for these populations and other species that require wetlands such as *Ambystoma altamirani*

(Heredia-Bobadilla and Sunny 2021; Reyes-Olivares et al. 2024; Ruiz-Reyes et al. 2024; Sunny et al. 2024).

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Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics Approval and Consent to Participate Not applicable.

Consent for Publication Not applicable.

Competing Interests The authors declare no competing interests.

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