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Implications of global climate change for the development and ecological interactions between two key Amazonian aquatic macrophytes

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ABSTRACT

Amazon wetlands are among the most vulnerable ecosystem to be impacted by climate change, which may increase the frequency of extreme droughts and floods. We used *Eichhornia crassipes* and *Pistia stratiotes*, two abundant aquatic plants in the Amazon floodplains, to evaluate the effects of combined temperature and [CO_2] increase on growth, physiology and ecological interactions. Individual and paired plants were deposited for three weeks in a microcosm under four IPCC scenarios: control (current temperature/CO_2), mild (control + 1.5 °C, 200 ppm CO_2), intermediate (control + 2.5 °C, 450 ppm CO_2) and extreme (control + 3.5 °C, 850 ppm CO_2). *P. stratiotes* died after three weeks in the intermediate and extreme treatments; *E. crassipes* experienced no mortality or change in any of the measured variables during the same period. *P. stratiotes* reduced root length in the mild treatment and reduced total dry biomass in intermediate and extreme treatments, revealing less tolerance to climate change. Ecological interactions between the two species changed with increasing [CO_2] and temperature neutral interaction changed to facilitation for *E. crassipes*, while competitive interaction changed to neutral for *P. stratiotes*. Global climate change may alter the composition, biomass and ecological interactions of Amazonian aquatic plant species.

Keywords: biomass, competition, *Eichhornia crassipes*, *Pistia stratiotes*, wetlands

Introduction

Global warming resulting from anthropogenic actions has been modifying the resilience of many ecosystems (Fuente *et al*. 2017), compromising the planet's biodiversity and human life (Buckeridge *et al*. 2007; IPCC 2013). As temperature rise and precipitation patterns change, resource inflows to ecosystems are entering novel ranges (Smith 2011). Forecasts from the fourth report of the Intergovernmental Panel on Climate Change (IPCC) indicate that global temperature will rise from 1.5 °C to 2 °C between 2030 and 2052. These changes could increase the temperature of continents and oceans, leading to extreme temperatures in some regions, with heavy rainfall and drought probability, as well as rainfall deficit in other regions (IPCC 2018; Marengo *et al*. 2018).

Alterations in CO_2 levels and temperature affect climate and change vegetation dynamics (Lashof *et al*. 1997;

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Schimel *et al*. 2001; Walther *et al*. 2002; Kelly & Goulden 2008). However, the long-term responses of plants to CO_2 and temperature increase depend on the physiological conditions and morphological acclimatization of each species. The effects of climate change in aquatic macrophyte communities, include changes in their phenology, biomass, productivity, and in species composition (Wetzel & Grace 1983; Liu *et al*. 2017; Lopes *et al*. 2018).

Climate can directly affect plants, inducing morphological and physiological responses, and indirectly interfering in biotic interactions (Tylianakis *et al*. 2008), therefore affecting the population dynamic (Olsen *et al*. 2016). For aquatic plants, temperature, light intensity and nutrient availability stand out as the most important abiotic factors (Bornette & Pujalon 2011), while competition resulting from interspecific relations has been identified as one of the most relevant biotic factors (Townsend *et al*. 2009). Interspecific competition is an important factor in determining which species can coexist or will be excluded from a habitat (Medina 1996). Positive interactions can also occur, such as facilitation, when the presence of one species favors the growth and development of the other, and neutral interactions, when the presence of one species does not interfere in the performance of the other. These interactions may have severe effects on individual development and growth, and population's distribution, as well as on species diversity and composition, and community dynamics (Bruno *et al*. 2003; Bagousse-Pinguet *et al*. 2014). Facilitation and competition mechanisms do not act isolated from each other but act together within a community producing complex and variable net effects (Callaway & Walker 1997). In addition, the conditions of the environment in which species interact are also relevant, and it is suggested that facilitation may be favored in environments with high abiotic stress (Bertness & Callaway 1994). In interspecific competition, there may be both mutual exclusion and coexistence of both species involved, depending on the differentiation of niches on an evolutionary scale (Townsend *et al*. 2009).

Little is known about the combined effects of such stressors on plant interactions (Weltzin *et al*. 2003; Darling & Côté 2008). This knowledge gap hinders predictions of ecosystem responses to global change (Tilman 2004; Thibault & Brown 2008), particularly in aquatic macrophytes communities (Lopes *et al.* 2018). Plant interactions, including competition and facilitation, are a complex phenomenon that are becoming increasingly unpredictable under climatic change (Ploughe *et al.* 2019). Recent studies reveal that plant interactions are highly dynamic, shifting from facilitative to competitive and back again as both resource availability and plant growth strategies change over time (Armas & Pugnaire 2005; Grant *et al*. 2014; Wright *et al*. 2015; Paterno *et al.* 2016). Experiments with *Pinus palustris,* demonstrate that although drought and invasive species suppressed the native tree species, the invader temporarily moderated stressful drought conditions, and at least some *Pinus* trees were able to survive despite increasingly strong competition (Alba *et al*. 2019). However, studies testing the combined effect of [CO_2] and temperature increase on the ecological relationships of aquatic plants are not available.

To understand the interactions between populations of a community is critical to comprehend their dynamics. Interactions depend, above all, on favorable environmental conditions (Gause 1934; Putman 1994). Basic knowledge on these interactions is of utmost importance, and it is most often used for biological control purposes (Bettiol & Ghini 1995). This knowledge may also be used in resistance induction, which consists in activating latent resistance mechanisms in response to treatment with biotic or abiotic (inducers) agents, and especially for maintaining the viability of natural communities (Thompson 2005; Oliveira & Del-Claro 2005).

About 400 aquatic herbaceous species occur in the fertile wetlands (várzeas) of the Amazon (Junk & Piedade 1993). They perform several key ecosystem functions and are well adapted to the variations in the hydrological cycle imposed by the flood pulse (Junk *et al.* 1989; Junk & Piedade 1997). However, changes in abiotic factors predicted by climate change scenarios will alter the dynamics of Amazonian aquatic ecosystems (Piedade *et al.* 2013). Consequently, the role of aquatic macrophyte communities in the functioning of these environments might be affect. Thus, this work was designed to answer the following questions: Will the increase in temperature together with CO_2 concentration influence the physiology and biomass increment of the aquatic macrophytes *Eichhornia crassipes* and *Pistia stratiotes*, which co-occur in the Amazonian floodplains? Will the increase in temperature together with CO_2 concentration change the interspecific ecological relationships between *E. crassipes* and *P. stratiotes*? We hypothesize that, since carbon contributes to the growth of aquatic plants, both species would be favored by the addition of mild [CO_2] and temperature level. On the other hand, the addition of extreme [CO_2] and temperature level could inhibit metabolic activities, resulting in death of individuals. Moreover, considering that *E. crassipes* is more adapted to many different habitats in the world, it will be facilitated while *P. stratiotes* will have a competitive disadvantage (Fig. 1).

Materials and methods

Studied species

The aquatic macrophytes used were chosen for their wide distribution in the floodplain, for being native to the Amazon, and having similar habits, forming monospecific and mixed stands (Lopes *et al.* 2011; Piedade *et al.* 2019). *Eichhornia crassipes* (Mart.) Solms, belonging to the Pontederiaceae family, is a native species of tropical South America (Sculthorpe 1985). The species' reproduction occurs vegetatively by stolons and seeds that are water dispersed (Gopal 1987; Piedade *et al.* 2019). Some ecosystem services provided by this species include the removal of water pollutants, paper and handcraft production and biogas. It occurs both in natural aquatic environments as in environments impacted by anthropic activities (Lopes & Piedade 2009). *Pistia stratiotes* L., belonging to the Araceae family, occurs in the tropical and subtropical regions (Pott & Pott 2000). It has extremely vigorous growth and can be dominant in the community (Junk & Piedade 1993; 1997). It inhabits especially still waters, preferably with large solar radiation and organic matter (Piedade *et al.* 2019). The species is used as food by the Amazon manatee when in captivity (Kissmann 1991), has medicinal potential (Rahman *et al*. 2011) and assists in the removal of heavy metals (Espinoza-Quiñones *et al.* 2009).

Plant collection area

The plants were collected on Marchantaria Island (3º15' S, 60º00' W), near the confluence of Solimões and Negro rivers, located 20 km southwest of Manaus (Irion *et al.* 1983). The minimum monthly average temperature in the area is 23 ºC with maximums between 30.2 ºC and 33.2 ºC; relative humidity ranges from 76 to 86 % (Piedade *et al.* 1991).

Similar specimens were collected, with an average of 10 leaves, and fresh weight around 40 g. The plants were conditioned in experimental units with water from the place of origin (Solimões River) and later taken to the Laboratório de Ecofisiologia of the Instituto Nacional de Pesquisas da Amazônia (INPA / MAUA). Prior to weighing, excess of water retained in the roots was removed by letting them drain for 5 minutes. Then, we sent the plants to the microcosm of the ADAPTA Project (Adaptações da Biota Aquática da Amazônia) in the Laboratório de Ecofisiologia e Evolução Molecular (LEEM), located at INPA.

Microcosm Experiment

The microcosm is composed of four climatic rooms of 3 × 4 m. The experimental conditions included the following: (a) Control - reproducing real-time changes in temperature and CO_2 levels that occur in a pristine forested area; (b) Mild - reproducing the B1 scenario (+ 200 ppm CO_2 and + 1.5 °C, in relation to Control); (c) Intermediate - reproducing the A1B scenario (+ 400 ppm CO_2 and + 2.5 °C, in relation to Control); and (d) Extreme - reproducing the A2 scenario (+ 850 ppm CO_2 and 4.5 °C, in relation to Control). The artificial light–dark cycle was 12:12 and humidity was set as a derived condition. The scenarios B1, A1B and A2 represent the climate conditions predicted by the IPCC (2007) for the year 2100 (Tab. 1; more details in Lopes *et al.* 2018).

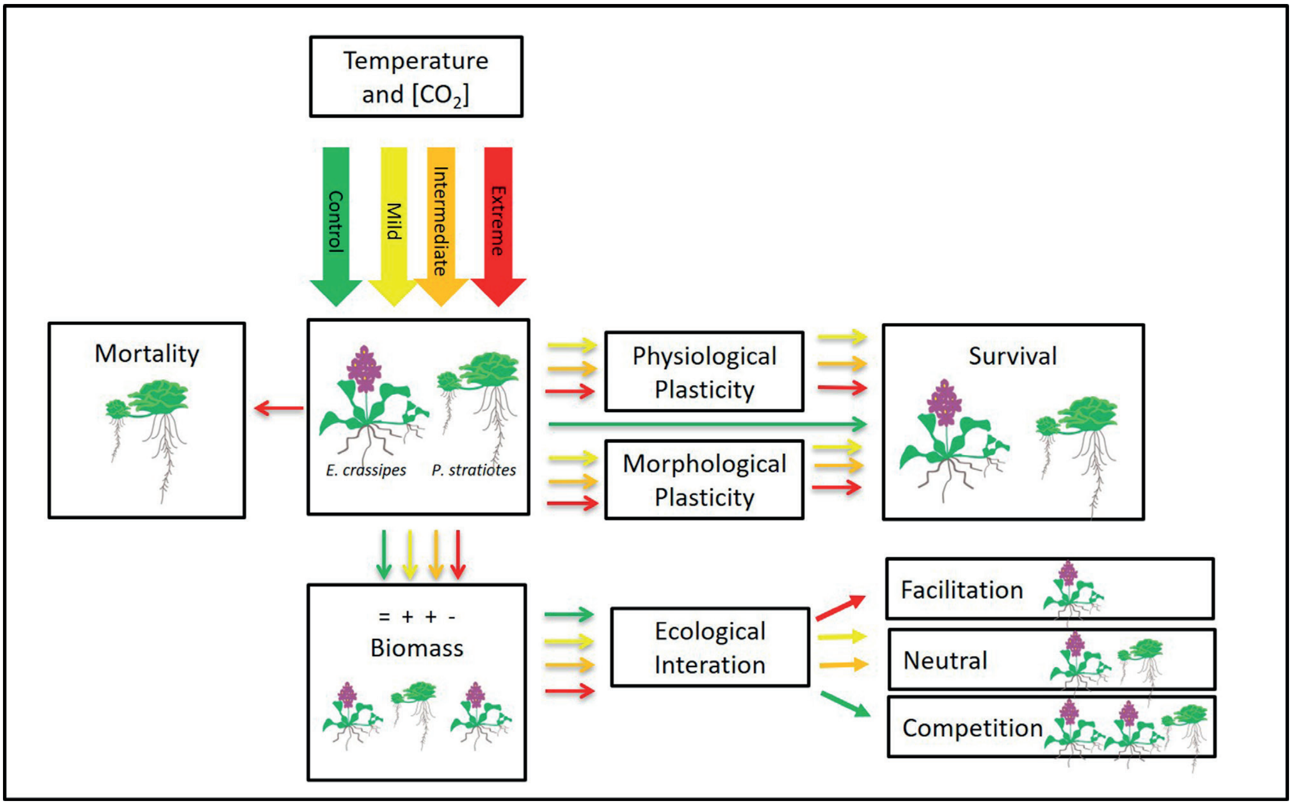

Figure 1. Impact hypothesis diagram for selected factors affecting ecological interaction between *E. crassipes* and *P. stratiotes* fronts to climate change. Different colors indicate the hypothesis for each climate scenario. The drawings of the species were gently ceded by Jefferson da Cruz.

Each room received nine experimental units: three with *E. crassipes*, three with *P. stratiotes* and three with the two species together, totaling 36 units, consisting of a 12-liter pot measuring 25.5 × 27 cm each, and containing water from the Solimões River, with 40 g of each species. In addition, a second control was established at the Casa da Vegetação of Grupo MAUA (INPA/Max-Planck), similar to the natural environment conditions. Plant monitoring was weekly and initially designed to last four weeks. Nevertheless, it was performed for three weeks due to plant mortality in some treatments.

Data collection

The variables of water (temperature and pH) were measured using a multiparameter meter (Hanna). Air temperature and CO_2 concentration data were obtained from sensors installed in the microcosm. During the experiment the number of live and dead leaves, root length, leaf length, the presence of shoots, petiole length and the appearance of chlorosis and necrosis were monitored. In addition, chlorophyll *a*, chlorophyll *b* and total chlorophyll content was measured with a portable Clorofilog meter (Falker, Brazil). At the end of the experiment, the dry biomass of the species was determined. To obtain the dry weight, the material was placed in a forced ventilation oven (70 °C) until constant weight and weighed in analytical balance (AG200) with precision degree 0.0001 g.

To measure the intensity of interaction, that is, the magnitude of the effect that one species has on another, regardless environmental factors (Brooker *et al*. 2008), the RII Relative Interaction Index (Armas *et al*. 2004) was calculated from the total biomass. For this we used the formula $RII = \frac{(B_P + N) - (B_P - N)}{(B_P + N) + (B_P - N)}$, in which BP + N is the total biomass value of the target plant in the presence of the neighbor, and BP - N is the total biomass value of the target plant in the absence of the neighbor.

To assess the importance of plant-plant interactions, that is, the impact of one species on another, expressed as a proportion of the impact of the entire environment on the species, we used the Iimp Importance Index (Seifan *et al*. 2010), calculated from total biomass using of the formula $Iimp = \frac{(N_{imp})}{\left|(N_{imp})\right| + \left|(E_{imp})\right|}$, N_{imp} is the neighbor's contribution to the total biomass of the target plant, defined by the formula $N_{imp} = B_{P+N} - B_{P-N}$; E_{imp} expresses the contribution of the environment to the total biomass of the target plant, defined by the formula $E_{imp} = B_{P-N} - MB_{P \pm N}$ where $MB_{P \pm N}$ is the maximum value of the total biomass of the target plant, regardless of neighbors.

Both RII and Iimp have values ranging from -1 to 1, and are symmetrical around zero, being negative for competition and positive for facilitation. Values closer to zero imply that the balance of interactions is neutral or unimportant for plant performance (Armas *et al*. 2004; 2011; Soliveres *et al*. 2011).

Statistical analysis

The effects of climate scenarios (temperature and $[CO_2]$) and ecological interaction between species (facilitation, neutral or competition) were evaluated on growth (number of live and dead leaves, root length, leaf length, presence of sprouts, petiole length) and also on the concentration of chlorophyll *a*, *b* and total, and water pH and temperature over time using block ANOVA of repeated measures, followed by Bonferroni test when a significative effect was found. For the effects on biomass incorporation and in the interaction index at the end of the experiment, we used randomized block ANOVA. This test considered the interaction between species as the main factor, and the climatic scenarios as a block factor, followed by Tukey test when a significative difference was found. All data were checked concerning the statistical assumptions by using a one-sample Kolmogorov–Smirnov test. Analyzes were performed using Systat 12.0 Software.

Results

During the experiment period, CO_2 concentration in microcosms ranged from 392 to 570 ppm in the control room, 494-781 ppm in the mild treatment, 750-978 ppm in the intermediate treatment and 1256-1466 ppm in the extreme treatment. The temperature ranged from 24.5 to 34.3 °C in the control room, 25.8-35.9 °C in the mild treatment, 26.2-40.3 °C in the intermediate treatment and 28.7-44.8 °C in extreme treatment. Humidity ranged from 45 to 85.6 % in all treatments during the experimental period (Tab. 2). The pH varied between 5.69 and 6.66 and water temperature 29.26 °C and 30.90 °C (Tab. 3).

Before the third week all the individuals in all treatments were alive. At the end of the third week of monitoring, individuals of *P. stratiotes* from the intermediate and extreme treatments showed a yellowish color around the central leaf veins, indicating a chlorosis process, unlike what was observed in the plants in the greenhouse, which showed no morphophysiological alteration (Fig. 2A-C). At the end of the same week, in the remaining individuals, chlorosis expanded from the central ribs to the whole plant, leading to the death of all *P. stratiotes* individuals (Fig. 2C). The species *E. crassipes* presented, in the intermediate and extreme treatment, necrosis at the margin's edges of the larger leaves. After the third week the leaves completely withered, leading to death of all individuals (Fig. 2D-F).

Effect of treatments and interspecific ecological interaction on ***E. crassipes***

There was no effect of climatic scenarios or species interaction over the three-week follow-up on the chlorophyll a index of *E. crassipes* (Tab. 4). Chlorophyll b index did not vary over time, but was higher in the presence of

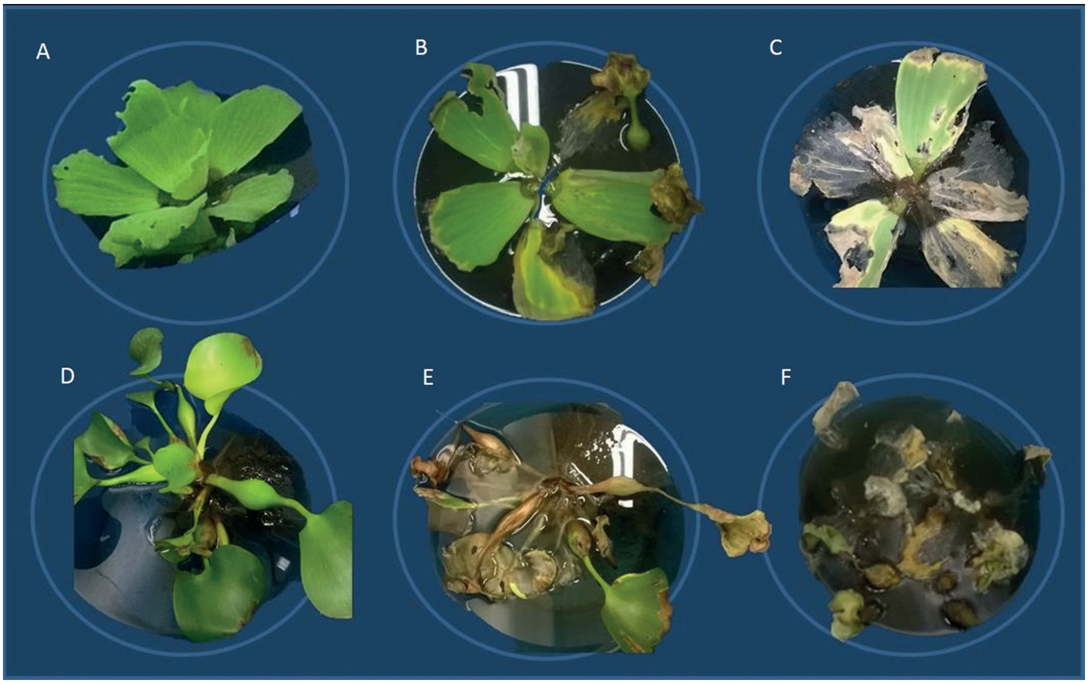

Figure 2. Third week of experiment with P. stratiotes in: **A)** control; **B)** intermediate with chlorosis; **C)** extreme with necrosis. *E. crassipes* in: **D)** control; **E)** intermediate with necrosis and **F)** extreme with dead plant.

Table 1. Programmed values of CO_2 concentration, temperature, and humidity for the microcosm.

Treatment	CO_2 (ppm)	Temperature (°C)	Humidity (%)	IPCC Scenario (2007)
Control	±400	±30	±75	–
Mild	Control +200	Control +1.5	±75	B1
Intermediate	Control +400	Control +2.5	±75	B2
Extreme	Control +850	Control +4.5	±75	A2

B1 comes closest to a “sustainable development” future where economic growth and environmental protection are considered compatible. It too has high economic growth (GDP is projected to be $350 trillion in 2100), although not as rapid as A1.

B2 is a less prosperous version of B1 with slower economic growth (GDP is projected to $250 trillion in 2100). Regional governance is more inward looking rather than global. Cultural pluralism is strong along with environmental protection.

A2 is a world of lower economic development (GDP reaches $250 trillion in 2100) and weak globalization. It is more prone to clashes between cultures and ideas, and places a high priority on indigenous values.

Table 2. Average values of microcosm climatic conditions in four weeks of the experiment period.

Weeks	CO_2 (ppm)				Temperature (°C)				Humidity (%)			
	C	M	I	E	C	M	I	E	C	M	I	E
1	486.17	666.83	885.57	1337.66	30.85	30.56	33.12	32.96	68.77	60.89	67.71	65.45
2	493.78	676.04	896.29	1350.11	30.97	31.10	33.49	33.74	69.62	60.84	68.44	65.68
3	482.34	662.91	883.04	1335.07	30.86	31.19	33.72	33.66	70.12	59.47	67.73	64.65
4	481.06	661.52	881.77	1336.03	30.31	31.27	33.35	33.92	71.30	59.99	68.36	65.90

Where C = control; M = mild; I = intermediate; E = extreme treatments

Table 3. Average (± standard deviation) of the water pH and temperature (°C) during experiment period.

Treatment	*E. crassipes*		Interaction		*P. stratiotes*	
	pH	Temperature	pH	Temperature	pH	Temperature
Greenhouse	5.69±0.57b	30.23±0.35a	6.34±0.69a	30.76±0.61a	6.08±0.38a	30,56±0.56ab
Control	6.50±0.16ab	29.90±0.29a	6.64±0.24a	30.16±0.70a	6.62±0.07a	30.20±0.43ab
Mild	6.39±0.15ab	29.26±0.15a	6.40±0.06a	29.76±0.35a	6.36±0.12a	29.43±0.11b
Intermediate	6.02±0.32ab	30.60±0.19a	6.50±0.07a	30.86±0.25a	6.48±0.05a	30.90±0.78a
Extreme	6.66±0.09a	29.90±0.29a	6.41±0.17a	30.06±0.51a	6.56±0.16a	30.20±0.43ab

Different letters indicate statistically significant differences ($p < 0.05$) between the treatments.

P. stratiotes, and higher in the mild climatic scenario (Tab. 4). There was an effect of climatic scenarios on the chlorophyll total index, with higher values in the mild scenario, but no effect of time or specie interaction (Tab. 5).

The number of *E. crassipes* leaves increased during the experiment, not affected by the presence of *P. stratiotes,* but influenced by the climatic scenario (Tab. 5), with higher values in mild scenario. Leaf length and petiole length of *E. crassipes* increased over time, with no effect of *P. stratiotes*, neither of climatic scenario (Tab. 4). The root length of *E. crassipes* increased over time, with no effect of *P. stratiotes* presence, but influenced by the climatic scenario (Tab. 4), with higher values in the mild scenario.

The total biomass of *E. crassipes* at the end of the 3-week treatment was higher in the presence of *P. stratiotes* ($F_{2.9}$ = 4.315, p = 0.023), and there was no effect of the climatic scenarios ($F_{2.9}$ = 1.166, p = 0.346).

Effect of treatments and interspecific ecological interaction on *P. stratiotes*

During the three weeks of the experiment there was an effect of climatic scenario on the chlorophyll *a* index, with lower values in mild and intermediate scenario (Tab. 6), but no effect of interspecific interaction or time (Tab. 5). There was no effect of climatic scenarios or specie interaction over the three-week follow-up on the chlorophyll *b* index (Tab. 5). Total chlorophyll was affected only by the climatic scenarios (Tab. 6), with lower values in mild and intermediate scenarios.

The number of leaves of *P. stratiotes* increased, but their size were reduced during the experiment, both affected by the presence of *E. crassipes* (Tab. 5). There was no effect of the climatic scenarios on the number of leaves (Tab. 6). Leaf length of *P. stratiotes* increased over time, with no effect of the presence of *E. crassipes* (Tab. 5), but an effect of the climatic scenarios, with longer leaves in the extreme treatment (Tab. 6). The root length of *P. stratiotes* did not increase over time and was not affected by the presence of *E. crassipes*, neither by the climatic scenarios (Tab. 6). The number of sprouts of *P. stratiotes* increased over time in the presence of *E. crassipes,* causing a reduction in the number of shoots, and the climatic scenario decreasing values in the extreme scenario (Tab. 6).

The presence of *E. crassipes* did not affect the total biomass of *P. stratiotes* (ANOVA, $F_{2.9}$ = 1.171, p = 0.290), but there was an effect of the climatic scenarios ($F_{2.9}$ = 23.886, p < 0.0001), with a reduction in the intermediate and extreme scenarios (Tab. 5).

Interspecific ecological interaction indices

RII index was not statistically different between species and treatments (p > 0.05). The Iimp index was significantly lower for *P. stratiotes* ($F_{2.9}$ = 2.648, p = 0.025), but there was no difference between treatments (p > 0.05). Relative intensity of interaction (RII) for the species *E. crassipes* in the greenhouse varied between competition and facilitation, and for *P. stratiotes* the intensity of competition was higher. In the control treatment the interaction between species changed in relation to the greenhouse, with *E. crassipes* competing in most experimental units, while *P. stratiotes* oscillated between competition and neutral interaction when *E. crassipes* were present. In the mild treatment *E. crassipes* showed competitive advantage, being facilitated in all experimental units when in the presence of *P. stratiotes*. In this treatment, *P. stratiotes* did not show a unique interaction pattern, oscillating between neutral interaction, facilitation and competition. In both intermediate and extreme treatment, *E. crassipes* suffered competition in most sample units, while for *P. stratiotes* facilitation was more important (Fig. 3A).

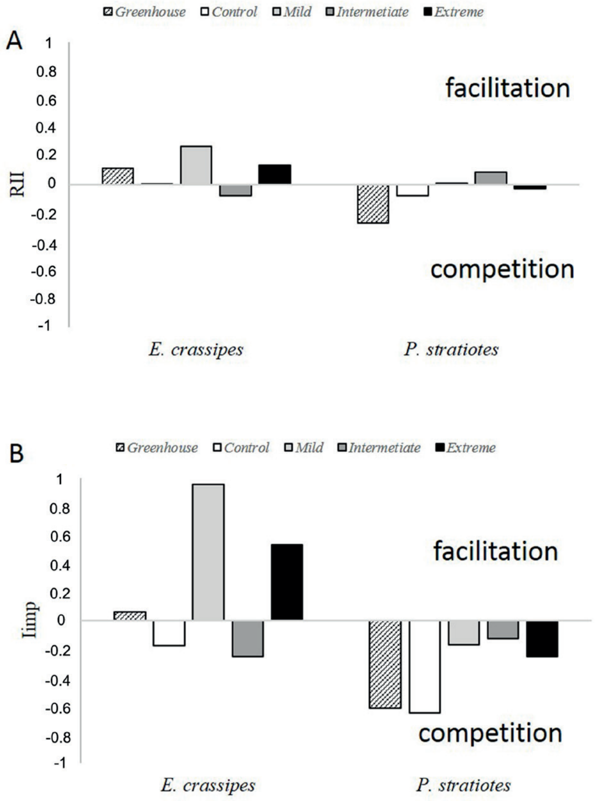

Figure 3. Indexes A) RII and B) Iimp demonstrating the ecological relationships between *E. crassipes* and *P. stratiotes* in the greenhouse and microcosm rooms after 3 weeks of the experiment. Where: Values = 0 indicate neutrality; < 0 competition; and > 0 facilitation.

In the greenhouse, the Importance index (Iimp) varied between competition and facilitation for *E. crassipes*, while competition was important for the performance of *P. stratiotes* species. In the control treatment for both *P. stratiotes* and *E. crassipes*, competition was more important. In the mild treatment, facilitation became important for both species. In the intermediate treatment competition was more important for *E. crassipes* and facilitation was

Table 4. Average (± standard deviation) of physiological, morphological, and biomass parameters of *E. crassipes* individually and in *P. stratiotes* presence (interaction) in the third week of the experiment.

	E. crassipes (individually)					*E. crassipes* (interaction)				
	GH	C	M	I	E	GH	C	M	I	E
Chlorophyll *a*	37.1±1.4a	37.7±4.5a	38.0±1.6a	36.3±1.7a	38.1±2.3a	37.5±2.7a	39.7±3.1a	39.1±3.0a	38.3±3.1a	35.8±4.6a
Chlorophyll *b*	7.8±1.2a	5.2±0.9a	7.5±0.9a	5.2±1.6a	5.3±0.4a	8.1±1.6a	6.6±0.6a	5.4±0.8a	6.2±1.2a	4.2±1.4a
Total chlorophyll	44.9±2.6a	42.8±4.3a	45.5±2.2a	41.5±0.7a	43.4±2.3a	45.6±2.7a	46.3±2.5a	44.6±3.6a	44.5±3.0a	39.9±6.0a
N° of leaves	14.0±1.6a	15.7±2.1a	16.7±2.5a	16.3±1.2a	13.3±1.2a	13.7±2.5a	15.3±2.1a	16.3±4.0a	14.3±1.7a	15.3±2.9a
Leaves length (cm)	14.0±0.8a	14.4±2.1a	13.6±1.3a	14.1±1.9a	12.3±1.7a	12.9±0.3a	13.1±1.3a	13.6±2.4a	13.0±2.2a	12.5±1.1a
Petiole length (cm)	10.5±1.5a	12.6±1.7a	11.7±0.9 a	8.7±2.2a	10.1±3.0a	10.2±1.3a	12.0±1.9a	12.5±1.9a	9.2±1.9a	9.4±3.1a
Root length (cm)	13.0±2.2a	13.7±0.7a	12.7±1.8a	10.4±0.8a	12.5±1.8a	12.5±1.9a	12.6±0.7a	14.9±3.4a	13.7±0.9a	13.5±0.8a
Total biomass (g)	2.3±0.5a	2.7±0.1a	2.4±0.0a	2.5±0.8a	2.4±0.7a	2.9±0.6a	2.7±0.5a	4.4±1.1a	2.2±1.0a	2.7±1.2a

Where GH = Greenhouse; C = control; M = mild; I = intermediate; E = extreme treatments. Different letters indicate statistically significant differences ($p < 0.05$) between the treatments.

Table 5. Summary of in block repeated measure ANOVA reults.

		E. crassipes			*P. Stratiotes*		
	Factor	F	gl	p	f	gl	p
Chlorophyll *a*	Specie Interaction	1.323	1	0.261	0.079	1	0.781
	Climatic Scenario	2.699	4	0.055	**3.272**	**4**	**0.028**
	Time	0.221	2	0.803	1.821	2	0.173
Chlorophyll *b*	Specie Interaction	**6.525**	**1**	**0.017**	1.947	1	0.176
	Climatic Scenario	**4.515**	**4**	**0.007**	0.2	4	0.936
	Time	0.247	2	0.782	0.35	2	0.707
Total chlorophyll	Specie Interaction	0.019	1	0.89	0.053	1	0.819
	Climatic Scenario	**3.444**	**4**	**0.023**	**2.911**	**4**	**0.043**
	Time	0.079	2	0.925	2.032	2	0.142
No leaves	Specie Interaction	0.064	1	0.803	**4.364**	**1**	**0.047**
	Climatic Scenario	**3.56**	**4**	**0.02**	2.577	4	0.063
	Time	**43.506**	**2**	**<0.001**	16.851	2	**<0.001**
Leaf length	Specie Interaction	1.049	1	0.316	1.031	1	0.32
	Climatic Scenario	2.74	**4**	0.052	**6.953**	**4**	**0.001**
	Time	**87.731**	**2**	**<0.001**	**73.549**	**2**	**<0.001**
Petiole length	Specie Interaction	0.288	1	0.596			
	Climatic Scenario	1.594	4	0.208			
	Time	**4.283**	**2**	**0.019**			
Root length	Specie Interaction	0.258	1	0.616	0.514	1	0.481
	Climatic Scenario	**3.431**	**4**	**0.024**	2.58	4	0.063
	Time	**5.502**	**2**	**0.007**	2.27	2	0.114
No sprouts	Specie Interaction				7.38	1	0.012
	Climatic Scenario				**3.036**	**4**	**0.037**
	Time				8.431	2	0.001

Table 6. Average (± standard deviation) of physiological, morphological, and biomass parameters of *P. stratiotes* individually and in *E. crassipes* presence (interaction) in the third week of the experiment.

	P. stratiotes (individually)					*P. stratiotes* (interaction)				
	GH	C	M	I	E	GH	C	M	I	E
Chlorophyll *a*	29.0±1.0a	29.7±2.7a	27.8±0.5a	27.3±1.5a	32.1±6.7a	30.4±2.3a	27.2±1.1a	27.2±1.1a	29.3±2.9a	26.8±1.2a
Chlorophyll *b*	3.8±0.2a	3.9±0.5a	3.2±1.0a	3.8±0.5a	5.0±1.3a	4.8±0.6a	3.5±0.0a	4.0±0.5a	4.1±0.0a	3.1±1.5a
Total chlorophyll	32.8±0.9a	33.6±3.2a	31.0±1.1a	31.1±1.0a	37.2±8.1a	35.1±1.7a	30.7±1.1a	31.2±1.6a	33.9±3.4a	29.8±0.3a
N° of leaves	13.7±1.7a	11.7±1.2a	11.3±0.9a	12.3±1.2a	14.0±1.6a	11.0±1.0a	10.5±1.5a	10.5±0.5a	11.0±1.0a	13.0±3.0a
Leaves length (cm)	13.4±1.0a	10.1±2.7a	12.1±1.4a	12.9±2.6a	11.6±0.7a	12.7±1.3a	9.0±0.9a	12.4±1.6a	11.0±0.9a	9.8±0.8a
Root length (cm)	11.8±0.6ab	12.4±1.2a	8.4±0.7b	10.7±1.6ab	11.3±1.3ab	13.3±0.8a	10.6±0.4ab	9.8±0.5ab	11.9±0.4ab	9.9±0.5ab
N° of sprout	2±0.8a	1.3±0.5a	1.3±0.5a	1.3±1.2a	0.3±0.5a	1±1.4a	0.5±0.5a	0.5±0.5a	1.0±1.0a	0.1±0a
Dry biomass (g)	1.3±0.3ab	2.2±0.0a	2.6±0.8a	0.6±0.4b	0.4±0.3b	0.9±0.1b	1.7±0.2ab	2.2±0.4a	0.7±0.4b	0.5±0.2b

Where GH = Greenhouse; C = control; M = mild; I = intermediate; E = extreme treatments. Different letters indicate statistically significant differences ($p < 0.05$) between the treatments.

more important for *P. stratiotes*. In the extreme treatment, both competition and facilitation were important for both species (Fig. 3B).

Discussion

Our results indicate that average temperatures of 30-34 ºC and average CO_2 concentrations of 881-1350 ppm are unfavorable to *P. stratiotes* and *E. crassipes*, either in isolation or when interacting. The RII and Iimp indices showed that there was a change in the type and intensity of interactions between species depending on the treatment (high temperature and CO_2). Bagousse-Pinguet *et al.* (2014) describe that any change in the environment can alter, modify, and even inhibit ecological interactions between plant species, causing effects on species diversity and abundance of these communities. Morphological and physiological responses of Amazonian aquatic plants were found in experimental conditions of higher [CO_2] and temperature (Lopes *et al.* 2018). In the present study, the change in the pattern of ecological interaction indicates that the combined rise in temperature and [CO_2] may result in changes in the communities of aquatic plants.

Heide *et al.* (2006) analyzed the effect of water temperature on the biomass of *Lemna minor* and *Azolla filiculoides* for 1.5 weeks, and verified the mortality of the species at 38 ºC, as well as the reduction of the biomass at temperatures above 29 ºC. In the present study, *P. stratiotes* presented lower biomass values in the intermediate and extreme treatments, where the average air temperatures were 31-34 °C in the intermediate treatment and 32-34 °C in the extreme treatment, showing relative lower susceptibility of this species to high temperatures, with mortality occuring only after three weeks. In a study of the same microcosm, Lopes *et al.* (2018) observed, for *Montrichardia arborescens*, an inhibition of biomass production in the extreme treatment of temperature and CO_2. *E. crassipes*, on the other hand, did not change biomass values in response to the treatments, indicating that this species is more tolerant to the imposed climate changes than *M. arborescens* and *P. stratiotes*. Although *E. crassipes* did not resist to intermediate and extreme treatments after 3 weeks. This higher tolerance to high temperatures can be explained due to ideal temperature differences for the species: between 28-31 ºC for *E. crassipes* (Pedralli & Meyer 1996); around 25 °C for *P. stratiotes* (Cancian *et al.* 2009); between 21-28 ºC for *A. filiculoides* and between 21-27 ºC for *L. minor* (Heide *et al.* 2006).

The occurrence of chlorosis is related to the deficiency of several elements responsible for chloroplast formation and chlorophyll synthesis (Breckle & Kahle 1992). This process impairs the photosynthetic metabolism of the plant and can lead to its death. For some aquatic macrophyte species as *M. arborescens*, photosynthesis rates were reduced in treatments with higher CO_2 and temperature (Lopes *et al.* 2018). In the present study, such differences were not observed. Also, unlike that observed by Cancian *et al.* (2009), who recorded chlorosis in *Pistia stratiotes* at a temperature of 30 °C, in this study chlorosis and necrosis only occurred in the leaves of both species in the treatments with the highest temperatures and CO_2 [intermediate (averages 30-34 °C and 881-896 ppm CO_2) and extreme (averages 33-34 °C and 1336-1350 ppm CO_2) treatments]. Therefore, when the average temperature exceeded 30 °C and the average CO_2 concentration exceeded 881 ppm, both species began to suffer damage that culminated in death.

In a competing habitat, what will ensure the success of one species over another is its ability to capture and use resources (Grime 1979). In this sense, *E. crassipes* showed a competitive advantage over *P. stratiotes*, since none of the morphological variables or biomass of this species was altered by the presence of *P. stratiotes*. Under natural conditions, several authors described *E. crassipes* competitive advantage and dominance over *P. stratiotes* (Parija 1934; Tag-El-Seed 1978; Reddy *et al.* 1983; Henry-Silva & Camargo 2005). This competitive advantage over other species may explain why *E. crassipes* is one of the most invasive species in the world (Gopal & Sharma 1981).

The importance of including facilitation in ecological invasion studies has already been pointed out (Bruno *et al.* 2003). The effects of facilitation are greatest in environments with high abiotic stress and low consumer pressure, and smaller when abiotic stress is low and consumer pressure is high. However, in intermediate environments of abiotic stress and consumer pressure, competition is more important (Bertness & Callaway 1994; Butterfield *et al.* 2016). This is consistent with what we observed in this study, where, according to the RII index, there was a higher occurrence of facilitation for *E. crassipes* in extreme and controls treatments compared to intermediates (Fig. 2A). This interaction is crucial for the permanence of species under extreme climate change (Lloret *et al.* 2012). As examples of facilitation in aquatic macrophytes we can mention: *Ipomoea aquatica*, which uses *E. crassipes* as a support structure for its growth; *Oxycaryum cubense*, an aquatic epiphyte that grows on other aquatic macrophytes such as *Eichhornia azurea* or *Salvinia auriculata* (Pott & Pott 2000), and *E. azurea*, with long floating roots that reduces the current resulting from wind waves, providing a favorable microhabitat for other floating macrophytes, such as *Salvinia* spp., *Azolla* sp. and *Ricciocarpos natans* (Thomaz & Bini 2005).

Among the indices analyzed in this study, neutralism was not a common relationship between the two species, occurring in a few experimental units. On the other hand, although neutralism is classified as the absence of physiological interaction and random occurrence between species, *E. crassipes* and *P. stratiotes* occur in mixed stands in the Amazon, which involves biological and physical factors

(Junk & Piedade 1997). This may explain the organization pattern of floodplain aquatic macrophyte assemblies (Boschilia *et al*. 2008).

Using neutral theory to predict extinction rates for tree species under climate change scenarios through 100 stochastic simulations, Hubbell *et al*. (2008) pointed to average total species extinction rates of 20 % and 33 % in the Brazilian Amazon. However, the analysis considers only the extinction rates of tree species, and not of other plants and animals that may also be extinct due to habitat loss. Considering the results of our study, we can assume that if scenarios such as intermediate and extreme are achieved, ecological interactions between *E. crassipes* and *P. stratiotes* will occur with greater intensity. As CO_2 concentration and temperature increase, the number of individuals will be reduced, and it may occur a competitive replacement or exclusion of these widely distributed species in all tropical regions of the planet (Sculthorpe 1985). If the increase in CO_2 concentration is accompanied by an increase in air temperature, as predicted by the IPCC (2013), several plant species will decrease growth and performance as a result of shortened developmental cycle and increased respiration (Taiz *et al*. 2013).

Amazon wetlands provide diverse ecosystem services to the population and this is associated with the high biodiversity, biomass production and ecological role of plants, including aquatic plants (Junk *et al*. 1989). The occurrence of different aquatic plant communities in the Amazon is known to vary according to the hydrological cycle (Junk & Piedade 1993); however, the deforestation and climate change in the region is causing local alterations, with increased frequency of flooding and extreme droughts (IPCC 2013; Gloor *et al*. 2015; Hilker *et al*. 2014). These alterations corroborate the model-based predictions proposed by Duffy *et al*. (2015), that the Amazon has entered a new climate regime, with a warmer and less humid climate which will promote reductions in species richness and productivity. If climate change continues, with a concomitant and progressive increase in temperature and CO_2, it is expected that these abundant key aquatic plants will also be reduced, with multiple negative impacts on Amazon wetlands.

In general, aquatic macrophytes have a wide ecological range (Thomaz & Bini 2003). The environmental changes interfere in the species distribution, causing ecosystems to disrupt their structure and functioning (Piedade *et al*. 2013). The combined effect of increased CO_2 and temperature caused significant physiological, morphological, and ecological interactions in the three aquatic macrophyte species studied to date (*ie*. *M. arborescens*, Lopes *et al*. (2018); *P. stratiotes* and *E. crassipes*, present study). Given the existence of almost 400 species of aquatic plants listed only for the Amazonian floodplains (Junk & Piedade 1993), and considering that species tolerance to climate change has been quite variable, we can expect large changes in the composition and dominance of some species, if IPCC forecasts take place.

Conclusion

The increase in temperature together with the CO_2 concentration affected morphology and physiology of both *E. crassipes* and *P. stratiotes*, with the latter being more sensitive to the effects of climate change. Although there is a wide variation between the types of interspecific ecological relationships in all treatments, the set of results indicates that these species are vulnerable to the predicted global climate change, both individually as in the complex relationships between them.

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