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ORIGINAL ARTICLE

Thrips biological control agent shows greater niche overlap with invasive alligatorweed than conventional agent in current and future climate scenarios

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Abstract *Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae: Caryophyllales) is an aquatic invasive weed from South America with a long history of biological control. The well-studied *Agasicles hygrophila* Selman & Vogt, 1971 (Coleoptera: Chrysomelidae) successfully controls *A. philoxeroides* in some parts of its invaded range, but is unsuitable in other areas due to its intolerance to cold temperatures. *Amynothrips andersoni* O'Neill, 1968 (Thysanoptera: Phlaeothripidae) has shown greater tolerance to cold temperatures, but no research has been conducted to determine its ecological niche with respect to *A. philoxeroides.* The aim of this study is to predict the environmental niches of *A. andersoni* and *A. hygrophila* and their overlap with that of *A. philoxeroides* in the North and South America under current and future climate scenarios. Accordingly, niche models were constructed in MaxEnt for all three species using environmental variables from the current climate and under two future climate scenarios (SSP1-2.6 and SSP5-8.5) for the year 2040. The niche overlap between the two biological control agents and the host were estimated for all three scenarios. Under both future climate scenarios, the total niche of *A. philoxeroides* is predicted to decrease by up to 10% whereas niche area is expected to increase by up to 10% for *A. andersoni* and *A. hygrophila*. *Amynothrips andersoni* had a greater niche overlap with *A. philoxeroides* than did *A. hygrophila* under all three scenarios, suggesting it is currently more widely suitable for *A. philoxeroides* biological control and should continue to be in 2040.

Keywords *Agasicles hygrophila* · Caryophyllales: Amaranthaceae · Climate change · Ecological niche model · Flea beetle · Thysanoptera: Phlaeothripidae

Introduction

Understanding the distribution of invasive species is important to the ecology and management of invasive

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species, but there are challenges when generating ecological niche models (ENMs) for invasive species (Peterson 2001; Lázaro-Lobo et al. 2020). Principal among these challenges is the assumption that the target species is in equilibrium with its environment. This study focuses on the invasive species *Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae), a globally distributed, aquatic invasive plant which is native to the Paraná River Basin of the South American countries Brazil, Paraguay, Uruguay, and Argentina. *A. philoxeroides* was first observed outside of its native range on the northern coast of the Gulf of Mexico and has since become widespread in freshwater ecosystems in the southeastern USA (Cohen GH01928487). Consequent with its early date of introduction is a long history of *A. philoxeroides* biological control with multiple biological control agents (Buckingham 1996). This study focuses on two of these agents: *Amynothrips andersoni* O'Neill, 1968 (Thysanoptera: Phlaeothripidae) and *Agasicles hygrophila* Selman & Vogt, 1971 (Coleoptera: Chrysomelidae; Maddox 1968; Maddox & Mayfield 1979). *A. hygrophila* has been studied and used extensively because its feeding defoliates affected *A. philoxeroides* shoots, causing high tissue mortality (Buckingham 1996). Comparatively, *A. andersoni* feeds primarily at the meristems, causing a stunting of alligator weed growth (Maddox and Mayfield 1979). These differences between *A. andersoni* and *A. hygrophila* have resulted in *A. andersoni* having received much less attention in use and research.

Although its high control efficacy has facilitated widespread use, *A. hygrophila* control is limited geographically because it poorly tolerates cold temperatures (Knight et al. 2023). This issue was first discussed in a niche modeling effort which suggested a discrepancy in the fundamental niches of *A. philoxeroides* and *A. hygrophila.* These findings have since been substantiated (Julien et al. 1995; Sánchez-Restrepo et al. 2023). This deficiency in the utility of *A. hygrophila* biological control has instigated investigation into alternative biological control methods. Specifically, recent evidence suggests that *A. andersoni* is much more tolerant to cold temperatures than *A. hygrophila* (Knight and Harms 2022). Additionally, a recent study suggests *A. andersoni* effectively reduces *A. philoxeroides* biomass under experimental conditions, thus improving the appeal of *A. andersoni* as a method of *A. philoxeroides* control (Schmid et al. 2024). Despite these promising findings, modern research literature regarding control of *A. philoxeroides* with *A. andersoni* is depauperate.

Although there are considerable gaps in *A. philoxeroides* research, multiple efforts to model the species ecological niche have been undertaken. Julien et al. (1995) authored the first peer-reviewed effort to model the niche of *A. philoxeroides* and were also the first to identify the poor niche overlap between *A. philoxeroides* and *A. hygrophila*. That study used CLIMEX models to predict suitable habitat of *A. philoxeroides* globally (Julien et al. 1995). The authors found that the modeled ecological niche of *A. philoxeroides* expanded far beyond its known distribution in East Asia, Australia, Sub-Saharan Africa, and Mediterranean Europe and Africa. However, they predicted very little suitable habitat outside of its then-known invaded range in the USA (Julien et al. 1995). Julien et al. (1995) was an early example of ENM utilization to study biological control of invasive species, and since then the importance of ENMs in biological control has been well-recognized (Julien et al. 1995; Kriticos et al. 2021). Since 1995, few efforts to model the ecological niche of *A. philoxeroides* have been undertaken and most have focus on regional range expansion in future climate scenarios (Yan et al. 2020; Hong-Qun et al. 2023; Sánchez-Restrepo et al. 2023). The consensus from all *A. philoxeroides* niche modeling efforts to date is that alligator weed is projected to expand its invaded range, particularly in North America.

When compared to *A. philoxeroides,* niche modeling efforts on *A. hygrophila* are fewer. An *A. hygrophila* ENM was first generated by Julien et al. (1995) where they observed a poor niche overlap with *A. philoxeroides.* The same poor overlap was observed in a 2023 study which also found that the range of suitable habitat in North America is expected to make few gains in future climate scenarios (Julien et al. 1995; Sánchez-Restrepo et al. 2023). While ENMs are scant for *A. philoxeroides* and *A. hygrophila,* our literature review produced no previous efforts to model the ecological niche of *A. andersoni.*

The objective of this study is to compare the niche overlap of *A. andersoni* and *A. hygrophila* with *A. philoxeroides* under current and future climate conditions using MaxEnt ENMs. This study assesses the following hypotheses: (1) In North America, climate change will facilitate the northward expansion of suitable habitat for all three species in the relatively short term, and (2) *A. andersoni* has greater niche overlap with *A. philoxeroides*, potentially giving this species broader biological control utility in North America than *A. hygrophila*.

Materials and methods

Data acquisition

Presence-only datasets were compiled for *A. philoxeroides, A. andersoni,* and *A. hygrophila* over the extent of the North and South American continents. Datasets were compiled using a combination of available records, reports from colleagues, and personal observations. Datasets for *A. philoxeroides* and *A. hygrophila* were compiled with occurrences from GBIF queries (GBIF.org 2024a, b). Records of *A. andersoni* on GBIF were scant, and so this dataset was compiled from multiple sources: records were sourced from Knight and Harms (2022), Smithsonian National Museum of Natural History (NMNH), Mississippi Entomological Museum (MEM), iNaturalist, and personal observation (iNaturalist community 2024). Records from iNaturalist were only used when sufficient evidence was provided to personally confirm the identity. In total, the datasets for *A. philoxeroides, A. andersoni,* and *A. hygrophila* contained 24,514, 38, and 682 records respectively. To account for heterogeneity in reporting effort and potential duplicate records, datasets were thinned using the R package "spThin" to eliminate records within 10 km of other records (Aiello-Lammens et al. 2019; Sánchez-Restrepo et al. 2023). After datasets were thinned, the *A. philoxeroides* dataset contained 1804 records, the *A. andersoni* dataset contained 35 records, and the *A. hygrophila* dataset contained 111 records (Supplementary Fig. S1).

Multiple bioclimatic variables were identified a priori as potential environmental factors to be used in ecological niche modeling. Of these variables, three (BIO1, BIO7, and BIO12) were selected because of their biological relevance and that they are not highly multicollinear ($|\rho| < 0.80$; Supplementary Table S1). Definitions of these bioclimatic variables are as follows: BIO1 = annual mean temperature, BIO7 = temperature annual range, and BIO12 = annual precipitation. The environmental variables used in this modeling effort was limited to three to mitigate the effect of model overfitting on the very limited *A. andersoni* dataset (Vaughan and Ormerod 2003). Raster files of these bioclimatic variables were obtained from the WorldClim consortium at the 30 arc second resolution (Fick and Hijmans 2017). Three different sets of these bioclimatic variables were used in this study, all obtained from WorldClim (Fick and Hijmans 2017). One set (present day) comprised variables generated with historical data from 1970 to 2000 and represents current conditions. The other two sets (SSP1-2.6 and SSP5-8.5) were generated from the HadGEM3 family of global climate models and prepared for the Coupled Model Intercomparison Project Phase 6 (CMIP6; Roberts 2017). These latter two sets represent predicted conditions for 2040 and were generated following two Shared Socio-economic Pathways (SSPs): SSP1-2.6 and SSP5-8. The SSP1-2.6 dataset represents a "best-case" scenario for near-future greenhouse gas emissions and warming for climatic conditions in 2040, while SSP5-8.5 represents a "worst-case" scenario. Values at present day for each bioclim variable (BIO1, BIO7, and BIO12) were determined for all occurrence records from all three species used in this study. Principal component analysis (PCA) was performed on these bioclim values, specifically bioclim variables were loaded onto two principle components (PC1 and PC2). Bioclim values extraction and PCA were conducted in R and RStudio (RStudio Team 2020; R Core Team 2021) using packages, "factoextra" (Kassambara and Mundt 2020), "FactoMineR" (Husson et al. 2023), and "raster" (Hijmans et al. 2023a).

Ecological niche modeling

Generation of ENMs was primarily conducted using ENMeval which can run MaxEnt in tandem to build ENMs (Phillips et al. 2020; Kass et al. 2023). The modeling process was conducted on *A. philoxeroides, A. andersoni,* and *A. hygrophila* using a compilation of all three aforementioned bioclimatic variables (ENV) as environmental predictors for the ENMs. All models were trained with the present-day set of bioclimatic variables. Background points were generated randomly based on the geographic extent of records for the target species. For *A. philoxeroides* models, 5000 background points were generated whereas for *A. andersoni* and *A. hygrophila* models, 2000 background points were generated. The models for *A. philoxeroides* had more background points because the occurrences spanned over a larger area than *A. andersoni* and *A. hygrophila.* Occurrences were partitioned for evaluation using the "block" function native to ENMeval (Kass et al. 2023). Ecological niche models were tuned using four feature classes (linear, linear-quadratic, linear-quadratic-hinge, and hinge) and five regularization multipliers (1–5) native to MaxEnt (Phillips et al. 2020). From these combinations of feature classes and regularization methods, 20 candidate models were generated for each species. The predictive power for each candidate model in each iteration was determined using the area under the curve (AUC). Candidate model performance was determined principally by the corrected Akaike information criterion (AICc) where candidate models with lower values performed better, but models with a $\Delta\text{AICc} < 2$ were considered not significantly different in performance. For candidate models with similar AICc, performance was determined secondarily via omission rate (OR), with model parsimony being the tertiary criterion. Candidate models with $\text{OR} > 0.05$ were excluded from selection. The candidate model that performed best based on these criteria was selected as the best fit model for its respective species.

Best fit models from each species were used to predict habitat suitability, which was projected over the North and South American continents using "dismo" and probability values were scaled using the "cloglog" function native to MaxEnt (Phillips et al. 2020; Hijmans et al. 2023b). Habitat suitability values for all three species were binned into four classes: unsuitable: $x \leq 0.25$, poor suitability: $0.25 < x \leq 0.50$, moderate suitability: $0.50 < x \leq 0.75$, and high suitability: $x > 0.75$. To estimate niche overlap between *A. philoxeroides* and both biological control agents (*A. andersoni* and *A. hygrophila*), the "nicheOverlap" function in "dismo" was used to calculate Schoener's D and Hellinger's I indices (Hijmans et al. 2023b). These indices range from 0.0 to 1.0 with 1.0 indicating perfect overlap between niches of two species and 0.0 indicating no overlap. To estimate area of habitat suitability, number of pixels poorly, moderately, and highly suitable habitat were determined for each species. Pixels are roughly equal to 1 km^2. Predicted habitat suitability, niche overlap, and habitat area were estimated for present-day, SSP1-2.6, and SSP5-8.5 scenarios.

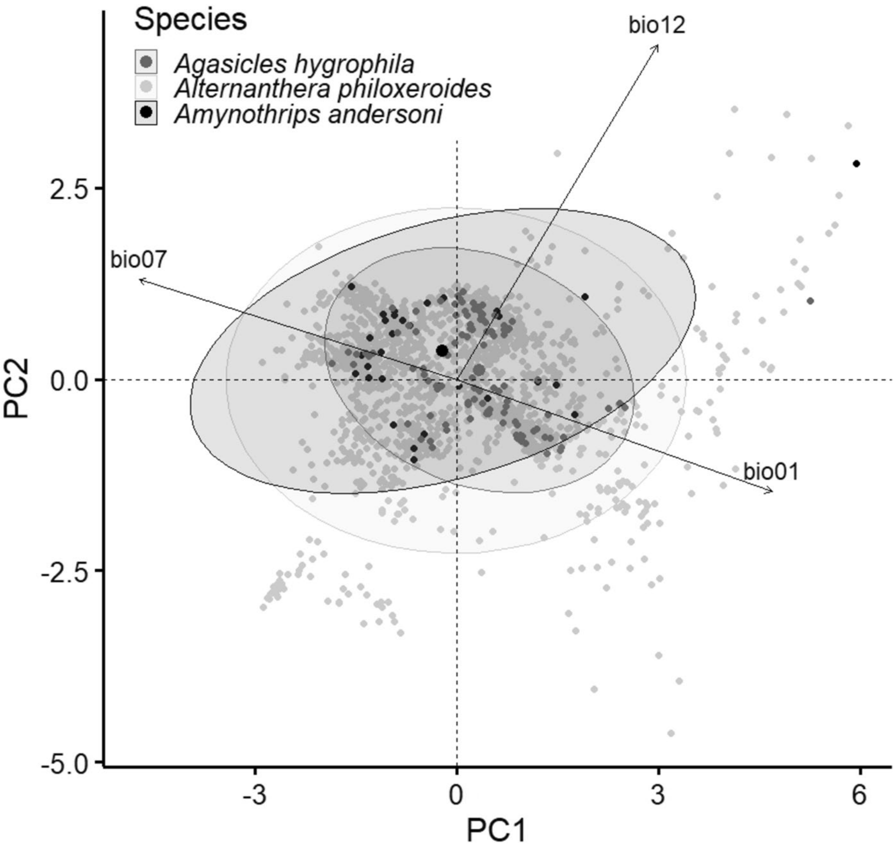
All modeling methods were conducted in R and RStudio using the packages "dismo" (Hijmans et al. 2023b), "ecospat" (Broennimann et al. 2023), "ENMeval" (Kass et al. 2023), "raster" (Hijmans et al. 2023a), and "sf" (Pebesma et al. 2023). Some functions used in these methods operated MaxEnt (Phillips et al. 2020) in tandem with R and RStudio (RStudio Team 2020; R Core Team 2021). Geoprocessing of spatial data was conducted using a combination of RStudio and ArcGIS Pro (RStudio Team 2020; Esri 2023). All mapping was conducted in ArcGIS pro (Esri 2023).

Results

Following PCA on bioclim variables, BIO1 and BIO7 were primarily loaded onto PC1 (loading values: $\text{BIO1} = 0.885$, $\text{BIO7} = -0.892$, $\text{BIO12} = 0.564$) whereas, BIO12 was primarily loaded onto PC2 (loading values: $\text{BIO1} = -0.278$, $\text{BIO7} = 0.246$, $\text{BIO12} = 0.826$). An ordination of the principal component coordinates of occurrence records for each species show the variance of the respective training dataset across the bioclim variables used for niche modeling (Fig. 1).

The principal component coordinates of training datasets show high overlap of bioclim values for *A. philoxeroides, A. andersoni,* and *A. hygrophila* (Fig. 1). Although the PCA seems to show high overlap among these species, the large discrepancy in training dataset size limits the statistical conclusions that can be drawn from the PCA results. A best fit model for each species was selected from twenty candidate models based on our model selection criteria (Supplementary Table S2). During model selection for *A. philoxeroides* none of the candidate models had $\text{OR} > 0.05$. For *A. andersoni,* nine candidate models had $\text{OR} > 0.05$ and were excluded from model selection. For *A. hygrophila,* two candidate models had $\text{OR} > 0.05$ and were excluded from model selection. All best fit models were highly predictive, as the AUC of best fit models for all three species neared or exceeded 0.80 (Supplementary Table S2). Of the environmental predictors used in these ENMs, all contributed greater than 20% to the best fit model

Fig. 1 Ordination of principle component coordinates of training datasets for *A. philoxeroides, A. andersoni,* and *A. hygrophila.* Principle component 1 (PC1) and PC2 explain 63.2% and 27.3% of the variance, respectively. Labeled arrows show loading weights and directions of bioclim variables onto PC1 and PC2. Ellipses represent ± 95% CI of the species means for both axes



with the exception of BIO12 in the *A. andersoni* model (Supplementary Table S3).

The total predicted niche area of *A. philoxeroides* in the present day consisted of 4.9 million poor pixels, 1.9 million moderate pixels, and 1.5 million high pixels, for a total of 8.3 million pixels of habitat area (Fig. 2a). The total predicted niche area of *A. andersoni* in the present day consisted of 12.8 million poor pixels, 2.2 million moderate pixels, and 1.0 million high pixels, for a total of 16.0 million pixels of habitat area (Fig. 3a). The total predicted niche area of *A. hygrophila* in the present day consisted of 4.5 million poor pixels, 2.7 million moderate pixels, and 1.0 million high pixels, for a total of 8.2 million pixels of habitat area (Fig. 4a). A pixel of niche area is roughly equal to 1 km^2. For the present day climate scenario, all three species had major regions of suitable habitat in the southeastern USA (Figs. 2a, 3a, 4a). Comparatively, *A. philoxeroides* and *A. andersoni* were predicted to have suitable habitat much further north in the eastern USA than *A. hygrophila* (Figs. 2a, 3a, 4a). The suitable habitat predicted for *A. hygrophila* was mostly relegated to the southernmost latitudes of the Gulf Coast and Atlantic Coast of the USA (Fig. 4a). Additionally, small portions of suitable habitat were predicted in California for *A. philoxeroides* and *A. andersoni,* whereas *A. hygrophila* was not predicted to have suitable habitat in California (Figs. 2a, 3a, 4a). In the native range, all three species had large regions of suitable habitat in and around the Paraná River Basin with the range *A. philoxeroides* being the most limited of the three (Figs. 2a, 3a, 4a). Aside from the Paraná River Basin, *A. philoxeroides* had very minor suitable habitat predicted in South America (Fig. 2a). In contrast, *A. andersoni* and *A. hygrophila* had a substantial region of suitable habitat in and around the Amazon River Basin (Figs. 3a, 4a).

Under both future climate scenarios, *A. philoxeroides* had marginal losses in predicted total niche area and *A. andersoni* and *A. hygrophila* had maginal gains in total niche area (Table 1). In the SSP1-2.6 and SSP5-8.5 scenario, all three species retain their major regions of suitable habitat in the southeastern USA and Paraná River Basin (Figs. 2b, c, 3b, c,

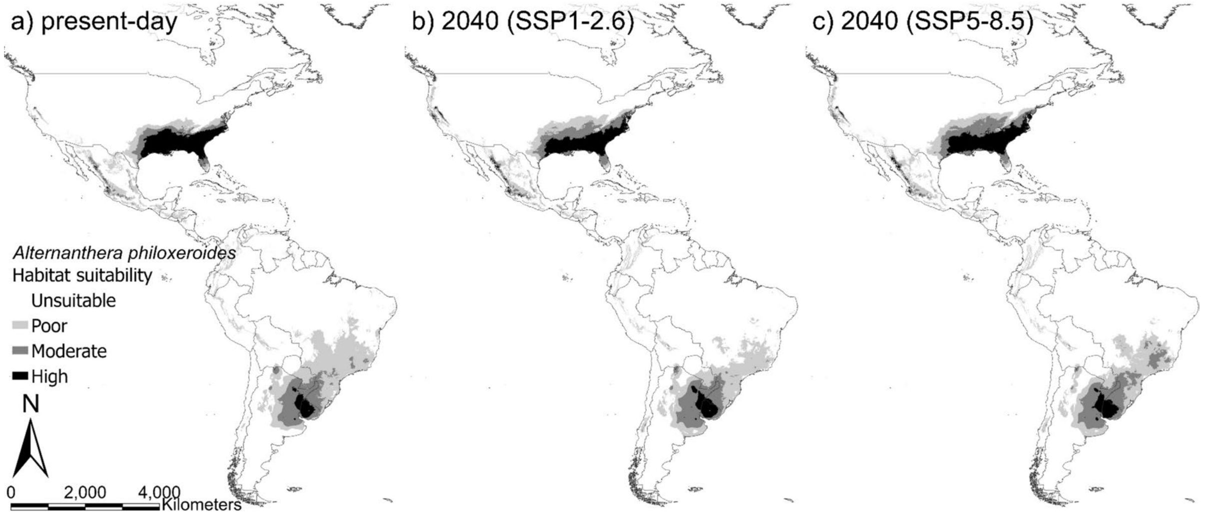


Fig. 2 Predicted habitat suitability for *A. philoxeroides* for **a** present day, **b** 2040 SSP1-2.6, and **c** 2040 SSP5-8.5

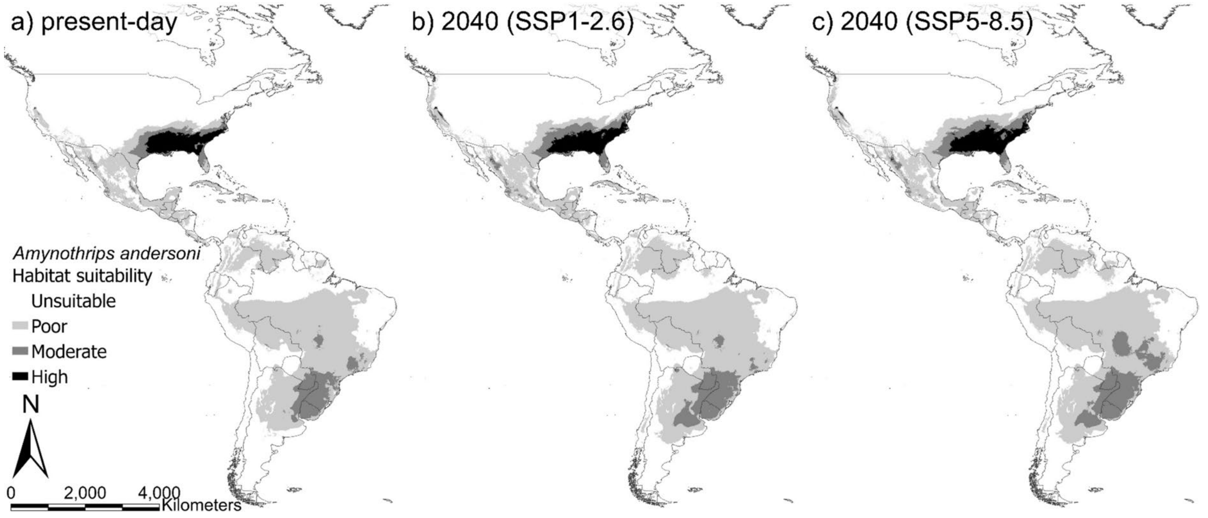


Fig. 3 Predicted habitat suitability for *A. andersoni* for **a** present day, **b** 2040 SSP1-2.6, and **c** 2040 SSP5-8.5

4b, c). The shifts of *A. philoxeroides* and *A. andersoni* expanded into the Midwest and Northeast of the USA, whereas with *A. hygrophila,* they were mostly relegated to the Southeast (Figs. 2, 3, 4). In the native range, all three species exhibit very minor shifts in suitable habitat (Figs. 2, 3, 4). *A. hygrophila* is predicted to exhibit the greatest gains in South America, particularly with highly suitable habitat in future scenarios. In all three species, the difference in ecological niche between SSP1 and SSP5 is very minor (Figs. 2, 3, 4; Table 1).

The niche overlap between *A. andersoni* and *A. philoxeroides* was greater than that of *A. hygrophila* and *A. philoxeroides* across all regions in each climate scenario according to both Schoener's D and Hellinger's I indices (Table 2). The discrepancy in *A. philoxeroides* niche overlap between *A. andersoni* and *A. hygrophila* was much less in South America comparatively, and much greater in North America and the Southeastern USA (Table 2). This discrepancy was at its greatest in the Southeastern USA in the present day scenario (Table 2).

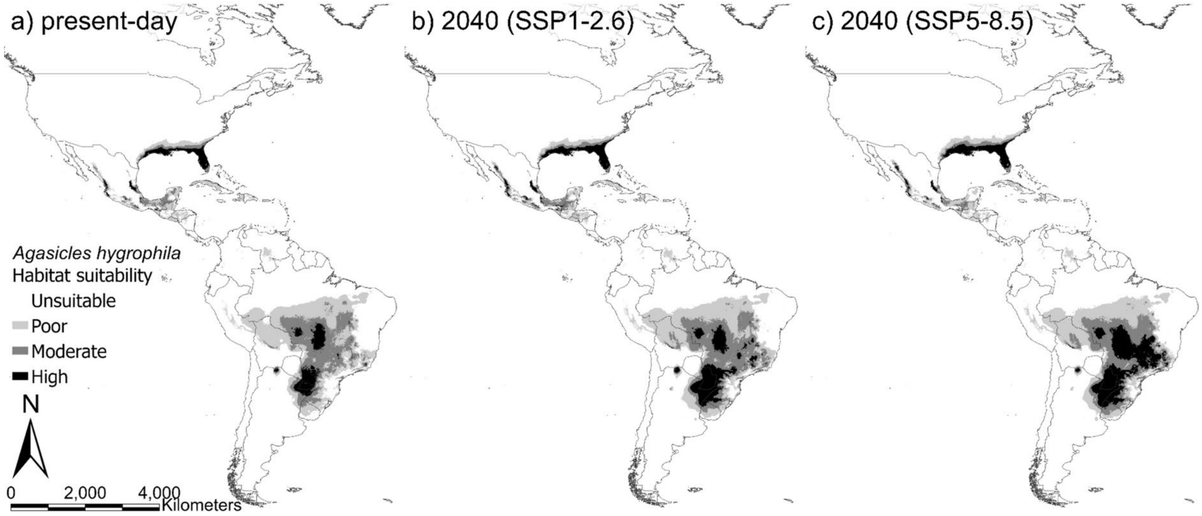


Fig. 4 Predicted habitat suitability for *A. hygrophila* for **a** present day, **b** 2040 SSP1-2.6, and **c** 2040 SSP5-8.5

Table 1 Percent change in predicted niche area in future scenarios (SSP1-2.6 and SSP5-8.5) compared to present day scenarios for *A. philoxeroides, A. andersoni,* and *A. hygrophila.* Changes in niche area represented in poorly suitable, moderately suitable, and highly suitable habitat as well as total niche area

Species	Future scenario	% of present scenario			
		Poor	Moderate	High	Total
A. philoxeroides	SSP1-2.6	85.2	114.7	93.3	93.4
	SSP5-8.5	84.2	135.1	99.9	98.5
A. andersoni	SSP1-2.6	104.8	129.1	105.7	108.1
	SSP5-8.5	102.0	151.9	109.6	109.3
A. hygrophila	SSP1-2.6	96.4	113.5	161.5	110.3
	SSP5-8.5	90.3	94.5	231.5	109.6

Discussion

While ENMs for these three species suggest some differences in ecological niches, suitable habitat of *A. philoxeroides* and *A. andersoni* are projected to expand similarly as climate change progresses. The northward invaded range expansion of all three species under climate change scenarios supports our first hypothesis (i.e., that climate change will facilitate the northward expansion of suitable habitat for all three species). Additionally, under all three scenarios the discrepancy between *A. andersoni* and *A. hygrophila* and their niche overlap with *A. philoxeroides* remains substantial, thus supporting our second hypothesis (i.e., that *A. andersoni* has greater niche overlap with *A. philoxeroides* than does *A. hygrophila*).

Whereas previous research on *A. philoxeroides* ENMs predicted little range expansion in the USA, our findings are much more congruent with Sánchez-Restrepo et al. (2023) predicting substantial, northward expansion in the USA (Julien et al. 1995). Specifically in the future climate scenarios, these ENMs predict that more of the eastern and midwestern USA will provide suitable habitat for *A. philoxeroides* by 2040 (Fig. 2). According to these predictions, the southern portions of the Midwest and Northeast of the USA are at risk for *A. philoxeroides* invasion by 2040. Comparatively, *A. hygrophila* makes gains in suitable habitat under future climate scenarios and, unfortunately, from a biological control standpoint, much of the eastern USA remains unsuitable (Table 1; Fig. 4). Additionally, a problem arises when using the fundamental niche of *A. hygrophila* to inform its utility as a biological control agent: *A. hygrophila* exhibits substantial seasonal migration (Harms and Shearer 2017). Specifically, *A. hygrophila* adults will migrate and are sometimes recorded outside of their overwintering range, thus explaining why this species is observed in regions where long-term *A. hygrophila* control has not been observed (Harms and Shearer 2017). This creates a discrepancy between the ecological niche of *A. hygrophila* and its effective range of biological control that must be accounted for. Harms and Shearer (2017) suggest that

Table 2 Continental and regional values for Schoener's D and Hellinger's I indices of niche overlap of *A. andersoni* and *A. hygrophila* with *A. philoxeroides* at present day, SSP1-2.6, and SSP5-8.5 scenarios

Region	Scenario	*A. andersoni*		*A. hygrophila*			
		D	I	D	I	ΔD	ΔI
North and South America	Present day	0.754	0.947	0.544	0.819	0.210	0.128
	SSP1-2.6	0.689	0.919	0.491	0.774	0.198	0.145
	SSP5-8.5	0.690	0.918	0.505	0.779	0.185	0.139
North America	Present day	0.824	0.949	0.470	0.776	0.354	0.173
	SSP1-2.6	0.809	0.950	0.462	0.768	0.347	0.182
	SSP5-8.5	0.810	0.950	0.470	0.772	0.340	0.178
South America	Present day	0.727	0.949	0.615	0.870	0.112	0.079
	SSP1-2.6	0.632	0.905	0.554	0.826	0.078	0.079
	SSP5-8.5	0.630	0.903	0.573	0.835	0.057	0.068
Southeastern USA	Present day	0.942	0.997	0.542	0.846	0.400	0.151
	SSP1-2.6	0.938	0.995	0.544	0.844	0.394	0.151
	SSP5-8.5	0.941	0.996	0.550	0.844	0.391	0.152
California	Present day	0.868	0.982	0.489	0.804	0.379	0.178
	SSP1-2.6	0.851	0.978	0.545	0.846	0.306	0.132
	SSP5-8.5	0.849	0.977	0.552	0.850	0.297	0.127

D Schoener's D index, *I* Hellinger's I index, *ΔD* difference of Schoener's D Index with *A. philoxeroides* between *A. andersoni* and *A. hygrophila*. *ΔI* difference of Hellinger's I Index with *A. philoxeroides* between *A. andersoni* and *A. hygrophila*

this discrepancy can be overcome with regular spring releases of *A. hygrophila* as a form of inoculative biological control but, so far, this method has not been put into practice. Ultimately, while *A. hygrophila* exhibits excellent control in the southernmost extent of *A. philoxeroides* in the USA as a biological control agent, it will become increasingly inapplicable as *A. philoxeroides* expands northward (Buckingham 1996). When compared to *A. hygrophila, A. andersoni's* potential biological control utility translates over a much greater area as evidenced by its greater area of suitable habitat (particularly in the USA) and greater niche overlap with *A. philoxeroides.* Under future climate scenarios, *A. andersoni's* predicted niche overlap with *A. philoxeroides* exhibits substantial gains for SSP1-2.6 and SSP5-8.5 by 2040 and its suitable habitat covers much of the eastern USA (Table 2; Fig. 3). While the efficacy of *A. andersoni* control has shown promising results in experimental studies, it remains unclear whether this species can fill the gap in *A. philoxeroides* biological control left by the cold-intolerant *A. hygrophila* (Schmid et al. 2024).

Alternanthera philoxeroides biological control in the southeastern USA

When focusing on the extent of the southeastern USA, our niche models predict that *A. andersoni* is a much better climate match for *A. philoxeroides* than *A. hygrophila* (Supplementary Figs. S2, S3, S4; Table 2). *A. philoxeroides* has been a problem in the Southeast for nearly a century and its control by *A. hygrophila* has been thoroughly studied (Buckingham 1996). Consequently, while *A. hygrophila* remains effective in the southernmost extent of the invaded range, its poor climate match with *A. philoxeroides* has been documented for decades (Julien et al. 1995; Sánchez-Restrepo et al. 2023). Our findings are congruent with these results: *A. hygrophila* is predicted to have very little suitable habitat north of 33° N in the USA both at present and by 2040 (Supplementary Figure S4). This reflects poorly on its utility as an *A. philoxeroides* biological control agent as *A. philoxeroides'* niche is predicted to expand north of 38° N by 2040 (Supplementary Fig. S2). Although the climate match of *A. hygrophila* to *A. philoxeroides* remains relatively poor, in areas where *A. hygrophila* biological control is viable it is still a highly effective option (Harms and Shearer 2017). Comparatively, *A. andersoni* has a much greater niche overlap with *A. philoxeroides,* within the southeastern USA. In future climate scenarios, *A. andersoni* is predicted to expand its range northward to a very similar geographic extent as *A. philoxeroides* (Supplementary Figs. S2, S3), suggesting it will continue to be an excellent climate match by 2040. These suggest that *A. andersoni* will be a valuable control tool for *A.*

philoxeroides in the southeastern USA, although questions remain about its control efficacy.

Alternanthera philoxeroides biological control in California

In the USA, invasive *A. philoxeroides* is primarily associated with the Southeast. However, it has also established invasive populations in California, albeit to a much smaller spatial extent (Pratt et al. 2021). While initially relegated to southern California, *A. philoxeroides* has since spread to more northern parts of the state including the Sacramento-San Joaquin Delta (Walden et al. 2019). Its spread has prompted efforts to manage *A. philoxeroides* in California, particularly within the Sacramento-San Joaquin Delta (Pratt et al. 2021). In the 60s and 70s, releases of *A. hygrophila* and *A. andersoni* were conducted for the purposes of controlling *A. philoxeroides* but, presently, there appear to be no established populations of either biological control agent from these releases (Pratt et al. 2021). Recent efforts to establish both agents have been conducted in the Sacramento-San Joaquin Delta, but at present it is uncertain whether they have established or will establish (Pratt et al. 2021).

In this study, *A. philoxeroides* ENMs predicted two large clusters of suitable habitat within northern California: along the northeastern ridge of the Central Valley and along the North Coast (Supplementary Fig. S5). When compared to the present day scenarios, both future scenarios predict considerable increases in these clusters of suitable habitat by 2040 (Supplementary Fig. S5). Notably, the niche models predict almost no suitable habitat within the Sacramento-San Joaquin Delta, despite current record of *A. philoxeroides* invasion in this region (Supplementary Fig. S5). In all three climate scenarios of this study, predicted suitable habitat of *A. philoxeroides* extends well beyond its current known extent, suggesting a strong potential to spread within California.

In addition to *A. philoxeroides, A. andersoni* also has considerable predicted suitable habitat within northern California (Supplementary Fig. S6). *A. andersoni* is predicted to have a larger niche in California than *A. philoxeroides* but, within California, niche overlap between *A. andersoni* and *A. philoxeroides* is similarly high compared to the rest of the invaded range (Table 2). Our niche models predict no suitable habitat for *A. hygrophila* within California, and its niche overlap with *A. philoxeroides* is substantially lower than that of *A. andersoni* according to both overlap indices (Table 2). While this seems promising for *A. andersoni* biological control in California, these ENMs might have accuracy issues within California, particularly for the biological control agents. Ecological niche models accumulate uncertainty in their predictions the further they extrapolate beyond the extent of their occurrence data (Soley-Guardia et al. 2024). This loss of accuracy can be demonstrated in our data when *A. philoxeroides* ENMs are constructed using only data from the native range or only from the invaded range (Supplementary Fig. S7). Since there are currently no records of either biological control agent in California, the uncertainty of model predictions for this area is quite high. Until these species are successfully established, or until establishment attempt decisively fails, in this region, it is likely that the true status of their habitat suitability in California will remain undetermined. To date, all establishment efforts of *A. philoxeroides* biological control agents in California have seemingly failed, although this effort is ongoing (Pratt et al. 2021).

Considerations and future research

Results from this study suggest that the ecological niche of *A. andersoni* much more closely matches that of *A. philoxeroides* than *A. hygrophila.* While this is promising for the utility of *A. andersoni* as a biological control agent, there is little evidence whether *A. andersoni* can effectively control *A. philoxeroides* in the field. Recently, *A. andersoni* effectively reduced *A. philoxeroides* biomass in a controlled setting as a stand-alone control agent (and as part of an integrated biological-chemical control technique) but scaling biological control up to a field scale presents additional challenges (Schmid et al. 2024). Studies that examine the biological control efficacy of *A. andersoni* in the field are necessary to better assess its future as a biological control agent. Also, it is currently unknown how well the *A. andersoni* would integrate into a biological control program that includes *A. hygrophila.* Future studies that assess the combined control of *A. andersoni* and *A. hygrophila* would benefit resource managers tasked with controlling *A. philoxeroides.*

While *A. andersoni* seems to be one solution to the *A. hygrophila* cold tolerance problem of *A. philoxeroides* management, researchers are seeking other solutions. In California's Sacramento-San Joaquin Delta, neither *A. andersoni* nor *A. hygrophila* have been successfully established in the wild. The released insects were taken from wild populations in the southeastern USA, and their failure to establish is presumably because these populations are poorly adapted to northern California climate (Pratt et al. 2021). Although previous attempts at establishment have failed, researchers suspect that other biotypes of *A. andersoni* and *A. hygrophila* in the native range would be better suited for California than those currently in North America (Pratt et al. 2021). This is further evidence of the importance of native range research on invasive species, particularly in the field of biological control (Pratt et al. 2021).

While establishment of these species in new regions is beneficial from a control perspective, it also improves the accuracy of niche models. In the case of California *A. philoxeroides*, researchers and resource managers would benefit from niche models specifically tuned to western North America, but presence data are lacking to develop locally calibrated models for *A. andersoni* and *A. hygrophila.* Niche models often lose accuracy when extrapolating a prediction to a disjunct area, as is the case with the southeastern USA and California. Successfully establishing these biological control agents in new regions of the invaded range of *A. philoxeroides* should not only improve control but also increase accuracy of predictive biological control research. For these reasons, responsible establishment efforts for *A. andersoni* and *A. hygrophila* should be prioritized. Additionally, the occurrence dataset of both biological control agents (but particularly *A. andersoni*) is quite small, and larger datasets would greatly improve the accuracy of niche modeling efforts.

Although the results of this study show promise for the biological control utility of *A. andersoni,* there are some potential issues with accuracy inherent in the scant training data available for *A. andersoni.* MaxEnt has been used by ecologists to build ENMs for nearly two decades and while the methods have improved considerably, there are still no standard practices to using MaxEnt (Phillips et al. 2006; Elith et al. 2010). Other studies have tested the accuracy of ENMs on very small training datasets. These studies determined that, in order to maintain model accuracy, a minimum threshold of sample size, somewhere between 15 and 30 records, must be obtained (Sampaio and Cavalcante 2023; Shim et al. 2023). While the training dataset for *A. andersoni* met these theoretical thresholds, the area over which the *A. andersoni* models were predicted in our study was much greater than the area in the studies of Sampaio and Cavalcante (2023) and Shim et al. (2023), and it is possible that could affect the sample size threshold. Our *A. andersoni* ENMs were potentially subject to overfitting to at least some degree as a result of the small training dataset. While overfitting is a possibility with the *A. andersoni* ENM, the difference between training and validation AUCs for the best fit model was quite low ($x < 0.01$) which generally indicates a low degree of overfitting, and with a regularization multiplier of 2.0, overly complex models should have been adequately penalized (Phillips et al. 2006). Fortunately, the issue of a small training dataset is actively being mitigated, as over two thirds of the *A. andersoni* dataset has been added since 2017. With continued surveys for *A. philoxeroides* biological control agent records, the accuracy of these ENMs will continue to improve.

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Author contributions GT and GNE acquired funding that supported this study. SAS, GT, and GNE contributed to the study conception and design. SAS performed methods and collected and analyzed the data. SAS, AFSR, AJS, and GNE interpreted the data. SAS drafted the initial version of the manuscript. All authors critically revised subsequent versions of the manuscript. All authors read and approved the submitted version of the manuscript.

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Declarations

Conflict of interest The authors declare no competing interests relevant to this study.

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