



Biocontrol in a warmer world: anticipating the climate suitability of an aggressive invasive plant and its specialist herbivore

Mikaela Marques Pulzatto · Luiz Guilherme dos Santos Ribas · Raytha de Assis Murillo ·
Fernanda Moreira Florêncio · Montserrat Vilà · Sidinei Magela Thomaz

Received: 21 April 2024 / Revised: 15 January 2025 / Accepted: 25 January 2025
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2025

Abstract Climate change may exacerbate alien species expansion into previously unsuitable areas. This shift in species distributions can lead to mismatches between interacting species. We evaluated the potential worldwide distribution of the invasive plant *Alternanthera philoxeroides*, and its specialist herbivore, the flea beetle *Agasicles hygrophila*, under future global warming scenarios to identify overlapping and non-overlapping areas. We used species distribution models (SDMs) to predict the potential global distribution of both species in current, and in moderately optimistic and pessimistic scenarios. Climate change

is expected to significantly expand *A. philoxeroides* toward higher latitudes, increasing its global range and climatic suitability. *Agasicles hygrophila* is also predicted to expand, albeit to a lesser extent, with some loss of currently suitable areas and a decrease in suitability. The overlapping area between their distributions is projected to increase globally, except in the USA. This suggests promising biocontrol potential for alligator weed in many regions in the future, but portions of its distribution may remain unsuitable for the flea beetle, particularly at higher latitudes. The northward expansion of the plant beyond the flea beetle's range may create zones with low control efficiency. These findings can help management strategies for this invasive plant under its future potential distribution.

Handling editor: Koen Martens

Guest editors: Sidinei M. Thomaz, Cécile Fauvelot,
Lee B. Kats, Jonne Kotta & Fernando M. Pelicice /
Aquatic Invasive Species IV

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10750-025-05808-2>.

M. M. Pulzatto · F. M. Florêncio · S. M. Thomaz (✉)
Graduate Program in Ecology of Inland Water Ecosystems (PEA), Department of Biology (DBI), Center of Biological Sciences (CCB), State University of Maringá (UEM), Av. Colombo, 5790, Bloco G90, Jardim Universitário, Maringá, Paraná CEP 87020-900, Brazil
e-mail: smthomaz@nupelia.uem.br

L. G. dos Santos Ribas
Laboratório de Biologia da Conservação, Departamento de Biodiversidade, Universidade Estadual Paulista, Av. 24 A, 1515, São Paulo, Rio Claro CEP 13.506-692, Brazil

R. de Assis Murillo
Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada

M. Vilà
Doñana Biological Station (EBD-CSIC), Americo Vesputio S/N, Isla de La Cartuja, 41092 Seville, Spain

M. Vilà
Department of Plant Biology and Ecology, University of Seville, Seville, Spain

Keywords *Agasicles hygrophila* · Alligator weed · *Alternanthera philoxeroides* · Global warming · Biological control efficiency · Climate change · Flea beetle · Species distribution model

Introduction

Biological invasions and climate change are recognized as two major anthropogenic drivers of global change, with significant negative impacts on biodiversity, economy, ecosystem services, and human health (Bellard et al., 2012, 2016, Mollot et al., 2017, IPBES, 2019, Rai and Singh, 2020, WWF, 2020). In addition to their individual impacts, climate change is expected to intensify biological invasions by increasing the probability of some alien species expanding into previously unsuitable areas (Walther et al., 2009). Climate change can influence all stages of the invasion process. Firstly, it can facilitate species introduction through the intensification of extreme climatic events or changes in human activities (Hellmann et al., 2008; Walther et al., 2009). Subsequently, it creates new environmental conditions that can enhance the survival, growth rate, reproduction, and competitive ability of invasive species (Hellmann et al., 2008; Walther et al., 2009). Consequently, climate change can lead to shifts in the geographic distribution of invasive species and affect their management by influencing the effectiveness of control strategies, particularly biological control (Hellmann et al., 2008).

The shifting of species distributions driven by climate change can lead to mismatches between the occurrence areas of interacting species, such as plants and their herbivores (Parmesan 2006), or in the case of invasive species, their biocontrol agents (Hellmann et al., 2008). Evidence in the literature suggests that under future climate scenarios, invasive plants have a significant potential for expanding their global distribution (e.g., Bradley et al., 2009; Osland & Feher, 2019; Wang et al., 2019). This expansion is often attributed to the broad thermal niche tolerance of highly invasive plants (Bustamante et al., 2020) that may benefit from “invasion windows” that arise due to extreme climatic events (Diez et al., 2012). The situation is particularly concerning at higher latitudes, where changes in temperature and precipitation create new suitable habitats for plant species that

were previously limited by winter-induced poleward expansion constraints (Osland & Feher, 2019; Osland et al., 2021).

On the other hand, many plant biocontrol agents, such as insects, are small ectothermic organisms, and ambient environmental temperature plays a crucial role in regulating their distribution by influencing various physiological functions, including respiration, metabolism, growth, reproduction, overwintering, and diapause (Harvey et al., 2020). Consequently, extreme temperature events can, for instance, adversely affect the survival and biomass of certain insect species (Harvey et al., 2020). Some species are ill-suited to cope with temperature extremes, and their survival may depend on their ability to migrate toward more suitable thermal environments (Chapman et al., 2015; Harvey et al., 2020), which can lead to a contraction of these organisms range due to climatic changes (e.g., Chen et al., 2011).

Alternanthera philoxeroides (Mart.) Griseb. (Amaranthaceae), commonly known as alligator weed, is a herbaceous amphibious macrophyte native to the Paraná River basin in South America. It has invaded all continents except Africa and Antarctica (Bulletin OEPP/EPPO Bulletin, 2016, Arana & Murillo, 2021). Alligator weed is considered a troublesome weed in at least 30 countries, identified as one of the 12 most harmful invasive species in China, and classified as a Weed of National Significance in Australia (Geng et al., 2007; Pan et al., 2007; CHAH, 2021). Its success as an invasive species can be attributed, in part, to its high phenotypic plasticity (Geng et al., 2016).

While alligator weed prefers a warm, stable, and rainy climate (Yan et al., 2020), with an optimal temperature range around 30–35°C (Shen et al., 2005), it has a wide tolerance to temperatures. Genetic adaptation for cold tolerance has been observed in some alligator weed populations in China, enabling its spread to northern regions of the country (Luo et al., 2020). Additionally, experiments investigating the effects of warming have shown that temperature increases of 1°C and 2°C do not significantly impact its growth (Meza-Lopez et al., 2017). In fact, regional studies have indicated a potential poleward expansion of this invasive plant in areas where it is already established in response to climate change (e.g., USA – Konkki et al., 2015, China – Tu et al., 2021). However, there is a notable lack of global-scale studies for this species.

On the other hand, the specialist herbivore of alligator weed, and its primary biological control agent in invaded areas, *Agasicles hygrophila* Selman & Vogt, 1971 (Coleoptera), commonly known as flea beetle, has a much smaller global distribution compared to alligator weed, resulting in some gaps between their distributions (Julien et al., 1995; Lu et al., 2013). Native to southern Brazil and northern Argentina (Center et al., 2009), this specialist herbivore is restricted to subtropical regions. This reflects the narrow temperature range tolerated by the insect, which exhibits low tolerance to both cold temperatures (below 15°C) and hot temperatures (above 30°C) (Stewart et al., 1999; Zhao et al., 2015; Harms & Cronin 2019; Jin et al., 2020; Jia et al., 2020).

Field surveys and experiments have indicated that global warming may lead to increased flea beetle populations, enhanced herbivory, and the establishment of this species in new habitats previously limited by cold winters (Hruska et al., 1985; Hellmann et al., 2008; Lu et al., 2013). However, global warming may also restrict the establishment, expansion, and effectiveness of this insect in hot areas (Jia et al., 2020) due to its strong sensitivity to high temperatures. This sensitivity is particularly notable in the eggs, which exhibit a low tolerance of 37.5°C. Lu et al. (2013) suggested that under climate change, the existing geographical gap between *A. philoxeroides* and its herbivore *A. hygrophila* may shift toward higher latitudes due to global warming, creating a new zone with low or no control efficiency, rather than eliminating it entirely.

Despite the available regional evidence, we still lack a global perspective on the potential distribution of both the invasive plant, *A. philoxeroides*, and its biocontrol agent, *A. hygrophila*, under future climate scenarios, especially evaluating their overlap. In this study, we employed species distribution models (SDMs) to determine the new areas that could be suitable for both species in future global warming scenarios. Additionally, we aimed to identify the potential overlapping and non-overlapping areas across the globe for these species. Due to their distinct thermal requirements and tolerances, as described previously, we anticipate the following outcomes: (i) the climate suitability for alligator weed will increase, resulting in an expanded potential distribution, particularly in higher latitudes where temperature is expected to rise; (ii) the distribution of *A. hygrophila* will contract,

leading to a decrease in suitability; and consequently, (iii) there will be fewer overlapping areas between the distributions of these two species under future climate scenarios.

Material and methods

Occurrence and climate data

We obtained occurrence records for both alligator weed and the flea beetle on a global scale, encompassing their native and invaded ranges, from the Global Biodiversity Information Facility (GBIF) online database (<https://www.gbif.org>) (GBIF.org, 2022). Additionally, we collected occurrence information for both species from the literature by searching for terms such as '*Alternanthera philoxeroides*,' '*A. philoxeroides*,' 'alligator weed,' '*Agasicles hygrophila*,' '*A. hygrophila*,' and 'alligator weed flea beetle' in the Web of Science Thompson Institute for Scientific Information (ISI; www.isiknowledge.com; accessed on July 14, 2021). A total of 595 articles, spanning from 1967 to 2021, were obtained, including the recent contribution by Arana and Murillo (2021). Out of these, 376 articles contained occurrence information which allowed us to extract the corresponding coordinates. We removed duplicate points that fell within the same pixel that we used to determine species occurrence.

We obtained current climate data from the WorldClim database (www.worldclim.org) for the period between 1970 and 2000. The data were retrieved at a spatial resolution of 10 min (~340 km²). We utilized all 19 available bioclimatic variables based on temperature and precipitation. These variables are widely recognized as biologically significant for most species and are commonly used in ecological modeling (Woodward and Williams 1987). Previous studies on *A. philoxeroides* and *A. hygrophila* also incorporated some of these variables in their species distribution models (SDMs), highlighting their importance for these species (e.g., Julien et al. 1995; Stewart et al. 1995; Koncki & Aronson, 2015; Wang et al., 2017; Yan et al., 2020; Tu et al., 2021).

To identify non-collinear variables, we conducted a scree plot analysis (Fig. S1) to determine the number of factors required to capture the environmental variation without collinearity. The plot indicated that four factors, represented by variables, would be

adequate (Fig. S1). Subsequently, we performed a factorial analysis to select the variables that would account for the greatest amount of environmental variation while maintaining the number of factors indicated by the scree plot. For both species, we included the following four selected non-collinear variables in our models: Maximum Temperature of Warmest Month (BIO 5), Temperature Annual Range (BIO 7), Precipitation of Wettest Month (BIO 13), and Precipitation of Driest Quarter (BIO 17) (Fig. 1).

We obtained future climate predictions for the same variables from the Intergovernmental Panel on Climate Change, Sixth Assessment Report (IPCC-AR6) (www.worldclim.org), for three time periods (2021–2040, 2041–2060, and 2061–2080), and gathered them in a single period, representing the future scenario (Fig. 1). For the climate scenarios, we selected one moderately optimistic scenario (Shared Socioeconomic Pathways; SSP2-4.5) and one pessimistic scenario (SSP5-8.5) of CO₂ emissions (Fig. 1; for more details, see Riahi et al., 2017). The SSP scenarios, more comprehensive than the previous Representative Concentration Pathways (RCPs) from the

IPCC-AR5, incorporate socioeconomic factors such as population, economic growth, education, urbanization, and technological development, and project how these factors may evolve by 2100 (Riahi et al., 2017). These factors can have significant implications for invasive species predictions. To account for uncertainties and capture variations among models, we used an ensemble of six General Circulation Models (GCMs) (Fig. 1). These models were provided by the BCC (Beijing Climate Center), CCCma (Canadian Centre for Climate Modelling and Analysis), CNRM (National Center for Meteorological Research, Météo-France), and MIROC (Model for Interdisciplinary Research on Climate).

Species distribution models (SDMs)

To predict the potential global distribution of the alligator weed and the flea beetle under current and future climate scenarios, we utilized species distribution models (SDMs). These models are correlative in nature and estimate potential occurrence points of a species beyond its known distribution range by

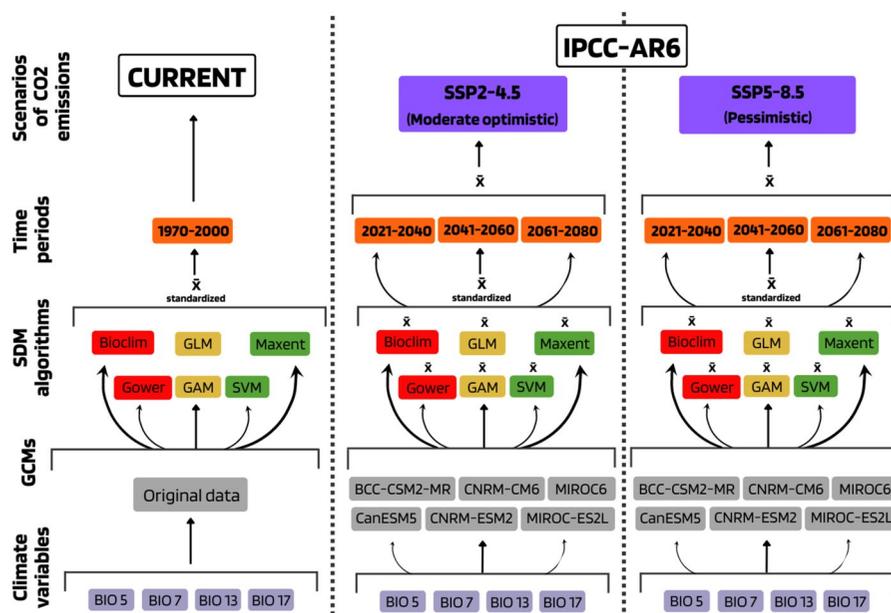


Fig. 1 Flowchart of the species distribution models (SDM) analyses for *Alternanthera philoxeroides* and *Agasicles hygrophila* in current and two different future climate scenarios based on IPCC-AR6 projections. The climate variables used in the analysis are as follows: BIO5=Maximum Temperature of Warmest Month, BIO7=Temperature Annual Range,

BIO13=Precipitation of Wettest Month, and BIO17=Precipitation of Driest Quarter. The analysis incorporates an ensemble of General Circulation Models (GCMs) to account for variations. SDM algorithms are represented by colors: red for envelope models, yellow for statistical models, and green for machine learning models

using a species occurrence matrix and environmental-climate predictors (Peterson et al., 2011). SDMs have been widely employed to forecast distribution shifts of invasive species, particularly in the context of climate change scenarios (e.g., Koncki & Aronson, 2015; Wang et al., 2017; Petsch et al., 2020). Predictive models are invaluable tools for this purpose due to the uncertainties associated with the magnitude and impact of climate change. Moreover, they are highly effective for large-scale modeling, as they do not require waiting for complete data sampling, which could take years to obtain.

In this study, we employed six distinct SDM algorithms to generate predictions: Bioclim and Gower (Envelope models), GLM and GAM (Statistical models), Maxent and SVM (Machine Learning models) (Fig. 1). Envelope models are based on distances in two and multidimensional spaces, utilizing only presence data of the target species. Statistical models involve various types of statistical analyses, such as correlations and regressions, and utilize presence-absence data. Machine learning models utilize construction algorithms and require both presence data and background information. By combining these different algorithms, we were able to incorporate the uncertainties associated with each approach and obtain a more robust ensemble model.

We utilized a species occurrence matrix and climate predictors to conduct the SDMs. These models generated climate suitability matrices, which were employed to project the potential distribution of the alligator weed and flea beetle for current and future scenarios worldwide. To construct and evaluate SDMs for current and future years, we randomly divided the species occurrence data into 75% for calibration (training) and 25% for evaluation (testing), repeating this process 25 times for each algorithm. Consequently, we obtained a total of 150 SDMs for each species for the current period, representing 25 repetitions for each of the six model algorithms. For future scenarios, we repeated this process and additionally incorporated information on three different sets of future climatic scenarios, six variations of General Circulation Models (GCMs), and two carbon emission scenarios. This resulted in a total of 5400 SDMs for future scenarios (Fig. 1).

We evaluated the performance of the models by assessing the area under the curve (AUC), which is derived from the receiver operating characteristic

(ROC) curve. AUC values range from 0 to 1, with higher values indicating more accurate predictions of species presence or absence using the testing dataset. Our models demonstrated high AUC values (>0.8) (Table S1), indicating their predictive solid capability. As a result, all the models were included for subsequent analysis.

We calculated a threshold for each SDM using the spec sens metric (Table S1) and applied this cut value to the climate suitability matrices of all the models. A threshold is used to maximize the sensitivity (true positive rate) plus the specificity (true negative rate), i.e., to maximize the percent of points correctly predicted as “presence” or “absence”. Finally, we created ensemble models by calculating the average predictions for each modeling algorithm and standardizing the predictions across algorithms for each species (Fig. 1). To achieve this, we standardized the predictions of the various SDMs and then combined them into a single model. Likewise, for future scenarios, we followed the same approach as in the current period. Additionally, we summarized the models developed for different GCMs and future time windows (covering the period from 2021 to 2080) by calculating the average suitability for each species, while keeping the two carbon emission scenarios separate.

Based on the final average models, we projected the potential distribution of each species for each scenario of CO₂ emissions. We then estimated the difference in the number of suitable grid cells between current and future climate scenarios for alligator weed and flea beetle. If our first hypothesis is correct, the future scenarios will present more suitable grid cells for alligator weed than the present. In addition, there would be new suitable grid cells toward higher latitudes on the predicted maps of future scenarios. For our second hypothesis to not be rejected, we expect to find more suitable grid cells at the present than in the future for the flea beetle. We also expect them to be concentrated at mid-latitudes on the predicted maps of future scenarios. Finally, we compared the number of suitable grid cells between the potential distribution of alligator weed and flea beetle in present and future scenarios. We expect to find fewer grid cells shared between the species distributions in the future so as not to reject our third hypothesis.

We conducted all data manipulation, analyses, and figure generation using the R software (R Core Team, 2021). Our analysis relied on several R packages,

including rJava (Urbanek, 2022), vegan (Oksanen et al., 2020), ggplot2 (Wickham, 2016), rnaturland (South, 2017), raster (Hijmans, 2022), and dismo (Hijmans et al., 2020) packages.

Results

In general, the potential distribution of alligator weed is projected to significantly expand under global warming. When comparing the future scenarios (SSP2-4.5 and SSP5-8.5) to the present, there is a substantial increase in the number of suitable grid cells for *A. philoxeroides*. Specifically, there is a 48.56% increase in suitable cells for SSP2-4.5 and a 64.5% increase for SSP5-8.5 (Figs. 2a, c, e, and 3a, c; Videos S1 and S3). When comparing the two future scenarios, the distribution of alligator weed

is expected to expand even further by 19.49% in the more pessimistic scenario (Fig. 3e – red cells). While the species may potentially lose 4.77% and 2.62% of the currently suitable cells in the SSP2-4.5 and SSP5-8.5 scenarios, respectively, there will still be a considerable increase in overall suitable habitat (Figs. 3a, c – yellow cells; Video S3). Additionally, not only will the potential area increase, but the climate suitability of the grid cells will also improve, as evidenced by the increase in red cells in the future maps (Fig. 2a, c, e; Video S1).

The expansion of suitable habitat for alligator weed is projected to occur predominantly toward higher latitudes in the northern hemisphere and in specific regions, such as the interior of the Amazon, Western Argentina, Central America, central Africa, Eastern Europe, and Western China (Figs. 2a, c, e, and 3a, c; Video S1 and S3). In the USA, there is a

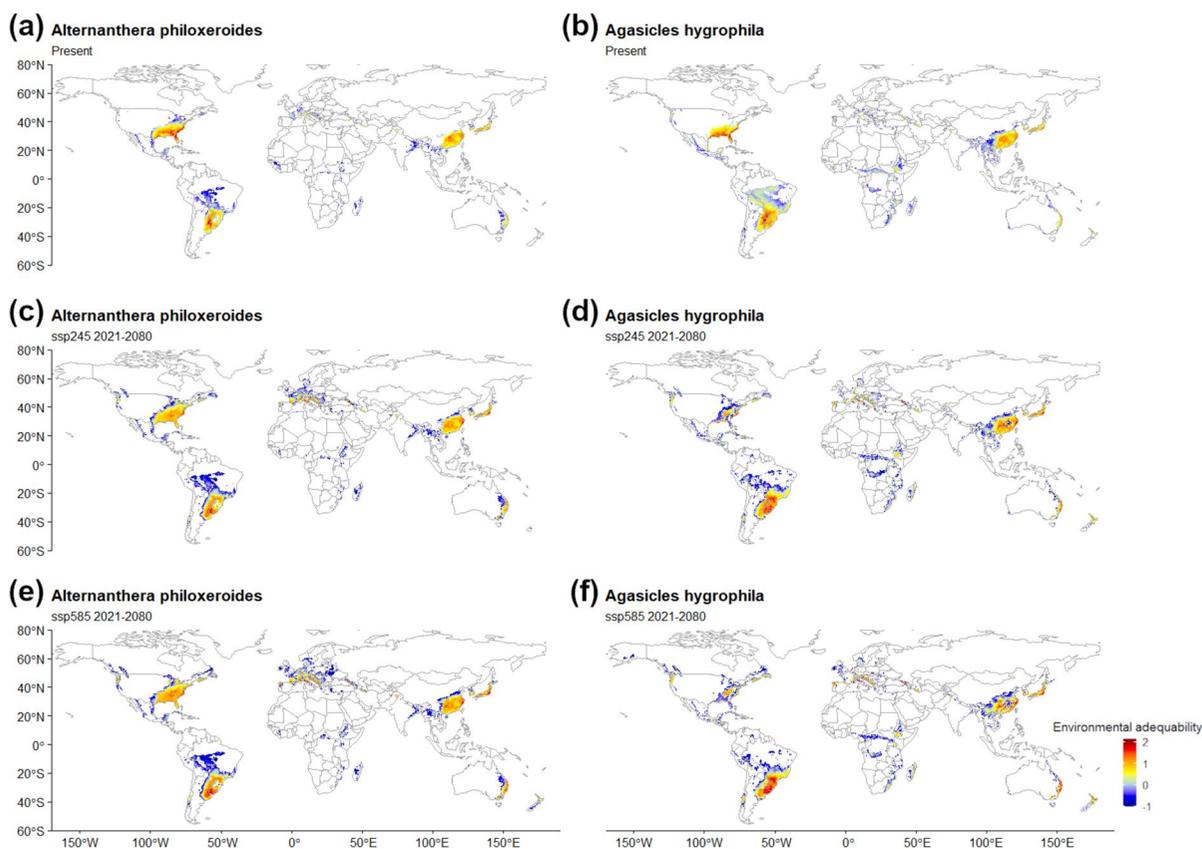


Fig. 2 Potential global distribution of *Alternanthera philoxeroides* (alligator weed) **a, c, e** and *Agasicles hygrophila* (flea beetle) **b, d, f** based on their climatic niches. The maps illus-

trate the current distribution (**a, b**) as well as two future CO₂ emission scenarios: a moderately optimistic scenario (**c, d**) and a pessimistic scenario (**e, f**)

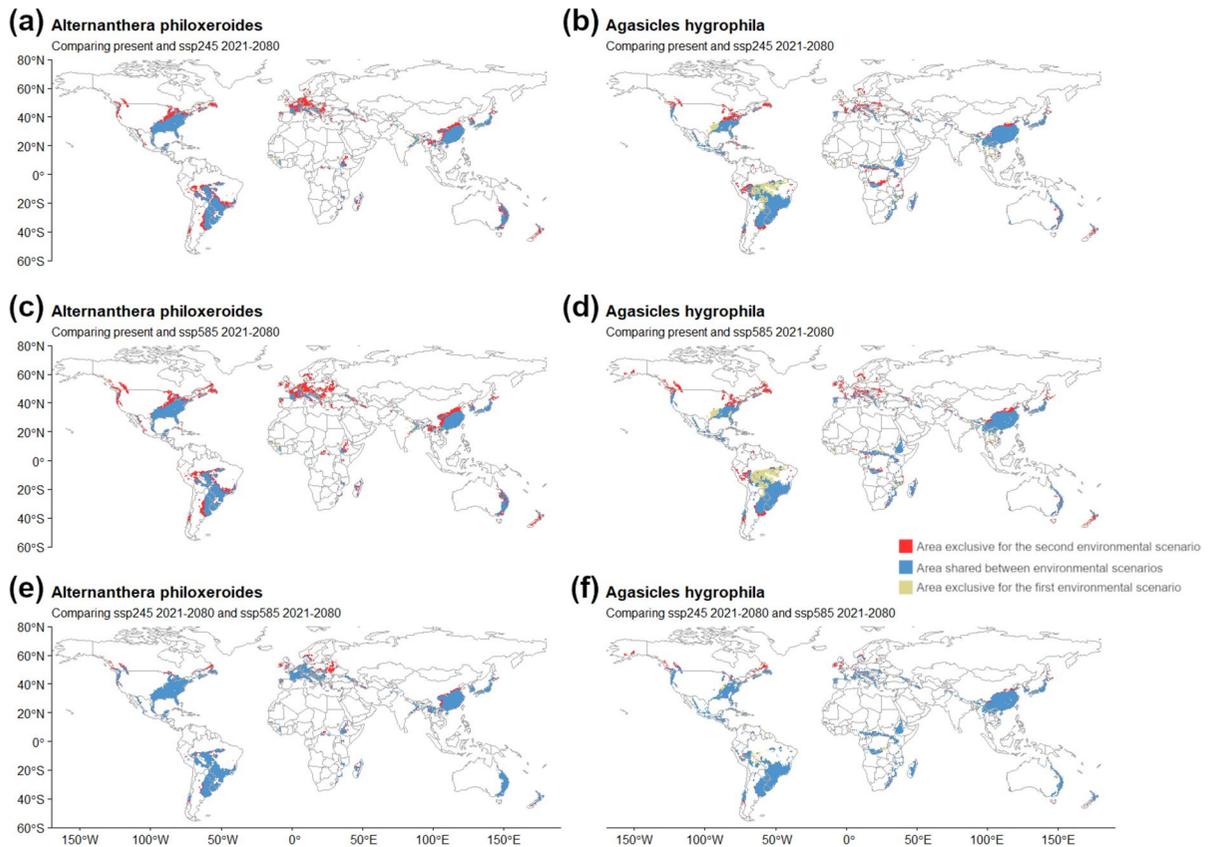


Fig. 3 Comparisons of the potential global distributions of *Alternanthera philoxeroides* (alligator weed) **a, c, e** and *Agasicles hygrophila* (flea beetle) **b, d, f** between different scenarios. Panel (**a** and **b**) compares the distributions between the current

scenario and a moderately optimistic CO₂ emission scenario, while panel (**c** and **d**) compares the current scenario with a pessimistic scenario. Panel (**e** and **f**) presents a comparison of both future scenarios

significant potential for northward expansion, extending into southern Canada on both coasts (Fig. 3a, c; Video S3). However, it is worth noting that the suitability level is expected to decrease, particularly along the southeast coast of the USA, where it is currently highly suitable to the species (Fig. 2a, c, e; Video S1). There is also a smaller predicted southward expansion toward Mexico but with lower suitability (Figs. 2a, c, e, and 3a, c; Video S1 and S3). Additionally, the areas that will become unsuitable for the species in the future are primarily located in Texas, the USA, and the east coast of Mexico (Fig. 3a, c – yellow cells; Video S3).

Alligator weed distribution will potentially reach higher latitudes in South Korea and Japan, and the climate suitability in these countries will tend to increase in future scenarios (Figs. 2a, c, e and 3a,

c; Videos S1 and S3). In China, the distribution can expand north and west to the center of the country, but with lower suitability (Figs. 2a, c, e and 3a, c; Videos S1 and S3). Expansion and greater suitability are expected across the east coast of Australia and the north island of New Zealand (Figs. 2a, c, e and 3a, c; Videos S1 and S3). Lastly, we observed several suitable areas for colonization in many European countries, even where it has not yet been recorded (Figs. 2a, c, e and 3a, c; Videos S1 and S3).

For the flea beetle, there is also a projected expansion in future scenarios, although to a lesser extent compared to alligator weed (SSP2-4.5 vs. Present = %; and SSP5-8.5 vs. Present = % increase in suitable cells; Figs. 2b, d, f and 3b, d; Videos S2 and S4). The difference between the SSP2-4.5 and SSP5-8.5 scenarios is small, with a 8.61% increase

in suitable cells expected in the pessimistic scenario (Fig. 3f – red cells). Also, there is an increase in the number of cells that are currently suitable for the flea beetle under climate change (Present vs. SSP2-4.5=23.89%; and Present vs. SSP5-8.5=28.06%; Fig. 3b, d – yellow cells; Video S4). However, the climate suitability for the flea beetle has the potential to decrease substantially in the future, as indicated by the increase in blue cells globally (Fig. 2b, d, f; Video S2).

In general, the expansion of the flea beetle's distribution follows similar patterns to the plant (Figs. 2b, d, f and 3b, d; Videos S2 and S4). The most significant loss of suitable area and suitability occurs in the USA, resulting in very few areas with moderate to high climate suitability, mainly concentrated on the west coast near the Canadian border, as well as in Louisiana, Tennessee, and North Carolina (Figs. 2b, d, f and 3b, d; Videos S2 and S4). In China, there is an increase in suitability in areas where it is currently moderate, but a sharp decrease in surrounding regions (Fig. 2b, d, f; Video S2). Higher latitudes in South Korea and most of Japan have the potential to become suitable for the flea beetle, with coastal regions maintaining a relatively high level of climate suitability, although to a lesser extent compared to

the plant (Fig. 2). Additionally, there is an increase in suitability predicted under climate warming in regions such as the east coast of Australia, north of the Iberian Peninsula, central Europe, and the east coast of the Black Sea (Fig. 2b, d, f; Video S2).

Comparing the distributions of the two species, the model(s) predicted an increase of 32.74% and 41.42% in the number of shared cells in the SSP2-4.5 and SSP5-8.5 future scenarios, respectively (Fig. 4 – blue cells; Video S5). However, this increase will not occur uniformly across all regions. There will be a potential decrease in the overlapping area in the USA. Furthermore, in these shared locations, high climate suitability is expected for the plant, but low suitability for the flea beetle, particularly in the southeast region (Figs. 2 and 4). Overlapping areas with high climate suitability for both species will be concentrated in Louisiana, Tennessee, and North Carolina, where they will remain highly suitable for the flea beetle (Figs. 2 and 4). Similarly, the southeast of China, the coast of South Korea, Japan, and the east coast of Australia are territories highly suitable for both species, resulting in large areas of overlap (Figs. 2 and 4). In Europe, there will be numerous overlapping areas in several countries (e.g., north of the Iberian Peninsula), but a significant portion of the plant's

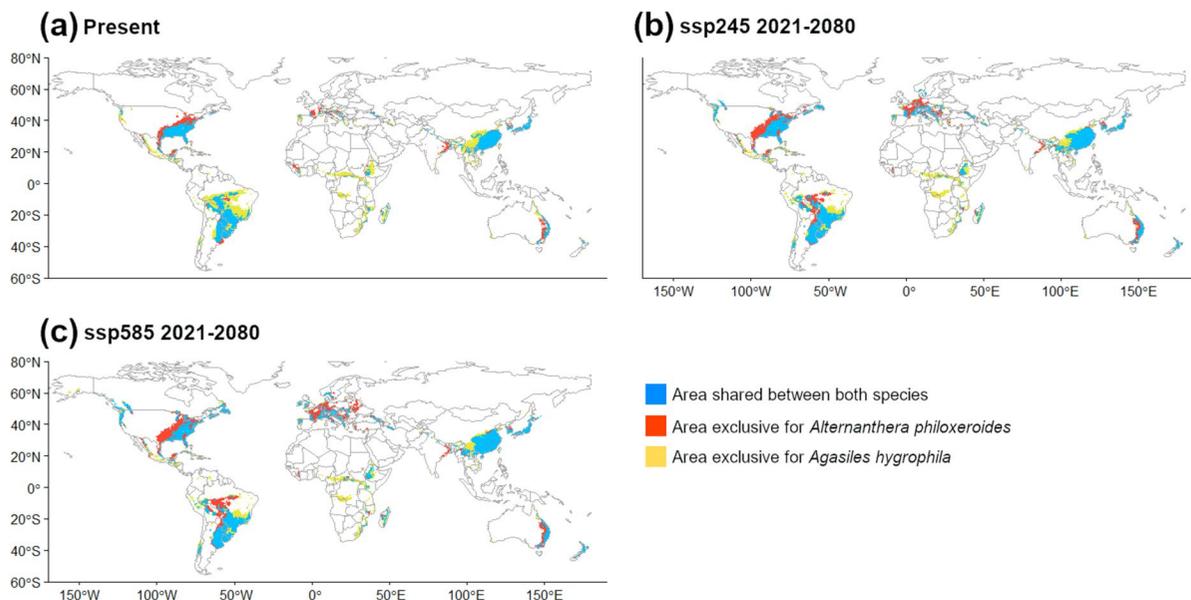


Fig. 4 Comparison of the potential global distributions of *Alternanthera philoxeroides* and *Agasicles hygrophila* in **a** the present, **b** a moderately optimistic future CO₂ emission scenario, and **c** a pessimistic future CO₂ emission scenario

distribution will remain unsuitable for the flea beetle, especially in higher latitudes (Fig. 4; Video S5).

Discussion

Our models for alligator weed support our first hypothesis. Not only does alligator weed have great potential for expansion worldwide, but the number of highly suitable sites will also increase with global warming. This expansion has been predicted in specific countries such as the USA (Koncki et al., 2015) and China (Tu et al., 2021). As climate change leads to warmer areas on the globe (IPCC, 2021), species adapted to high temperatures, like alligator weed, are expected to gain more climatically suitable areas for their establishment. This is consistent with the fact that alligator weed thrives at optimal temperatures of 30–35°C and has an upper threshold temperature for population growth of 36°C (Julien et al., 1995; Shen et al., 2005), which explains our predictions.

Precipitation, also included as a response variable in our models, is expected to increase globally by an average of 5 to 10% by 2100 (under the SSP2-4.5 and SSP5-8.5 scenarios, respectively), although not uniformly across the globe. Alligator weed, being an amphibious plant, can grow in both aquatic and terrestrial habitats due to its high phenotypic plasticity in response to water availability (Geng et al., 2007). It can tolerate a wide range of soil moisture levels, with optimal shoot emergence, plant height, and biomass occurring at around 30–35%, while no shoot emergence or growth occurs below 5% or above 60% moisture levels (Shen et al., 2005). Therefore, it is reasonable to expect that a species with such plasticity would possess mechanisms to cope with the predicted changes in precipitation associated with global warming.

As also anticipated in our first hypothesis, the potential distribution of alligator weed is expected to expand toward higher latitudes from its current established areas. These regions, in general, are projected to experience increased temperatures and precipitation in the future, except for certain areas such as the Iberian Peninsula, southern France, Italy, and the east coast of Australia, which are expected to become drier (IPCC, 2021). As we mentioned earlier, alligator weed thrives in warm and rainy climates (Yan et al., 2020), but it is also capable of tolerating different

levels of water availability and growing successfully in terrestrial habitats (Geng et al., 2007). Therefore, the anticipated drier conditions in these specific regions do not appear to pose a significant challenge for the species in the future.

Contrary to our second hypothesis, our models indicate that the distribution of the flea beetle is also projected to expand toward higher latitudes in future climatic scenarios, although to a lesser extent compared to alligator weed. Climate change is expected to result in warmer conditions, particularly in regions where the flea beetle is currently absent or has limited distribution (IPCC, 2021). The flea beetle is constrained by cold temperatures and cannot successfully overwinter in high-latitude areas (Coulson, 1977; Julien et al., 1995; Stewart et al., 1999; Zhao et al., 2015; Wang et al., 2019). However, with the emergence of new warm areas in the future, the flea beetle will have the potential to survive winter conditions and establish populations in regions that are currently unsuitable.

However, as predicted, the flea beetle is also expected to lose a significant number of currently suitable areas, leading to an overall decline in suitability. This species has a narrow range of environmental tolerances, with optimal conditions falling within non-extreme values (Julien et al., 1995). Consequently, it is unlikely that the extreme conditions projected for the future in some locations (IPCC, 2021) will create a suitable environment for optimal flea beetle fitness. Therefore, despite the slight increase in total area, the flea beetle will have limited availability of highly suitable sites for its establishment in a changing climate.

In terms of geographic distributions, the expansion of the flea beetle and the location of its most suitable sites appear to align with the patterns observed for the alligator weed. As a result, the overlapping areas between these two species are expected to increase and shift toward higher latitudes, contradicting our third hypothesis. However, due to the significantly greater expansion of the plant, a large portion of its potential future distribution will remain unsuitable for the flea beetle, resulting in numerous non-overlapping areas worldwide. Lu et al. (2013) previously suggested that the existing geographic gap between alligator weed and its specialist herbivore could shift to higher latitudes under global warming, thereby creating a new zone with low or no control efficiency.

Our models support this notion by demonstrating the presence of such non-overlapping areas at the global scale.

The USA was the pioneering country in using the flea beetle as a biological control agent for alligator weed, with varying levels of effectiveness across different latitudes (Coulson, 1977). However, our models indicate that climate change impacts will be particularly detrimental to the flea beetle's suitability in the USA, including areas where biological control has previously been successful (as noted by Coulson, 1977). In contrast, our models predict a northward expansion of the plant with moderate to high climate suitability, surpassing the predictions made by Konkki & Aronson (2015). Consequently, there is likely to be a substantial mismatch between the plant and herbivore distributions, resulting in a considerable gap where the plant can thrive more easily than the flea beetle. Many regions where the plant is currently considered a weed will also become unsuitable for the flea beetle in the future, such as Florida. Therefore, the use of biological control for alligator weed will no longer be a viable and effective option in these areas, requiring the exploration of alternative control methods.

In China, both alligator weed and the flea beetle have already been observed to expand northward (Lu et al., 2013). Northern regions of China have experienced a temperature increase in recent decades, and this trend is expected to continue along with increased precipitation (Gao et al., 2015; Yang et al., 2018). In response to these changing conditions, alligator weed and the flea beetle have been gradually spreading northward. However, the plant's distribution limit currently remains farther north than that of the flea beetle (Lu et al., 2013). Our models indicate that this expansion trend will persist into the future, but it will be more pronounced for the plant. This implies that while the flea beetle may potentially control the plant at higher latitudes than it does presently, the plant will still be able to occupy regions beyond the flea beetle's reach in the northward direction. Moreover, alligator weed has shown increased invasiveness with higher latitudes in China, and there is evidence suggesting that warming temperatures may enhance its competitive ability against native species (Wu et al., 2017). Consequently, in the absence of effective biocontrol measures predicted for the northernmost regions, it can be expected that the alligator weed will have even

more detrimental impacts on the native biota in these areas under climate change (Wu et al., 2017).

Despite the decoupling observed between alligator weed and the flea beetle in certain areas due to climate changes, there are still numerous regions worldwide where biological control using the flea beetle appears promising for the future. In Southeast Asia, France, Italy, and the Iberian Peninsula, the invasion process of alligator weed is relatively recent, and the extent of the invaded area remains small (Bulletin OEPP/EPPO Bulletin, 2016, Arana & Murillo, 2021). Focusing efforts on invasive plants during the early stages of invasion can greatly enhance the likelihood of successful biocontrol (Culliney 2005). Additionally, the presence of many overlapping areas with high climate suitability for both species in these regions suggests that biocontrol programs may remain viable, even in the face of climate change.

Although alligator weed has not yet been reported in many European countries, South Korea, and Japan, our models indicate that there are numerous areas highly suitable for its establishment in these regions. The projected climate suitability for the plant in these areas shows a similar increasing trend to that observed in the USA and China, where the species has been invasive since the late nineteenth century (Coulson, 1977; Chen et al., 2008). Considering the rapid spread of alligator weed within a span of three decades in the USA, forming extensive mats that caused various negative impacts such as hindering navigation in slow-moving rivers (Coulson, 1977), it is likely that alligator weed would quickly expand and become a troublesome invader in these areas if the species is introduced. Additionally, these regions also have the potential to provide suitable conditions for the flea beetle in the future, making biocontrol using the flea beetle an option to consider in case of a future invasion.

The southern regions of Canada, the Amazon, Mexico, the South Island of New Zealand, and the Nordic countries are projected to have low suitability for the establishment of alligator weed under global warming. Additionally, these areas will be entirely unsuitable for the flea beetle. It is crucial for these countries to remain vigilant and monitor any signs of the introduction of this invasive plant. In the event of an invasion, alternative control methods should be considered to effectively manage it. Furthermore, although Julien et al. (1995) indicated that many areas

in Africa would be favorable for alligator weed, our models showed very few areas with low suitability in Ethiopia, Mozambique, and Madagascar. Currently, this species is not regarded as a pest on the African continent, and it appears unlikely that it will become one in the future.

Model limitations and future perspectives

Our predictions for future climate scenarios are based on the assumption of niche conservatism for both species. Wang et al. (2017) found that alligator weed does not exhibit a significant shift in its niche between native and invaded areas in the present. However, Luo et al. (2020) observed genetic adaptation in alligator weed for cold tolerance, enabling its colonization of colder regions in China. Additionally, due to its high phenotypic plasticity (Geng et al., 2016), it is plausible that this species possesses mechanisms to tolerate the significant changes projected for the future. Therefore, it is reasonable to expect some niche changes for this species under future climate scenarios.

The same possibilities may apply to the flea beetle as well. Ectothermic organisms have the potential to mitigate the effects of warmer maximum temperatures resulting from climate warming through behavioral thermoregulation (Kearney et al., 2009). Insects can also gradually adjust their thermal tolerance and expand their range accordingly (Guo et al. 2012). In fact, there is evidence suggesting that the flea beetle can develop cold tolerance within a few years through a naturalization process involving bet-hedging strategies (Guo et al., 2012). Furthermore, microhabitats can provide refuge for the flea beetle, protecting it from low non-freezing temperatures for short periods and enabling successful overwintering (Guo et al., 2012).

Therefore, it is important to interpret our predictions for future scenarios with caution, as both species have the potential to modify their physiological traits and adapt to climate warming through phenotypic plasticity or long-term evolutionary changes. Future research should aim to investigate how these species may evolve over time in response to climate warming and how such changes may influence their future distribution. Nonetheless, our results align closely with the existing knowledge for particular regions and we hope that they can provide valuable insights for governments, stakeholders,

and managers in effectively managing the control of this invasive plant in the context of future climate changes.

Acknowledgements We would like to thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for granting MMP and FMF Ph.D. scholarships. LGR acknowledges the National Institutes for Science and Technology (INCT) in Ecology, Evolution and Biodiversity Conservation (EECBio), founded by MCTIC/CNPq (Grant #465610/2014-5), FAPEG (proc. 201810267000023), and the Universidade Estadual Paulista for granting his postdoctoral research (PROPe—UNESP edital 13/2022). RAM acknowledges the support of the Natural Sciences and Engineering Research Council of Canada (NSERC, Discovery Grant RGPIN-2019-05937). SMT acknowledges the Brazilian Council of Research (CNPq) for constant funding through a Productivity Research Grant. This study is a product of the Research Center on Biodiversity and Climate Change (CBioClima) from UNESP.

Author contributions All authors contributed to the study's conception and design. Material preparation, data collection, and analysis were performed by Mikaela Marques Pulzatto, Luiz Guilherme dos Santos Ribas, Raytha de Assis Murillo, and Fernanda Moreira Florencio. The first draft of the manuscript was written by Mikaela Marques Pulzatto and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding MMP and FMF have received Ph.D. scholarships from the Coordination for the Improvement of Higher Education Personnel (CAPES). LGR was founded by MCTIC/CNPq (Grant #465610/2014-5), FAPEG (proc. 201810267000023), and his postdoctoral research was granted by the Universidade Estadual Paulista (PROPe—UNESP edital 13/2022). RAM has received the support of the Natural Sciences and Engineering Research Council of Canada (NSERC, Discovery Grant RGPIN-2019-05937). SMT is constantly granted by the Brazilian Council of Research (CNPq) through a Productivity Research Grant.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

References

- Arana, J. J., P. G. Murillo, 2021. Primera cita de *Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae) en el sur de la Península Ibérica (Sevilla, España). Acta Botanica Malacitana 46. <https://doi.org/10.24310/abm.v46i0>
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller & F. Courchamp, 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15: 365–437. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>.

- Bellard, C., P. Cassey & T. M. Blackburn, 2016. Alien species as a driver of recent extinctions. *Biology Letters* 12: 1–4. <https://doi.org/10.1098/rsbl.2015.0623>.
- Bradley, B. A., D. S. Wilcove & M. Oppenheimer, 2009. Climate change increases risk of plant invasion in the Eastern United States. *Biological Invasions* 12(6): 1855–1872. <https://doi.org/10.1007/s10530-009-9597-y>.
- Bulletin OEPP/EPPO Bulletin, 2016, *Alternanthera philoxeroides* (Mart.) Griseb. 46(1):8–13. <https://doi.org/10.1111/epp.12275>
- Bustamante, R. O., L. Alves, S. Gonçalves, M. Duarte & I. Herrera, 2020. A classification system for predicting invasiveness using climatic niche traits and global distribution models: Application to alien plant species in Chile. *Neobiota* 63: 127–146. <https://doi.org/10.3897/NEOBIOTA.63.50049>.
- Center, T. D., J. P. Cuda, A. J. Grodowitz & C. R. Minter, 2009. Alligatorweed flea beetle *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae: Halticinae). University of Florida: IFAS Extension. <http://edis.ifas.ufl.edu/pdf/IN/IN83100.pdf>. Accessed 19 April 2022
- Chapman, J. W., D. R. Reynolds & K. Wilson, 2015. Long-range seasonal migration in insects: Mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters* 18(3): 287–302. <https://doi.org/10.1111/ele.12407>.
- Chen, L., Y. Yu & H. He, 2008. Historical invasion and expansion process of *Alternanthera philoxeroides* and its potential spread in China. *Biodiversity Science* 16(6): 578–585. <https://doi.org/10.3724/SP.J.1003.2008.08195>.
- Cheng, I. C., J. K. Hill, H. J. Shiu, J. D. Holloway, S. Benedick, V. K. Chey, H. S. Barlow & C. D. Thomas, 2011. Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography* 20(1): 34–45. <https://doi.org/10.1111/j.1466-8238.2010.00594.x>.
- CHAH (Council of Heads of Australasian Herbaria) (2021) *Alternanthera philoxeroides* (Mart.) Griseb. Department of Sustainability, Environment, Water, Population and Communities. <https://profiles.ala.org.au/opus/weeds-australia/profile/Alternanthera%20philoxeroides>
- Coulson, J. R., 1977. Biological control of alligatorweed, 1959–1972: A review and evaluation. Technical Bulletin, United States Agricultural Research Service 1547: 1–98.
- Culliney, T. W., 2005. Benefits of classical biological control for managing invasive plants. *Critical Review in Plant Sciences* 24(2): 131–150. <https://doi.org/10.1080/07352680590961649>.
- Diez, J. M., C. M. D'Antonio, J. S. Dukes, E. D. Grosholz, J. D. Olden, C. J. Sorte, D. M. Blumenthal, B. A. Bradley, R. Early, I. Ibanez, S. J. Jones, J. J. Lawler & L. P. Miller, 2012. Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and Environment* 10(5):249–257. <https://doi.org/10.1890/110137>
- Gao, J., X. Yang, C. Dong & K. Li, 2015. Precipitation resource changed characteristics in arid and humid regions in Northern China with climate changes. *Transactions of the Chinese Society of Agricultural Engineering* 31(12):99–110. <https://doi.org/10.11975/j.issn.1002-6819.2015.12.014>
- GBIF.org (2022) GBIF Occurrence Download. <https://doi.org/10.15468/dl.tkhstr>
- Geng, Y. P., X. Y. Pan, B. Li, J. K. Chen, B. R. Lu & Z. P. Song, 2007. Phenotypic plasticity rather than locally adapted ecotypes allows the invasive alligator weed to colonize a wide range of habitats. *Biological Invasions* 9(3): 245–256. <https://doi.org/10.1007/s10530-006-9029-1>.
- Geng, Y., R. D. van Klinken, A. Sosa, B. Li, J. Chen & C. Y. Xu, 2016. The relative importance of genetic diversity and phenotypic plasticity in determining invasion success of a clonal weed in the USA and China. *Frontiers in Plant Science* 7: 1–13. <https://doi.org/10.3389/fpls.2016.00213>.
- Guo, J. Y., J. W. Fu, X. Q. Xian, M. Y. Ma & F. H. Wan, 2012. Performance of *Agasicles hygrophila* (Coleoptera: Chrysomelidae), a biological control agent of invasive alligator weed, at low non-freezing temperatures. *Biological Invasions* 14: 1597–1608. <https://doi.org/10.1007/s10530-010-9932-3>.
- Harms, N. E. & J. T. Cronin, 2019. Variability in weed biological control: Effects of foliar nitrogen on larval development and dispersal of the alligatorweed flea beetle, *Agasicles hygrophila*. *Biological Control* 135: 16–22. <https://doi.org/10.1016/j.biocontrol.2019.05.002>.
- Harvey, J. A., R. Heinen, R. Gols & M. P. Thakur, 2020. Climate change-mediated temperature extremes and insects: From outbreaks to breakdowns. *Global Change Biology* 26(12): 6685–6701. <https://doi.org/10.1111/gcb.15377>.
- Hellmann, J. J., J. E. Byers, B. G. Bierwagen & J. S. Dukes, 2008. Five potential consequences of climate change for invasive species. *Conservation Biology* 22(3): 534–543. <https://doi.org/10.1111/j.1523-1739.2008.00951.x>.
- Hijmans, R. J., 2022. raster: Geographic Data Analysis and Modeling. R package version 3.6–11. <https://CRAN.R-project.org/package=raster>
- Hijmans, R. J., S. Phillips, J. Leathwick & J. Elith, 2020. dismo: Species Distribution Modeling. R package version 1.3–3. <https://CRAN.R-project.org/package=dismo>
- Hruska, A. J., S. M. Gladstone & K. G. Wilson, 1985. Expanded range of the Alligatorweed Flea Beetle (*Agasicles hygrophila* Selman and Vogt) in South Carolina. *Journal of Aquatic Plant Management* 23: 92–93.
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services (summary for policy makers). IPBES Plenary at its seventh session (IPBES 7, Paris, 2019). Zenodo. <https://doi.org/10.5281/zenodo.3553579>
- IPCC 2021: Summary for Policymakers. In: Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, B. Zhou (eds). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp 3–32). Cambridge University Press. <https://www.ipcc.ch/report/ar6/wg1/#SPM>. Accessed 11 June 2022
- Jia, D., X. F. Yuan, Y. H. Liu, C. Q. Xu, Y. X. Wang, L. L. Gao & R. Y. Ma, 2020. Heat sensitivity of eggs attributes to the reduction in *Agasicles hygrophila* population. *Insect*

- Science 27(1): 159–169. <https://doi.org/10.1111/1744-7917.12611>.
- Jin, J. S., M. T. Zhao, Y. Wang, Z. S. Zhou, F. H. Wan & J. Y. Guo, 2020. Induced thermotolerance and expression of three key Hsp genes (Hsp70, Hsp21, and sHsp21) and their roles in the high temperature tolerance of *Agasicles hygrophila*. *Frontiers in Physiology* 10 <https://doi.org/10.3389/fphys.2019.01593>
- Julien, M. H., B. Skarratt & G. G. Maywald, 1995. Potential geographical distribution of Alligator Weed and its biological control by *Agasicles hygrophila*. *Journal of Aquatic Plant Management* 33: 55–60.
- Kearney, M., R. Shine & W. P. Porter, 2009. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences* 106(10): 3835–3840. <https://doi.org/10.1073/pnas.0808913106>.
- Koncki, N. G. & M. F. J. Aronson, 2015. Invasion risk in a warmer world: Modeling range expansion and habitat preferences of three nonnative aquatic invasive plants. *Invasive Plant Science Management* 8(4): 436–449. <https://doi.org/10.1614/ipsm-d-15-00020.1>.
- Lu, X., E. Siemann, X. Shao, H. Wei & J. Ding, 2013. Climate warming affects biological invasions by shifting interactions of plants and herbivores. *Global Change Biology* 19: 2339–2347. <https://doi.org/10.1111/gcb.12244>.
- Luo, L. D., X. X. Kong, Z. A. Gao, Y. Zheng, Y. W. Yang, X. Li, D. N. Yang DN, Y. P. Geng & Y. P. Yang, 2020. Comparative transcriptome analysis reveals ecological adaptation of cold tolerance in northward invasion of *Alternanthera philoxeroides*. *BMC Genomics* 21(1). <https://doi.org/10.1186/s12864-020-06941-z>
- Meza-Lopez, M. M. & E. Siemann, 2017. Nutrient enrichment increases plant biomass and exotic plant proportional cover independent of warming in freshwater wetland communities. *Plant Ecology* 218(7): 835–842. <https://doi.org/10.1007/s11258-017-0733-y>.
- Mollot, G., J. H. Pantel & T. N. Romanuk, 2017. The effects of invasive species on the decline in species richness: a global meta-analysis. *Advances in Ecological Research* 56: 61–83. <https://doi.org/10.1016/bs.aecr.2016.10.002>.
- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlenn, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs & H. Wagner, 2020. vegan: Community Ecology Package. R package version 2.5–7. <https://CRAN.R-project.org/package=vegan>
- Osland, M. J., P. W. Stevens, M. M. Lamont, R. C. Brusca, K. M. Hart, J. H. Waddle, C. A. Langtimm, C. M. Williams, B. D. Keim, A. J. Terando, E. A. Reyier, K. E. Marshall, M. E. Loik, R. E. Boucek, A. B. Lewis & J. A. Seminoff, 2021. Tropicalization of temperate ecosystems in North America: The northward range expansion of tropical organisms in response to warming winter temperatures. *Global Change Biology* 27: 3009–3034. <https://doi.org/10.1111/gcb.15563>.
- Osland, M. J. & L. C. Feher, 2019. Winter climate change and the poleward range expansion of a tropical invasive tree (Brazilian pepper – *Schinus terebinthifolius*). *Global Change Biology* 26(2): 607–615. <https://doi.org/10.1111/gcb.14842>.
- Pan, X. Y., Y. P. Geng, A. Sosa, W. J. Zhang, B. Li & J. K. Chen, 2007. Invasive *Alternanthera philoxeroides*: Biology, ecology and management. *Acta Phytotaxonomica Sinica* 45(6): 884–900. <https://doi.org/10.1360/aps06134>.
- Parnesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37: 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>.
- Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura & M. B. Araújo, 2011. *Ecological Niches and Geographic Distributions* (MPB-49). Princeton University Press. <http://www.jstor.org/stable/j.ctt7stnh>
- Petsch, D. K., L. G. S. Ribas, T. Mantovano, M. M. Pulzatto, A. T. Alves, G. D. Pinha & S. M. Thomaz, 2020. Invasive potential of golden and zebra mussels in present and future climatic scenarios in the new world. *Hydrobiologia* 848: 2319–2330. <https://doi.org/10.1007/s10750-020-04412-w>.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rai, P. K. & J. S. Singh, 2020. Invasive alien plant species: Their impact on environment, ecosystem services and human health. *Ecological Indicators* 111: 106020. <https://doi.org/10.1016/j.ecolind.2019.106020>.
- Riahi, K., D. P. van Vuuren, E. Kriegler et al., 2017. The shared socioeconomic pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change* 42:153–168. <https://https://doi.org/10.1016/j.gloenvcha.2016.05.009>.
- Shen, J. Y., M. Q. Shen, X. H. Wang & Y. T. Lu, 2005. Effect of environmental factors on shoot emergence and vegetative growth of alligatorweed (*Alternanthera philoxeroides*). *Weed Science* 53(4): 471–478. <https://doi.org/10.1614/WS-04-198R>.
- South, A., 2017. rnaturalearth: World Map Data from Natural Earth. R package version 0.1.0. <https://CRAN.R-project.org/package=rnaturalearth>
- Stewart, C. A., R. B. Chapman, R. M. Emberson, P. Syrett & C. M. A. Frampton, 1999. The effect of temperature on the development and survival of *Agasicles hygrophila* Selman & Vogt (Coleoptera : Chrysomelidae), a biological control agent for alligator weed (*Alternanthera philoxeroides*). *New Zealand Journal of Zoology* 26(1): 11–20. <https://doi.org/10.1080/03014223.1999.9518172>.
- Stewart, C. A., M. H. Julien & S. P. Worner, 1995. The potential geographical distribution of alligator weed (*Alternanthera philoxeroides*) and a biological control agent, *Agasicles hygrophila*, in New Zealand. *Forests and Environment* 48:270–275. <https://doi.org/10.30843/nzpp.1995.48.11556>
- Tu, W., Q. Xiong, X. Qiu & Y. Zhang, 2021. Dynamics of invasive alien plant species in China under climate change scenarios. *Ecological Indicators* 129: 107919. <https://doi.org/10.1016/j.ecolind.2021.107919>.
- Urbanek S (2022) rJava: Low-Level R to Java Interface. R package version 1.0–8, <http://www.rforge.net/rJava/>
- Walther, G. R., A. Roques, P. E. Hulme, M. T. Sykes, P. Pyšek, I. Kühn & M. Zobel, 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology and*

- Evolution 24(12): 686–693. <https://doi.org/10.1016/j.tree.2009.06.008>.
- Wang, C. J., J. Z. Wan, H. Qu & Z. X. Zhang, 2017. Climatic niche shift of aquatic plant invaders between native and invasive ranges: a test using 10 species across different biomes on a global scale. *Knowledge Management of Aquatic Ecosystems* 27: 418–426. <https://doi.org/10.1051/kmae/2017019>.
- Wang, C. J., Q. F. Li & J. Z. Wan, 2019. Potential invasive plant expansion in global ecoregions under climate change. *Peer J* 7: e6479. <https://doi.org/10.7717/peerj.6479>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*, Springer-Verlag, New York.
- Woodward, F. I. & B. G. Williams, 1987. Climate and plant distribution at global and local scales. *Vegetatio* 69: 189–197. <https://doi.org/10.1007/BF00038700>.
- Wu, H., M. Ismail & J. Ding, 2017. Global warming increases the interspecific competitiveness of the invasive plant alligator weed, *Alternanthera philoxeroides*. *Science of the Total Environment* 575: 1415–1422. <https://doi.org/10.1016/j.scitotenv.2016.09.226>.
- WWF (2020) Living Planet Report 2020 - Bending the curve of biodiversity loss. In: Almond REA, Grooten M, Petersen T (eds). WWF (2020). WWF, Gland, Switzerland. <https://www.zsl.org/sites/default/files/LPR%202020%20Full%20report.pdf>
- Yan, H., L. Feng, Y. Zhao, L. Feng, D. Wu & C. Zhu, 2020. Prediction of the spatial distribution of *Alternanthera philoxeroides* in China based on ArcGIS and MaxEnt. *Global Ecology and Conservation* 21: e00856. <https://doi.org/10.1016/j.gecco.2019.e00856>.
- Yang, Y., Z. Wu, H. He, H. Du, L. Wang, X. Guo & W. Zhao, 2018. Differences of the changes in soil temperature of cold and mid-temperate zones, Northeast China. *Theoretical and Applied Climatology* 134: 633–643. <https://doi.org/10.1007/s00704-017-2297-0>.
- Zhao, L., D. Jia, X. Yuan, Y. Guo, W. Zhou & R. Ma, 2015. Cold hardiness of the biological control agent, *Agasicles hygrophila*, and implications for its potential distribution. *Biological Control* 87: 1–15. <https://doi.org/10.1016/j.biocontrol.2015.02.007>.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.