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RESEARCH ARTICLE

Climate change scenarios differentially modulate the impact of invasion in a native macrophyte species

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Abstract

Biological invasion and climate change threaten freshwater ecosystems, potentially amplifying their impacts through interaction. However, empirical evidence on how future climate scenarios influence the invasion process and their interactive effects on native species remains limited. We conducted a full-factorial experiment to evaluate the independent and interactive effects of *Hydrilla verticillata* invasion and future climate scenarios (baseline, mitigation, and business-as-usual) on the native macrophyte *Cabomba caroliniana*. We also assessed the response of the non-native *H. verticillata* to these climate scenarios. The climate change mitigation scenario maintained the invasive potential of *H. verticillata*, as indicated by its vertical growth and colonization potential via vegetative propagules, which were comparable to baseline conditions. Simultaneously, the mitigation scenario supported the vertical growth and production of *C. caroliniana* at levels similar to those under the baseline. Under the business-as-usual scenario, *H. verticillata* exhibited enhanced vertical growth and colonization capacity via vegetative propagules. Interestingly, its presence under the business-as-usual scenario was associated with increased vertical production of the native species. Although invasion appeared to buffer the adverse effects of extreme climatic stress, it merely enabled *C. caroliniana* to recover vertical production to baseline and mitigation levels, rather than providing a long-term advantage. Our findings highlight the ecological benefits of climate change mitigation and the complex outcomes arising from the interaction between invasion and future climate scenarios for native species.

Biological invasion is a significant global threat to biodiversity, contributing to species extinctions, habitat alterations, and disruptions to ecosystem functioning and the provision of ecosystem services (Bellard et al. 2016; Cacabelos et al. 2020; Liu et al. 2020; IPBES 2023). The introduction of non-native species with high invasive potential leads to biotic homogenization, which is the increasing similarity among biological communities on a global scale (Olden et al. 2004; Lockwood et al. 2007; Petsch et al. 2022; Bando et al. 2023). Biotic homogenization is primarily driven by the greater dispersal abilities of non-native species, along with their competitive and predation advantages (Rahel 2002; Olden et al. 2004), which interfere with important ecosystem processes (Carvalho et al. 2016; Pyšek et al. 2020). These ecological shifts result in substantial economic costs associated with ecosystem degradation and the management of invasive species, totaling trillions of dollars (Cuthbert et al. 2021). While biological invasion threatens biodiversity globally, freshwater ecosystems are particularly vulnerable due to intensive trade and natural linkages, making them more susceptible than marine and terrestrial ecosystems (Sala et al. 2000; Bolpagni 2021). In addition to their individual impacts, biological invasion is expected to synergistically interact with climate change as both threats co-occur in space and time (Isbell et al. 2023).

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Climate change is expected to facilitate multiple stages of biological invasion through three main mechanisms: (1) by creating new opportunities for species introduction that overcome geographic barriers, (2) by altering abiotic conditions, and (3) by reshaping biotic communities within recipient environments (Robinson et al. 2020). Among the stages of the biological invasion process, the colonization stage is particularly critical in the context of potential climate change effects on freshwater ecosystems. This stage is pivotal because non-native species must primarily survive and thrive in the new recipient environment to successfully establish themselves (Theoharides and Dukes 2007; Walther et al. 2009). The colonization process is even more complex for certain non-native macrophytes, which can float in the water column for extended periods before attaching their roots to the sediment (Umetsu et al. 2012; Petruzzella et al. 2020; Hussner et al. 2021). Climate change can alter abiotic conditions, such as temperature and water levels, thereby modifying constraints that previously limited the colonization of non-native species (Walther et al. 2009). Overall, non-native species typically exhibit greater environmental tolerance, phenotypic plasticity, and rapid growth compared to native ones, which enables them to better cope with environmental changes (Rejmánek and Richardson 1996; Bradley et al. 2010).

Most reviews and theoretical projections on the combined effects of climate change and biological invasions suggest that non-native species will be favored due to their broader climatic range, while native species will face increasing disadvantages (Essl et al. 2020; IPBES 2023). This trend is expected to be exacerbated under a climate business-as-usual (BAU) scenario, where no significant efforts are made to mitigate climate change. This scenario supports temperature increases and altered rainfall patterns that will likely continue to create unfavorable conditions for native species to thrive. However, the results of climate change mitigation strategies could provide an alternative, potentially limiting temperature increases and stabilizing rainfall patterns. Climate mitigation could alleviate pressures on native species and reduce the competitive advantages of non-native species compared to the BAU scenario. Therefore, climate change mitigation may lead to different outcomes for native and non-native species compared to the BAU scenario, underscoring the need for studies to determine the possible effects under distinct future climate scenarios (Lengyel et al. 2023).

Our study aimed to assess the effects of future climate scenarios on the early stages of the biological invasion process, focusing on their impacts on the growth and biomass production of the non-native macrophyte *Hydrilla verticillata*. As a highly invasive species across multiple freshwater ecosystems (Sousa 2011), *H. verticillata* serves as an excellent model for evaluating the impact of invasion. We also evaluated the individual and combined effects of future climate scenarios and *H. verticillata* invasion on the growth and biomass production of a native macrophyte. We conducted a full-factorial outdoor experiment using an innovative climate experimental simulation that incorporates two major climatic components (i.e., temperature and rainfall) predicted under both climate change mitigation and BAU scenarios. We expected that (1) the climate BAU scenario would have positive impacts on the growth and biomass production of the non-native macrophyte species, while (2) climate change mitigation would buffer the anticipated negative impacts of the BAU scenario on the growth and biomass production of the native macrophyte species. Furthermore, we predicted that (3) the interaction with biological invasion would reduce the climatic mitigation effectiveness on the growth and biomass production for the native macrophyte species while enhancing the negative effects of the BAU scenario.

Methods

Experimental setup

We conducted a 35-d outdoor mesocosm experiment from July to August 2021 at the Federal University of Rio de Janeiro campus (latitude: −22.84, longitude: −43.23) to evaluate the early floating phase of the colonization stage of the non-native *Hydrilla verticillata*. The duration of the experiment was not pre-established but was instead determined by the critical water depth thresholds set by the climate scenarios. As our primary goal was to assess the responses of aquatic macrophytes, it was essential to maintain a minimum viable water column. Therefore, the experiment was conducted until water levels reached the lowest threshold that still supported macrophyte viability.

We used 50-L plastic containers as mesocosms, measuring 65.8 cm in height and 31.0 cm in diameter, with a 20-cm edge above the ground to buffer daily temperature variations. A total of 36 mesocosms were filled with a 5-cm layer of sediment that simulated natural conditions, with a bottom layer of organic substrate (Mega fértil—Box Reef, 1 cm deep; initial nutrient composition: 0.14% phosphorus and 0.08% nitrogen) and a top layer of sand (commercially acquired washed sand, 4 cm deep). Each mesocosm was then filled with approximately 30 L of dechlorinated tap water, which was filtered through a 50 μm plankton net. This setup simulates a shallow lagoon environment, which is particularly vulnerable to the effects of climate change, as fluctuations in water level and temperature can influence the abundance and metabolism of primary producers, particularly macrophyte species (Lind et al. 2022).

We selected the rooted-submerged macrophyte species *Cabomba caroliniana*, native to South America, as a model in our study (Schooler et al. 2009). We established the native species by planting four apical stem fragments (15 cm in length, without lateral branches) into the substrate layer of each mesocosm. This shoot density falls within the natural range observed in submerged macrophyte communities (Li et al. 2015). The chosen fragment size was intended

to decrease mortality and maximize the growth potential of the species (Riis and Sand-Jensen 2006; Riis et al. 2009). All fragments of the native species were acquired commercially (Flora Aquática, Brazil) and were cultivated under standardized conditions for 10 d prior to the experimental manipulation to ensure similar starting conditions. In each of the 36 mesocosms, four fragments were individually planted simultaneously, all using the same water source. The mesocosms were placed under a transparent roof to prevent interference from local rainfall while remaining exposed to the natural photoperiod. During this pre-experimental period, abiotic conditions were maintained consistently across mesocosms, with the following average values ± standard deviation (SD): water column height = 46 ± 0 cm, turbidity = 0 ± 0 Nephelometric Turbidity Unit, salinity = 0.005 ± 0.0006%, dissolved oxygen = 5.38 ± 0.35 mg L^{-1}, conductivity = 0.113 ± 0.011 mS cm^{-1}, and pH = 5.47 ± 0.29 (n = 36).

Experimental design

We established six treatments through a factorial combination of three climate change treatments (baseline, mitigation, and BAU) and two invasion conditions (presence or absence of the non-native species). Each treatment combination was replicated six times; resulting in 36 mesocosms arranged in a spatial block design. In the invasion treatments, individuals of the non-native species were introduced, whereas in the noninvaded treatments, only the native species were present.

Biological invasion treatments

Hydrilla verticillata has a native dispersal range that encompasses Asia and Australia, but it currently exhibits a cosmopolitan distribution due to its human-mediated introduction (Sousa 2011). This non-native species has reached an extensive geographic distribution through its use of aquariophily and has become invasive in numerous freshwater ecosystems (Sousa 2011).

We introduced the rooted-submerged non-native macrophyte species *Hydrilla verticillata* 10 d after this pre-experimental period, allowing sufficient time for the native species to establish in the mesocosms. We established the non-native species by adding two apical stem fragments (15 cm in length, without lateral branches) to the surface water of the mesocosms (*i.e.,* fragments were not planted), representing a moderate propagule pressure according to our mesocosm area (Li et al. 2015). This method mimics the colonization stage observed in natural conditions, as *H. verticillata* regenerates from floating fragments in the water column (Umetsu et al. 2012; Louback-Franco et al. 2020). Hydrilla shoots can be broken by external forces, giving rise to new individuals that develop roots and anchor themselves in the sediment (Li et al. 2015; Louback-Franco et al. 2020). These fragments can remain floating for weeks before settling and rooting, allowing for an extended growth phase prior to effectively colonizing the new environment (Chadwell and Engelhardt 2008; Petruzzella et al. 2020). All fragments of the non-native species were acquired commercially (Flora Aquática, Brazil).

Climate change treatments

We established two climate change treatments based on Representative Concentration Pathways (RCP) 4.5 and 8.5 for the 2080–2099 period, respectively termed as mitigation and BAU, to reflect projected future climate scenarios (IPCC 2023). Additionally, a baseline treatment was included as a control, representing historical climatic conditions observed from 1985 to 2004. The mitigation treatment represents the RCP 4.5 scenario, which assumes policies to reduce greenhouse gas emissions, leading to moderate changes in temperature and rainfall patterns (Thomson et al. 2011). The BAU treatment corresponds to the RCP 8.5 scenario, reflecting current trends in greenhouse gas emissions and predicting more severe changes in temperature, rainfall, and the frequency of extreme climatic events (Riahi et al. 2011).

We gathered data on 20 yr of temperature and rainfall for each climate change treatment generated by the Brazilian Center of Weather Forecasting and Climate, part of the National Institute for Space Research (CPTEC/INPE), and obtained through the PROJETA platform (Chou et al. 2014a, 2014b; Lyra et al. 2018; https://projeta.cptec.inpe.br/). They employed a high-resolution climate model (0.5 km, continental, HADGEM2-ES) for the municipality of Rio de Janeiro, Brazil (latitude: −22.90, longitude: −43.20), where our experiment was conducted. The PROJETA platform provided data on air temperature at 2 m height from the ground surface in 3-h intervals, as well as daily precipitation values for each climate treatment.

As a previous approach (Rodrigues et al. 2024), we selected a representative year from the 20-yr time series interval for each climate change treatment, considering both temperature and rainfall modeling data. First, we calculated the SD for each year within the selected time series interval in relation to the mean values of temperature and rainfall over that same period (Eq. 1). Next, we summed the SD of temperature and rainfall for each year, resulting in the total SD (Eq. 2).

$$SD_{y1} = \sum \left(|y|_{t1} - \bar{x} \right) + \ldots + \left(|y|_{t960} - \bar{x} \right) \quad (1)$$

$$SD_{total} = \sum SD_{y1} + \ldots + SD_{y20} \quad (2)$$

where y = a year within the 20-yr time series interval; $|y|$ = temperature or rainfall absolute value for a year y, $\bar{x}$ = mean temperature or rainfall of the selected time interval, t = temperature (every 3 h) and rainfall (daily) of the selected time interval.

We selected the year with the lowest total SD compared to the average of the 20-yr time series interval for each treatment. Specifically, (1) the year 1998 best represented the

baseline conditions relative to the 1985–2004 time interval, and (2) the year 2097 best represented both mitigation and BAU climate change scenarios relative to the 2080–2100 time interval (Fig. 1). Choosing a representative year for each climate treatment ensured (1) an accurate representation of the average climate conditions for each treatment, (2) the continuity and variability of temperature and precipitation patterns, and (3) a robust basis for comparison among the experimental treatments in this study.

We used a custom-made automated heating system (NAYAD Limno) to manipulate the water temperature regime in the mesocosms. This system consisted of a temperature sensor and an 80 W aquarium heater (Master, Rio de Janeiro, Brazil) placed at the top of each mesocosm. Both devices were connected to a control system that monitored the difference between the current and previously uploaded predicted temperature for each climate treatment. The control system turned on the heat whenever the current temperature fell below the predicted one. Over 90% of the predicted temperatures were accurately achieved within a 3-h time frame across all climate treatments. Regarding warming, the mitigation and BAU treatments showed a mean temperature of $1.0°C \pm 2.0°C$ (mitigation, mean $\pm$ SD) to $2.6°C \pm 1.8°C$ (BAU, mean $\pm$ SD) higher than the baseline treatment mean temperature. The mean difference in temperature between the mitigation and BAU treatment was $1.7°C \pm 2.4°C$ (mean $\pm$ SD) (Fig. 1).

We carried out daily rainfall manipulation by adding dechlorinated tap water that had been filtered through a 50 μm mesh plankton net. We tracked water volume variation throughout the experiment; the BAU treatment showed the lowest water volume compared to the baseline and mitigation treatments (Supporting Information Fig. S1).

Nutrient concentration

Additionally, we measured water ammonium and orthophosphate concentrations throughout the experiment to assess potential responses to water level variation across the climate treatments. Nutrient concentrations were recorded at the start of the experiment, during three intermediate sampling events, and at the end of the experiment for all treatments (*see* Supporting Information Fig. S2). Mean initial concentrations were $1.44 \pm 4.55\ \mu g\ L^{-1}$ for orthophosphate and $38.08 \pm 43.08\ \mu g\ L^{-1}$ for ammonium ($n = 36$). No nutrients were added during the experiment; thus, the measured concentrations reflect natural inputs from the water and sediment used to fill the mesocosms. The ammonium and orthophosphate analyses were performed using the methods outlined by Bower and Holm-Hansen (1980) and Golterman (1978), respectively.

Native and non-native species responses

At the end of the experiment, we harvested all fragments of both native and non-native species and separated them into (1) roots from shoot structures and (2) main shoots from the lateral new shoots. Each fragment was individually examined to count the number of lateral new shoots attached to the main fragment. We measured the size of each structure and separately dried roots, main shoots, and lateral new shoots at 60°C for 48 h. We weighed all structures using a laboratory precision balance to determine the dried weight of the fragments. We calculated the length and biomass of the total main shoot and the lateral new shoots of both native and non-native macrophyte species by summing the individual fragments. Then, we calculated the root-to-shoot ratio using their total shoot and total root biomass. Vertical growth was determined as the total mean length (cm) of the main fragments, and lateral growth as the mean length (cm) of the lateral new shoots. Then, we evaluated vertical and lateral biomass production (hereafter production) of both native and non-native macrophyte species, using dry weight as an indicator for these traits.

Vertical growth and production enable us to evaluate the structural dynamics of both species across treatments and their ecological role in light competition. Lateral growth and production (i.e., the emergence of new shoots) were assessed to understand the dispersion and propagule pressure potential of both species. Lateral growth is particularly important in assessing vegetative propagules and colonization of the non-native species *H. verticillata*. It is essential to note that both species can also absorb nutrients from their shoots, thereby contributing to their overall growth and production. Although these species also absorb nutrients from their shoots and leaves, we evaluated root production to assess colonization potential and complement our understanding of the nutrient acquisition of both species. Finally, the root-to-shoot biomass ratio was calculated to assess the relative investment in root and shoot biomass production.

Although we initially added two fragments of the non-native species, we found additional unattached fragments of *H. verticillata* at the end of the experiment, referred to as invasive vegetative propagules, which originated from the fragmentation of their lateral shoots. Following the same steps described above, we evaluated the number, vertical growth, production, radicular production, and root-to-shoot biomass ratio of these vegetative propagules across different treatments. In mesocosms where no invasive vegetative propagules were detected, we assigned a value of zero for all responses evaluated.

Data analysis

We fitted a general linear mixed-effects model (GLMM) to evaluate the independent and combined effects of climate change and biological invasion on the vertical and lateral growth, vertical and lateral production, radicular production, and root-to-shoot biomass of the native macrophyte species. We also evaluated the responses of the non-native macrophyte *Hydrilla verticillata* to the climate change treatments, considering its vertical and lateral growth, vertical and lateral

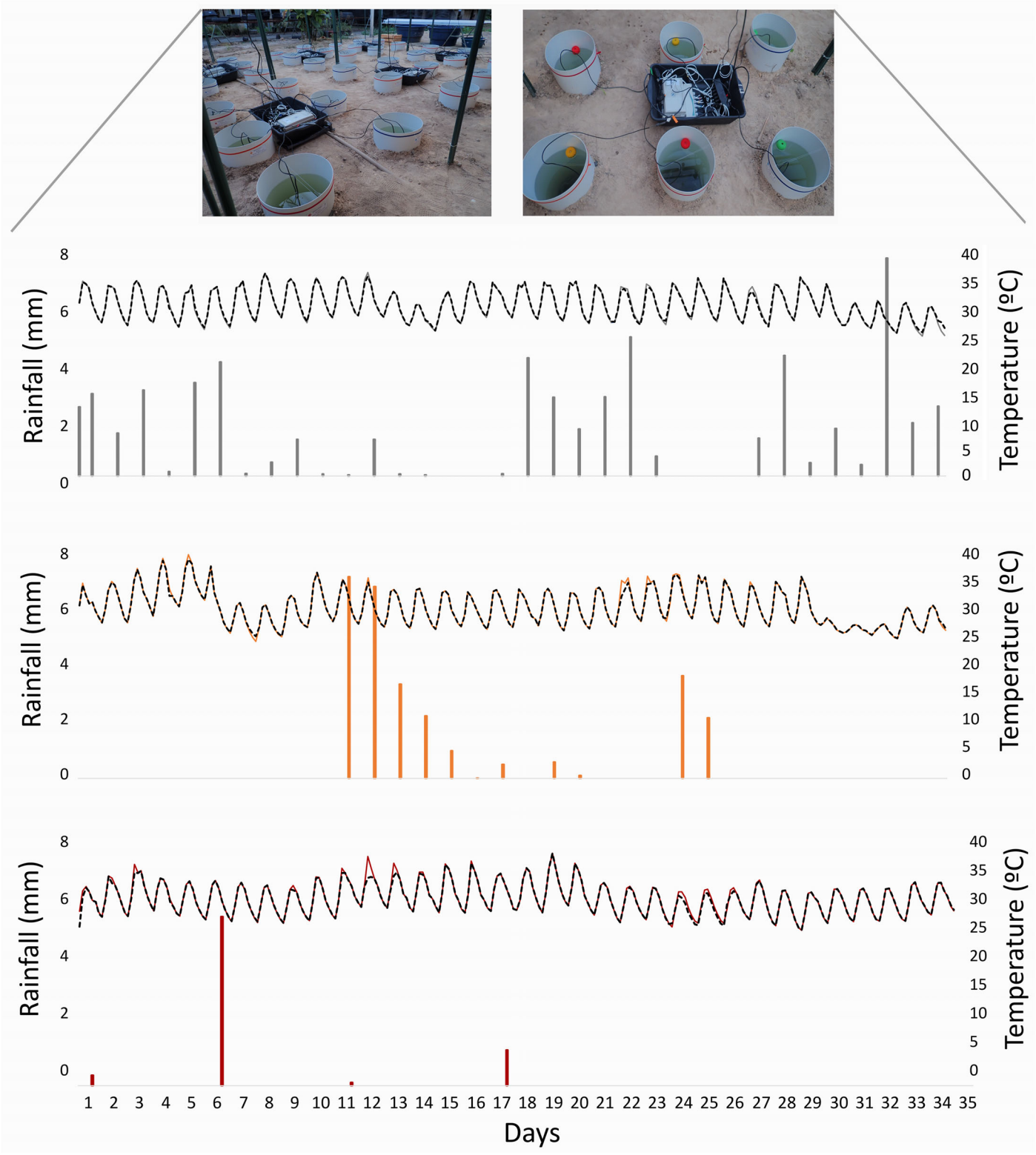


Fig. 1. Modeled and observed temperature variations within 3-h intervals and daily rainfall variation data for each climate treatment during the 35-d experiment. Filled lines represent the modeled temperature, and dashed lines represent the observed temperature. Baseline treatment was represented by the year 1998 of the 1985–2004 interval. Mitigation and business-as-usual (BAU) treatments were represented by the year 2097 of the 2080–2100 interval. Rainfall data closely matched the model predictions, and temperature deviations from the models were minimal and nonsignificant, attributed to the automated control system. Climate treatments are color-coded as follows: gray for baseline, orange for mitigation, and red for BAU treatment.

production, radicular production, and root-to-shoot biomass as response variables. We used the *lme* function for normally distributed data and the *glmmTMB* function for beta-distributed data in the R package *nlme* (version 3.1.165) and *glmmTMB* (version 1.1.9), respectively (Bates et al. 2015; Pinheiro 2023). In all models, block was included as a random factor. When analyzing the effects on native species, both climate and invasion treatments were included as fixed factors. In contrast, when assessing the responses of the non-native species, only climate treatments were included as fixed effects. To assess the effects of climate and invasion treatments on nutrient concentrations (ammonium and orthophosphate), we also used GLMMs with block as a random factor and climate and invasion as fixed factors. The analyses considered nutrient dynamics throughout the experiment, not only initial or final values. We performed a Tukey post hoc test to compare differences between climate and invasion treatments for each response variable evaluated using the R package *emmeans* (version 1.10.3; Searle et al. 1980). All statistical analyses were carried out using the R platform (version 4.4.1; R Core Team 2023).

Results

The effects of climate change treatments on the non-native macrophyte species

Climate change significantly affected the growth rather than the production of *H. verticillata* (GLMM; Table 1), which increased its vertical and lateral growth under the BAU treatment compared to the baseline treatment (Fig. 2a, b). Only non-native vertical growth was significantly higher under the BAU treatment compared to the mitigation treatment (Fig. 2a). There were no significant differences between the baseline and mitigation treatments for the vertical and lateral growth of the non-native species (Tukey's HSD post hoc test, Fig. 2a, c). We did not observe a significant effect of climate change treatments on the vertical, lateral, and radicular production, or the root-to-shoot biomass ratio, of the non-native species *H. verticillata* (Table 1).

Table 1. Generalized linear mixed model results on the effects of climate change treatments (*i.e.*, baseline, mitigation, and business-as-usual) on the growth and production responses of the non-native species *Hydrilla verticillata*, including vertical growth, lateral growth, vertical production, lateral production, radicular production, and root-to-shoot biomass ratio. Block was used as a random effect, and treatments as fixed effects. Significant effects are represented in bold ($p < 0.05$). df is split into between-groups degrees of freedom and within-groups degrees of freedom, respectively. Marginal and conditional R^2 values for the models are provided in Supporting Information Table S1.

	Climate change		
Non-native responses	X^2	p	df
Vertical growth	6.60	**0.033**	2.25
Lateral growth	12.54	**0.001**	2.25
Vertical production	1.28	0.527	2.25
Lateral production	1.14	0.564	2.25
Radicular production	0.27	0.871	2.25
Root-to-shoot biomass ratio	3.45	0.177	2.25

Climate change had no significant effect on the number, vertical growth, vertical production, and radicular production of the invasive vegetative propagules of the non-native species *H. verticillata* compared to the baseline treatment (Supporting Information Table S2). However, their root-to-shoot biomass ratio was significantly increased under the BAU treatment compared to the baseline and mitigation treatments (Supporting Information Fig. S3; GLMM: $X^2 = 3.80$, df = 2, $p < 0.005$).

Although no significant effect of climate change was observed on the radicular production of the non-native *Hydrilla verticillata*, all invasive propagules and introduced fragments developed roots across climate treatments. None of the fragments had their roots anchored in the sediment. After 35 d, root development occurred in 83% of fragments under baseline conditions and in 100% of fragments under mitigation and BAU treatments. Additionally, *H. verticillata* fragments gradually sank toward the sediment, starting in the first week after introduction and remained there for the duration of the experiment.

Independent and interactive effects of climate change and biological invasion on native species

Climate change significantly decreased the vertical growth of the native species *C. caroliniana* (GLMM; Table 2). This result was primarily driven by the smaller plant elongation of the native species under the BAU treatment compared to the baseline and mitigation treatments (Tukey's Honestly Significant Difference post hoc test; Fig. 3a).

The presence of biological invasion significantly decreased the root-to-shoot biomass ratio of the native species *C. caroliniana* (GLMM; Table 2). Thus, we observed a higher investment of the native species in the vertical production in response to biological invasion. This was reflected in the interactive effects between climate change and biological invasion treatments, which significantly increased the shoot production of *C. caroliniana* (GLMM on the root-to-shoot biomass; Table 2), especially under the BAU treatment (Tukey's HSD post hoc test; Fig. 3c). There were no significant differences between the baseline and mitigation treatments on the vertical production of the native species, regardless of invasion treatment (Fig. 3c). We did not observe a significant independent and interactive effect between climate change and biological invasion treatments on lateral growth, lateral production, and radicular production of *C. caroliniana* (Table 2).

The effects of climate change and biological invasion on nutrients

We observed an interactive effect of climate change and invasion on the total orthophosphate concentration (GLMM,

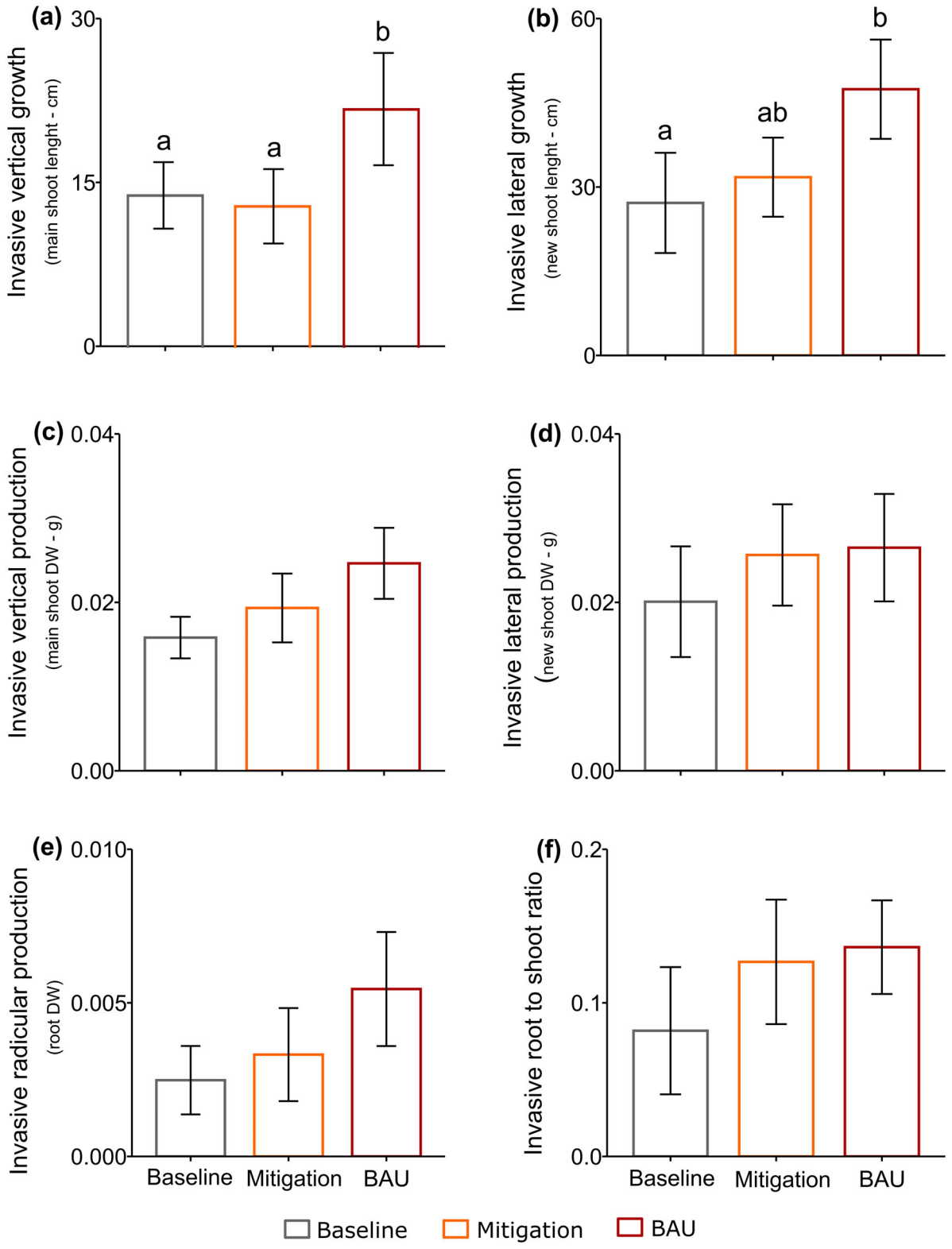


Fig. 2. Effects of climate change treatments (i.e., baseline, mitigation, and business-as-usual [BAU]) on the non-native species *Hydrilla verticillata* growth and production responses, described as vertical growth (**a**), lateral growth (**b**), vertical production (**c**), lateral production (**d**), radicular production (**e**), and root-to-shoot biomass ratio (**f**). The colors represent climate treatments: gray = baseline, orange = mitigation, and red = BAU. Different lowercase letters indicate statistically significant differences among treatments, while their absence indicates nonsignificant effects (Tukey's Honestly Significant Difference post hoc test). The values are means ± standard error of the mean ($n = 6$).

Table 2. Generalized linear mixed model results on the effects of climate change treatments (*i.e.*, baseline, mitigation, and BAU), biological invasion treatments (*i.e.*, absence or presence of *Hydrilla verticillata*), and their interaction on the growth and production responses of the native species *Cabomba caroliniana*, including vertical growth, lateral growth, vertical production, lateral production, radicular production, and root-to-shoot biomass ratio. Block was used as a random effect, and treatments as fixed effects. Significant effects are represented in bold ($p < 0.05$). df is split into between-groups degrees of freedom and within-groups degrees of freedom, respectively. Marginal and conditional R^2 values for the models are provided in Supporting Information Table S3.

	Climate change			Biological invasion			Climate × invasion		
Native responses	X^2	p	df	X^2	p	df	X^2	p	df
Vertical growth	12.92	**0.001**	2.25	0.16	0.688	1.25	1.67	0.432	2.25
Lateral growth	0.81	0.666	2.25	0.01	0.894	1.25	1.16	0.559	2.25
Vertical production	4.19	0.123	2.25	0.26	0.607	1.25	7.54	**0.023**	2.25
Lateral production	1.48	0.476	2.25	0.85	0.354	1.25	2.03	0.361	2.25
Radicular production	1.25	0.532	2.25	2.06	0.152	1.25	2.13	0.344	2.25
Root-to-shoot biomass ratio	2.25	0.323	2.25	5.01	**0.025**	1.25	3.29	0.192	2.25

$X^2 = 27.77$, df = 2, $p < 0.005$), with higher concentrations observed under the mitigation and BAU treatments compared to the baseline treatment in the absence of invasion (Supporting Information Fig. S2). An opposite trend was observed in the presence of invasion: orthophosphate concentrations decreased under the mitigation and BAU treatments, whereas they increased under the baseline treatment (Supporting Information Fig. S2). We did not observe any individual effect of climate change (GLMM, $X^2 = 1.09$, df = 2, $p = 0.578$) or biological invasion (GLMM, $X^2 = 3.05$, df = 1, $p = 0.080$) on orthophosphate concentration. There was no individual or interactive effect of climate change and invasion on total ammonium concentration.

Discussion

Multiple reports emphasize the urgent need to avoid surpassing the critical climate tipping points (IPCC 2023; UN 2023), although empirical evidence on the effects of future climate change scenarios on aquatic ecosystems remains scarce (but *see* Carriel et al. 2023, Lengyel et al. 2023). In this context, we expected that climate change mitigation would buffer the anticipated negative impacts of the BAU scenario on the growth and production of native macrophyte species. While climate change did not affect all response variables, our results indicate that climatic mitigation has the potential to counteract the effects of BAU treatment on both native and non-native macrophyte species. Climate scenarios with moderate changes in temperature and rainfall, as represented by our mitigation treatment, appear to preserve the vertical growth and production of the native species *C. caroliniana*, while maintaining the invasiveness potential of the non-native macrophyte *H. verticillata* at levels comparable to those of the baseline treatment. These findings support our hypothesis regarding the buffering effect of climate mitigation on native macrophyte performance and highlight its potential to restrict the growth of non-native species. Although the presence of climatic mitigation can maintain baseline climate conditions, a future BAU scenario that supports higher warming and potential drought reveals divergent impacts on invasion outcomes and native species. Under the BAU treatment, the native species exhibited constrained vertical growth, whereas the non-native species showed higher vertical growth and a greater potential for invasive vegetative propagule colonization compared to the baseline and mitigation treatments.

These contrasting responses can be attributed to warming and reduced water levels driven by climate change, which may favor non-native species with broader climatic tolerance (Short et al. 2016; Hermann et al. 2023). Our results indicate higher concentrations of dissolved nutrients, such as orthophosphate, under the BAU treatment in the absence of invasion, likely due to water level reductions that concentrate these nutrients (Jeppesen et al. 2015; Ersoy et al. 2020; Li et al. 2021). However, in the presence of *H. verticillata*, PO_4 concentrations decreased under both the mitigation and BAU treatments compared to the baseline, suggesting that the increased nutrient availability caused by climate change scenarios was likely taken up by the invasive species when present. These conditions are critical during the early colonization stage of the invasion process as *H. verticillata* fragments occupy water surfaces, gaining an advantage in light and nutrient acquisition, which contributes to its growth. Therefore, our hypothesis anticipating that the BAU scenario would favor the growth and production of the non-native macrophyte *H. verticillata* is fully supported by our results. In contrast, reduced water levels constrained the vertical growth and production of native species, whose fragments are rooted in the sediment and rely directly on sediment-derived nutrients (Schooler et al. 2009).

In addition to the individual impacts of climate change, we hypothesized that the interaction with biological invasion would reduce the effectiveness of climate mitigation and intensify the negative effects of the BAU scenario on native species. Our hypothesis was only partially supported, as the

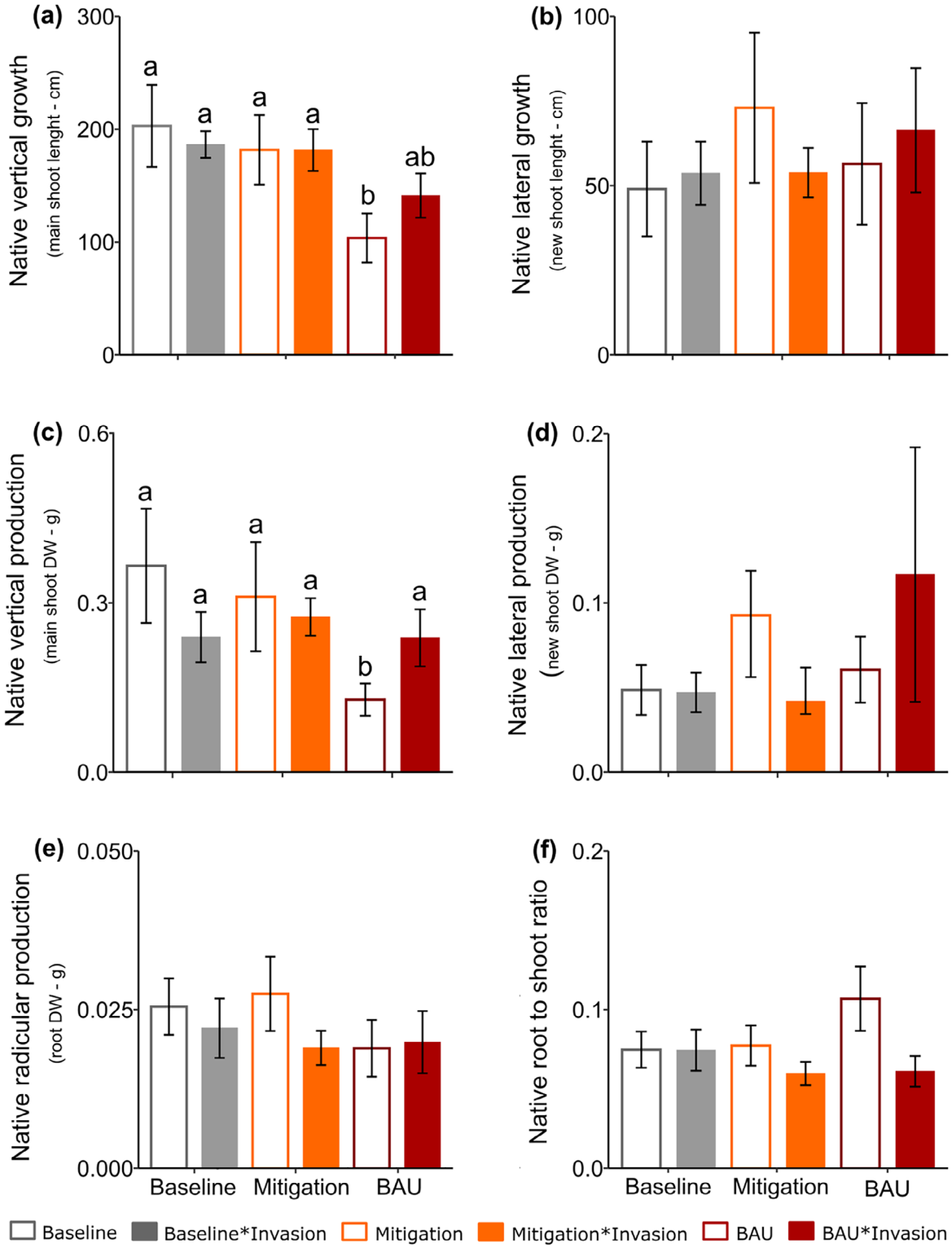


Fig. 3. Independent effects of climate change treatments (i.e., baseline, mitigation, and business-as-usual [BAU]) and their interaction with biological invasion on the native species *Cabomba caroliniana* growth and production responses described vertical growth (**a**), lateral growth (**b**), vertical production (**c**), lateral production (**d**), radicular production (**e**), and root-to-shoot biomass ratio (**f**). The colors represent climate treatments: gray = baseline, orange = mitigation, and red = BAU. The filled column indicates the presence of climatic treatments with biological invasion. Different lowercase letters indicate statistically significant differences among treatments, while their absence indicates nonsignificant effects (Tukey's HSD post hoc test). The values are means ± standard error of the mean ($n = 6$).

native species exhibited significantly higher vertical production in the presence of the non-native species under the BAU treatment; however, this difference was not statistically significant compared to that observed under the other climate treatments. This suggests that the presence of the non-native species under BAU conditions could offset the detrimental impacts of extreme climatic changes by restoring native vertical production to levels comparable with baseline and mitigation scenarios, rather than providing a lasting advantage. Previous studies have shown that water-level stress can shift interactions between native and non-native submerged macrophytes from competition to facilitation, as plants reallocate resources to cope with environmental stress rather than directly outcompeting one another (Li et al. 2022; Liu et al. 2023). In our study, however, the non-native species may have buffered the impacts of climate change on native macrophytes through light competition, potentially triggering a shift in native biomass allocation toward shoot production. Nonetheless, the long-term implications of this invasion-offset effect on native biomass production under future extreme climatic conditions remain uncertain and warrant further investigation as the invasion progresses.

In light of these dynamics, we further support the effectiveness of climate mitigation in reducing the detrimental effects of the climate BAU scenario on native species and the invasiveness potential of non-native species. While climate mitigation was not entirely effective in preventing the lateral growth of the non-native species compared to the BAU treatment, it significantly reduced the root-to-shoot biomass ratio of the observed invasive vegetative propagules. Thus, our findings suggest that climate mitigation can counteract the ability of *H. verticillata*'s vegetative propagules to invest in roots and colonize a new recipient environment. Mitigating climate conditions may reduce physiological stress, leading to lower urgency in allocating resources to traits related to dispersion and regeneration of non-native species. In contrast, the combination of warming, reduced water levels, and increased nutrient concentration observed under the BAU treatment may favor rapid lateral growth, allowing propagules to increase their buoyancy, dispersal potential, or photosynthetic capacity. Notably, the observed decrease in PO_4 concentration in the presence of invasion despite climate-driven nutrient enrichment suggests that the invasive species may have actively taken up these nutrients to support its accelerated lateral growth under future climate conditions. These longer fragments have a survival advantage due to increased photosynthetic tissue and reserves for shoot and root development (Riis et al. 2009). Thus, lateral growth is crucial for the regeneration of *H. verticillata*, especially since mechanical fragmentation of these structures under environmental stress generates vegetative propagules (Riis et al. 2009; Umetsu et al. 2012).

Although *H. verticillata* employs multiple dispersal strategies, lateral shoot fragmentation is among the most effective for producing new individuals and enabling long-distance dispersal (Madsen and Smith 1999; Umetsu et al. 2012). In our study, all observed invasive vegetative propagules originated through lateral fragmentation, regardless of climate change treatment. This indicates that even under varying climatic conditions, this dispersal mode remains a dominant and reliable mechanism for their spread. While the BAU treatment favored the growth of non-native species compared to the baseline and mitigation treatments, it also resulted in the lowest water volume and the highest potential for drought. The lower water volume observed under the BAU treatment was attributed to an extreme decrease in rainfall volume and frequency compared to the other treatments. Although such stressors can threaten the survival of both native and non-native species, *H. verticillata* may employ dormancy strategies to regenerate after disturbances, allowing it to persist more effectively than native species (Sousa 2011; Patrick and Florentine 2021). These combined traits underscore the resilience of *H. verticillata* under fluctuating water levels and highlight the vulnerability of native species that lack similar adaptive mechanisms.

It is essential to consider certain limitations when applying our findings to real-world systems. First, the short experimental duration may not fully capture long-term ecological dynamics, particularly those related to competitive displacement between species from a long-term perspective and nutrient cycling over seasonal or multi-year timescales. Additionally, while mesocosm experiments provide valuable control and replicability, they may not fully reflect the complexity of natural ecosystems, such as the biotic interactions between multiple species. Despite those limitations, we concluded that the effects of biological invasion on native species can vary depending on the climatic context, highlighting the complex interplay between invasion and future climatic conditions. Overall, the BAU treatment supported the growth of the non-native species *H. verticillata*, while constraining the vertical growth and production of the native species. Notably, the presence of the non-native species under the BAU treatment was associated with an increase in native vertical production, although this effect was not significantly different from that observed under the baseline and mitigation treatments. Thus, the presence of the invasive species appears to offset the effects of extreme climate stress, representing a recovery to baseline levels, rather than a net benefit for the native species. Overall, our results support that prioritizing climate mitigation efforts could help reduce freshwater vulnerability to invasion by limiting the invasive potential to levels comparable to those observed under current climatic conditions, thereby supporting the persistence of native species.

Author Contributions

Tauany Rodrigues: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, supervision, visualization, writing—original draft. Joseph L. S.

Ferro: data curation, investigation, methodology, writing—review and editing. Reinaldo L. Bozelli: funding acquisition, investigation, methodology, writing—review and editing. Aliny P. F. Pires: conceptualization, funding acquisition, supervision, writing—review and editing. Vinicius F. Farjalla: conceptualization, funding acquisition, supervision, writing—review and editing.

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Conflicts of Interest

None declared.

Data Availability Statement

All data are provided in the Figshare repository in the private link: https://figshare.com/s/529b73126c836cd8da8e.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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