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Effects of climate change conditions on the individual response and biotic interactions of the native and non-native plants of Antarctica

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Abstract

Anthropogenic pressure and climate change have generated important changes in the environmental conditions of Antarctic ecosystems. These changes include the introduction of non-native species, rising temperatures, changes in precipitation patterns, and the expansion of ice-free areas. These alterations can have adverse effects on the native flora. Therefore, our study aimed to assess the potential impact of the non-native plants: *Poa annua* and *Juncus bufonius* on native species *Colobanthus quitensis* and *Deschampsia antarctica* under climate change simulated conditions. Individuals of *C. quitensis*/*D. antarctica* and *J. bufonius*/*P. annua* were exposed to four different growth conditions: 6 °C/low water availability (LW); 8 °C/LW and 6 °C/high water availability (HW) and 8 °C/HW. We hypothesized that competition would be more intense at 8 °C/HW, whereas facilitation would be the predominant interaction at 6 °C/LW. The results revealed that under 8 °C/HW conditions, all species experienced a significant increase in biomass production. However, the mortality rate of native species shows the opposite trend. The Relative Interaction Index (RII) showed a competitive effect of both non-native species on *D. antarctica*, independent of temperature and water availability, while for *C. quitensis* competition is more intense at LW conditions. These findings demonstrate that the impact of climate change could exacerbate the effects of non-native species on native species in Antarctic ecosystems. This includes non-native species that have been reported but have not yet established stable populations in the maritime Antarctic.

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Introduction

Antarctic ecosystems have exhibited low levels of invasion (Hughes and Convey 2012; Hughes et al. 2015; Huiskes et al. 2014; Galera et al. 2018; Chwedorzewska et al. 2020). This limited invasion is primarily attributed to the low pressure of propagules due to geographical factors (Lee and Chown 2009; Hughes and Convey 2012) and physiological barriers (extreme climatic and edaphic conditions: low temperature, limited water availability, strong winds, specific light regime, and poor soil conditions) (Frenot et al. 2005; Convey 2011; Convey and Peck 2019; Hughes et al. 2020). However, during the last 50 years the increase in anthropogenic pressure associated with scientific and tourist activities, and the effect of regional climate change (particularly in the maritime Antarctic) has challenged this paradigm (Hughes et al. 2020). Instances of non-native plant propagule have notably increased in the maritime Antarctic, where human activities

are concentrated and, where the climatic conditions are more suitable for the growth of plant species, compared to the continental Antarctic (Chown et al. 2012; Chwedorzewska et al. 2015; Molina-Montenegro et al. 2015; Fuentes-Lillo et al. 2017a; Bokhorst et al. 2021), altering the distribution and conservation status of native terrestrial flora.

The maritime Antarctic terrestrial ecosystem has a very simple community structure with extremely low diversity of Magnoliophyta (*Deschampsia antarctica* Desv., Poaceae*, and *Colobanthus quitensis* (Kunth) Bartl., Caryophyllaceae), along with a relatively high richness of cryptogams (Convey et al. 2014). It has been suggested that the maritime Antarctic, due to its low species diversity, very low productivity, and presence of empty niches may exhibit high invasibility (Galera et al. 2018). This phenomenon is exacerbated by the increasing pressure of alien propagules transferred by human vectors (Chown et al. 2012; Fuentes-Lillo et al. 2017a; Hughes et al. 2020; Bokhorst et al. 2021). Furthermore, considering the current effect of global change processes (such as climate change and increased anthropogenic pressure) on the Antarctic ecosystem, the impact of non-native species could increase significantly during the next century (Convey and Lewis Smith 2006; Casanova-Katny and Cavieres 2012; Duffy et al. 2017; Atala et al. 2019; Chwedorzewska et al. 2020; Hughes et al. 2020; Pyšek et al. 2020).

Climate suitability analysis for 93 invasive species worldwide, including species present in the sub-Antarctic and Antarctic islands, has revealed that climate can serve as an abiotic filter for some non-native species. However, there is a wide range of non-native species, particularly herbaceous plants that are currently invading sub-Antarctic islands. By 2100, these species could potentially be established in the ice-free zones in the maritime Antarctic (Duffy et al. 2017). Recent research has demonstrated 16 non-native species of different growth forms have been able to germinate and grow under simulated climate change conditions in Antarctic soils. This suggests that the number of non-native species that can be established is higher than that determined by different distribution models (Bokhorst et al. 2021). In this context, it is crucial to understand how the synergies between climate change and anthropogenic pressure increase the risk of the establishment of non-native species and amplify the impacts on the Antarctic ecosystem, along with the changes in biotic interactions between native and non-native species. Such understanding is fundamental from a conservative perspective (Chown and Brooks 2019; McCarthy et al. 2019; Hughes et al. 2020).

The effect of climate change can enhance the invasion process by improving climatic conditions, removing the abiotic barrier, increasing propagule production, and modifying existing biotic interactions between native and non-native species (Blumenthal et al. 2016). In the Antarctic ecosystem, biotic interactions are expected to be mediated by the stress-gradient hypothesis, where under current climatic conditions (low temperatures: average temperature 0 °C and low precipitation: 250–500 mm per year). Facilitation is the predominant interaction between plants, while competition becomes more intense under more favorable climatic conditions resulting from climate change (Lortie and Callaway 2006; Atala et al. 2019). Furthermore, the intensity of these interactions between native and non-native species can be influenced by various factors, such as the growth temperature (especially an increase in the number of cumulative days with temperatures above 0 °C and the duration of the vegetation season; Cavieres et al. 2018), the phylogenetic closeness of the species (Dostál 2011), functional traits (Cahill et al. 2008; Burns and Strauss 2012), the ontogeny of the species analyzed (le Roux et al. 2013) and the phenotypic plasticity and genetically based trait differentiation (Alexander et al. 2016). Understanding these processes can enhance our understanding of how biotic interactions, particularly competition, may intensify due to climate change; and how nonnative species can establish and disperse through facilitative interactions under the extreme climatic conditions currently prevailing in the maritime Antarctic (Brooker et al. 2007, Casanova-Katny and Cavieres 2012; Hughes et al. 2020; Rew et al. 2020).

It has been experimentally established that the impact of climate change can affect the functioning of both native and non-native species in Antarctic ecosystems (Molina-Montenegro et al. 2012a, 2016, 2019; Torres-Díaz et al. 2016; Fuentes-Lillo et al. 2017b; Acuña-Rodríguez et al. 2017; Atala et al. 2019). Although progress has been made in understanding the competitive effect of *Poa annua* L. (the first alien plant that established a functional population under Antarctic conditions) on native species (*C. quitensis* and *D. antarctica*), there are still no studies evaluating the competitive effect of other non-native species reported in the ecosystems of the maritime Antarctic and even invading the sub-Antarctic ecosystems (Frenot et al. 2005; Duffy et al. 2017; Fuentes-Lillo et al. 2017a; Hughes et al. 2020). One of the non-native species that would function as a model species in the analysis of the effect of climate change on growth, survival, and the type of interaction (facilitation/competition) on native Antarctic plants is *Juncus bufonius* L. *Juncus bufonius* is a species whose propagules have been reported in soil samples from the vicinity of the Henryk Arctowski Polish Antarctic Station (Admiralty Bay, King George Is., South Shetlands), with a probable distribution area of approximately 300 m^2 (Cuba-Díaz et al. 2013, 2015). Additionally, this species has been reported to invading different sub-Antarctic islands (Frenot et al. 2005) and is considered one of the most dangerous species due to its high level of invasiveness (Convey 2010; Bazzichetto et al. 2021). *J. bufonius* is a cosmopolitan species, mainly associated with coastal areas and cool and temperate climates with

moderately high precipitation, and it can also tolerate saline conditions (Heywood et al. 2007). It has been proposed that, due to the morphological variability and adaptability of this species, the expected environmental conditions in Antarctica due to regional warming could be favorable for the successful establishment of *J. bufonius* in the Maritime Antarctic (Cuba-Díaz et al. 2015).

Based on these approaches, this research evaluates the impact of climate change on the individual response and biotic interactions of native and non-native plants of the maritime Antarctic. The study focuses on examining the competitive effect of non-native species (*P. annua* and *J. bufonius*) on native species (*C. quitensis* and *D. antarctica*). In this context, two main questions will be addressed: (1) How do simulated climate change conditions (increased temperature and increased water availability) affect biomass production and the mortality rate of both native and non-native species? (2) How does the impact of simulated climate change influence the interactions between coexisting native and non-native species in Antarctic ecosystems?

We hypothesize that the competitive effect of non-native species on native species will intensify with higher temperatures and increased water availability. Furthermore, due to the phylogenetic and morphological similarities between non-native species and *D. antarctica*, the competitive effect is expected to be greater for this native species. Additionally, we expect that under conditions of low temperature and low water content, facilitation will be the predominant interaction.

Materials and methods

Study species

Two natives species: *C. quitensis* and *D. Antarctica,* and two non-natives species: *J. bufonius* and *P. annua* collected in the vicinity of the H. Arctowski Polish Antarctic Station (King George Island, Antarctica; 62° 09'S, 50° 28'W, 3–23 m a.s.l.) were used for experiments. Individuals of the four species were collected as part of several research projects and from scientific collaborations since 2009. These plants are currently maintained and/or propagated in the Antarctic Vascular Plant Collection of the "Laboratorio de Biotecnología y Estudios Ambientales" at the Universidad de Concepción. *C. quitensis* and *D. antarctica* were propagated vegetatively for a period of more than 6 months, reaching 540 individuals of each species. While *J. bufonius* and *P. annua* were propagated from seeds collected from plants maintained in the laboratory under the growth conditions indicated below. The seeds of *J. bufonius* were germinated 2 months before the experiment, while those of *P. annua* were germinated two weeks earlier since their germination

and growth are much faster than that of *J. bufonius* under controlled conditions (540 individuals of each species were also generated for the experiments).

All plants were kept until the beginning of the experiments in polystyrene containers of 240 cm³ inside a growth chamber at a temperature of 13 ± 2 °C, photoperiod of 16/8 h light/dark, with a flow of photosynthetic photons of 100 ± 20 μmol photons m^{-2} s^{-1}, in a substrate formed by leaf soil: peat: perlite in the ratio 3:2:1 v/v, the relative humidity was $80 \pm 20\%$, maintain with manual watering. The propagation, germination, maintenance, and all the experiments were conducted under controlled conditions at the "Laboratorio de Biotecnología y Estudios Ambientales" of the "Universidad de Concepción in Chile."

Growth response and mortality percentage of native and non-native species under a climate change scenario (Experiment 1)

To determine the influence of climate change on biomass production and the percentage of mortality of *C. quitensis*, *D. antarctica*, *J. bufonius,* and *P. annua*; individuals of each species were subjected to four different water and temperature conditions: 6 °C/low level of water availability (LW), 8 °C/LW, 6 °C/ high level of water availability (HW) and 8 °C/HW. Based on climate data, it has been observed that during the summer in maritime Antarctica, the average air temperature is 3 °C (Angiel et al. 2010; Arażny et al. 2013). Additionally, the temperature at ground level is 2–4 °C higher than the air temperature (Arażny et al. 2013). Therefore, the temperature of 6 °C simulates the current mean temperature in the growing season during the Antarctic summer, while the second temperature considers an increase to 8 °C, based on estimators of moderate climate change indicating at least a 1.5 °C–2 °C increase for mean temperature (Duffy et al. 2017; Frame 2020; Hughes et al. 2020). Two used conditions of water availability simulate the current conditions LW (of an average of -20 kPa of water potential; (Molina-Montenegro et al. 2012b; Torres-Díaz et al. 2016; Fuentes-Lillo et al. 2017b) and the projected conditions (of an average of -14 kPa of water potential) due to the increase in the precipitation level and thaw because of the temperature increase (Molina-Montenegro et al. 2012b; IPCC 2019). Water content was regulated through manual irrigation every 48 h. For maintaining a soil water potential of − 20 kPa, 20 ml of water was added, while for a soil water potential of -14 kPa, 28 ml of water was added. Monitoring of the soil water potential was done using a TEROS 21 soil tensiometer from METER Group. Nutrient content was monitored by applying a solution of phostrogen (Solaris, Buckinghamshire, UK) every two weeks at a concentration of 0.2 g L^{-1}.

Ten individuals from each species under study were subject to the experimental condition described above for

2.5 months. Each experimental condition consisted of 6 replicates. At the end of this period, all individuals were collected and dried at 60 °C for four days, then weighed in an analytical balance (RADWAG AS 220/C/2) to evaluate the total biomass (both aboveground and root biomass; Cavieres et al. 2018). The number of dead individuals was evaluated during the entire experimental period, this variable was worked on as a percentage of mortality (the percentage of dead individuals based on the initial quantity).

Competition experiments (Experiment 2)

To evaluate the effect of temperature and water availability on the interaction between native and non-native species, a competition experiment was conducted. The experiment consisted of individuals of *C. quitensis* ($n = 10$) or *D. antarctica* ($n = 10$) growing together (240 cm^3 containers) with individuals of *J. bufonius* ($n = 10$) or *P. annua* ($n = 10$), as control 20 individuals from each species growing separately, under the same conditions as described above. Additionally, nutrient availability was monitored by applying a solution of phostrogen (Solaris, Buckinghamshire, UK) every two weeks at a concentration of 0.2 g L^{-1}. Each experimental condition consisted of 6 replicates and was maintained for 2.5 months in growth chambers. The biomass and the percentage of mortality were evaluated following the methodology described for Experiment 1. To determine the intensity of the interaction between non-native and native species and the different experimental conditions the Relative Interaction Index (RII) for biomass was used, which is a proxy that determines the intensity of the interaction. The following formula was employed to compute the index: RII = ($B_{native:non-native} - B_{nativealone}$)/($B_{native:non-native} + B_{nativealone}$), where $B_{native:non-native}$ represents the biomass of the native individuals growing in the presence of the non-native species, and $B_{nativealone}$ represents the biomass of the individuals growing without the presence of the non-native species. The values of RII range from −1 to 1, when there are negative values the competitive interaction is the predominant one, while when they are positive it is the facilitation, values equal to 0, indicate that the interaction is neutral (Armas et al. 2004; Cavieres et al. 2018).

Data analyses

All data analyses were run in R version 3.6.1 (Team 2019).

Experiment 1

To determine the effect of temperature and water availability on biomass production and the mortality rate of each species, a two-way ANOVA was performed using the *aov* function from the Stat package in Rstudio (R core Team),

where the two levels (6 °C and 8 °C) of growth temperature and two levels (LW and HW) of water availability and the interactions between both factors were the independent variables. To show significant differences between the different experimental conditions (temperature, water availability) a Tukey HSD test was performed using the *Tukey HSD* function from the Stat package in Rstudio (R core Team). Data were transformed using the root sine function to normalize the percentage mortality.

Experiment 2

To determine how the presence of individuals of non-native species, temperature and water availability affects the biomass and percentage of mortality of the native species, a three-way ANOVA analysis was performed, using *aov* function from Stat package in Rstudio (R core Team), where the growth temperature (6 °C and 8 °C), water availability (LW and HW), and the presence of non-native species and the interactions of these variables were the independent variables. To determine significant differences between the different experimental conditions (temperature, water availability, and presence of individuals of non-native species) a Tukey HSD using the *TukeyHSD* function from the Stat package in Rstudio (R core Team) analysis was performed. Data were transformed using the root sine function to normalize the percentage mortality.

Finally, to determine if the RII values differ from 0 and the differences between the two levels of water availability for each temperature, a t-test was performed. All the graphs were made with the *ggplot2* package of the R program (Core Team 2019).

Results

Growth response and mortality percentage of native and non-native species under a simulated climate scenario (Experiment 1)

The results revealed that temperature had a significant impact on biomass production of the four species under study, 46.6% for *C. quitensis*, 37.74% for *D. antarctica*, 60% for *J. bufonius*, and 25% for *P. annua* (Table 1, Fig. 1a-d). Additionally, only *J. bufonius* showed a significant effect on the water content, with greater accumulation of biomass to HW (57% more compared to LW) (Table 1, Fig. 1c). High temperature and water availability favored the increase in biomass of the three species under study, except for *D. antarctica,* which experienced a decreased in biomass (− 24.5%) (Fig. 1b). Overall, mortality rates were marginal, with values below 1%, and only in *C. quitensis* this value was higher but without exceeding 10% mortality

Table 1 Two-way ANOVAs the effects of temperature (6 °C or 8 °C) and water availability (LW or HW) on biomass accumulation of native (*Colobanthus quitensis* and *Deschampsia antarctica*) and non-native (*Juncus bufonius* and *Poa annua*) Antarctic vascular plants

Species	Variables effects on biomass	Statistical parameters			
		df	SS	F	p-value
C. quitensis	Temperature (T)	2	0.320	16.144	**0.001***
	Water Condition (WC)	2	0.034	1.717	0.211
	T×WC	2	0.006	0.315	0.583
	Error	14	0.019		
D. antarctica	Temperature (T)	2	0.544	24.550	**< 0.001***
	Water Condition (WC)	2	0.029	1.323	0.269
	T×WC	2	0.005	0.263	0.615
	Error	14	0.031		
J. bufonius	Temperature (T)	2	0.293	5.920	**0.029***
	Water Condition (WC)	2	0.160	3.232	**0.043***
	T×WC	2	0.001	0.002	0.962
	Error	14	0.695		
P. annua	Temperature (T)	2	0.020	0.451	**0.050***
	Water Condition (WC)	2	0.023	0.526	0.480
	T×WC	2	0.006	0.141	0.713
	Error	14	0.621		

df degree of freedom; SS sum of squares; *F* test F

*p-value with significant differences

(Online resource 1 1 a-d). Regarding this variable, the influence of the environmental factors studied was differential, the water content showed significant effects in *C. quitensis* and *J. bufonius*, while in *P. annua* the factor that exerted significance was the temperature, and for *D. antarctica* both factors and their interaction significantly influenced the mortality (Table 2, Online resource 1 1 a-d).

Competition experiments (Experiment 2)

The presence of both non-native species had a significant impact on the biomass accumulation of the native species (Table 3). Specifically, the presence of non-native individuals (both species) and water availability led to a significant decrease in *C. quitensis* biomass, with the most pronounced decrease observed under conditions of 6 °C/LW (Table 3, Fig. 2a, c). The presence of *J. bufonius* individuals, temperature, and their interaction significantly affected the biomass accumulation of *D. antarctica* (Table 3), with the greatest decrease recorded at 6 °C (− 13,2%) (Fig. 3a, b). Similarly, the presence of *P. annua* individuals and water availability and the interaction of these variables had a significant effect on the accumulation of biomass of *D. antarctica* (Table 3), with the lowest biomass production observed at 6 °C/LW (− 51%) (Fig. 3c).

The mortality of *C. quitensis* individuals was influenced by the presence of *J. bufonius*, temperature, water availability, and their interaction (Table 4). An increase in mortality was observed at 6 °C/LW (~ 25%), compared to the control where no mortality was observed (Online

resource 1 2a). The same trend was evident at 6 °C/HW, where a mortality rate of 33% compared to 10% in the control (Online resource 1 2b). The interaction between *C. quitensis* and *P. annua* temperature, and water availability significantly affected the mortality of *C. quitensis* individuals (Table 4, Online resource 1 2 d). For *D. antarctica*, the presence of *J. bufonius* and the interaction between temperature (CxT) and water availability (CxWC), showed significant effects on mortality (Table 4), reaching a 30% mortality at 6 °C/HW (Online resource 1 3b). A similar trend was observed in the interaction of the presence of *P. annua* with temperature (CxT) and water availability (CxWC), which significantly affected the mortality of *D. antarctica* (Table 4), where the mortality of *D. antarctica* was higher (27%) at 6 °C/LW (Online resource 1 3 c).

The RII interaction between *C. quitensis/J. bufonius* and *C. quitensis/P. annua* indicates that when water availability is the limiting factor (LW) at 6 °C, the predominant interaction is competition (Fig. 4a, b). However, if water availability increases, the presence of *J. bufonius* generates a competitive interaction at 8 °C (Fig. 4a), while in the interaction *C. quitensis/P. annua* predominates is facilitation, independent of temperature (Fig. 4b). In the interaction between *D. antarctica* and both non-native species, the competition was the predominant interaction, being more intense at 8 °C for *J. bufonius*, independent of the level of water availability (Fig. 5a). For *P. annua*, the interaction was more intense at 6 °C/LW (Fig. 5b).
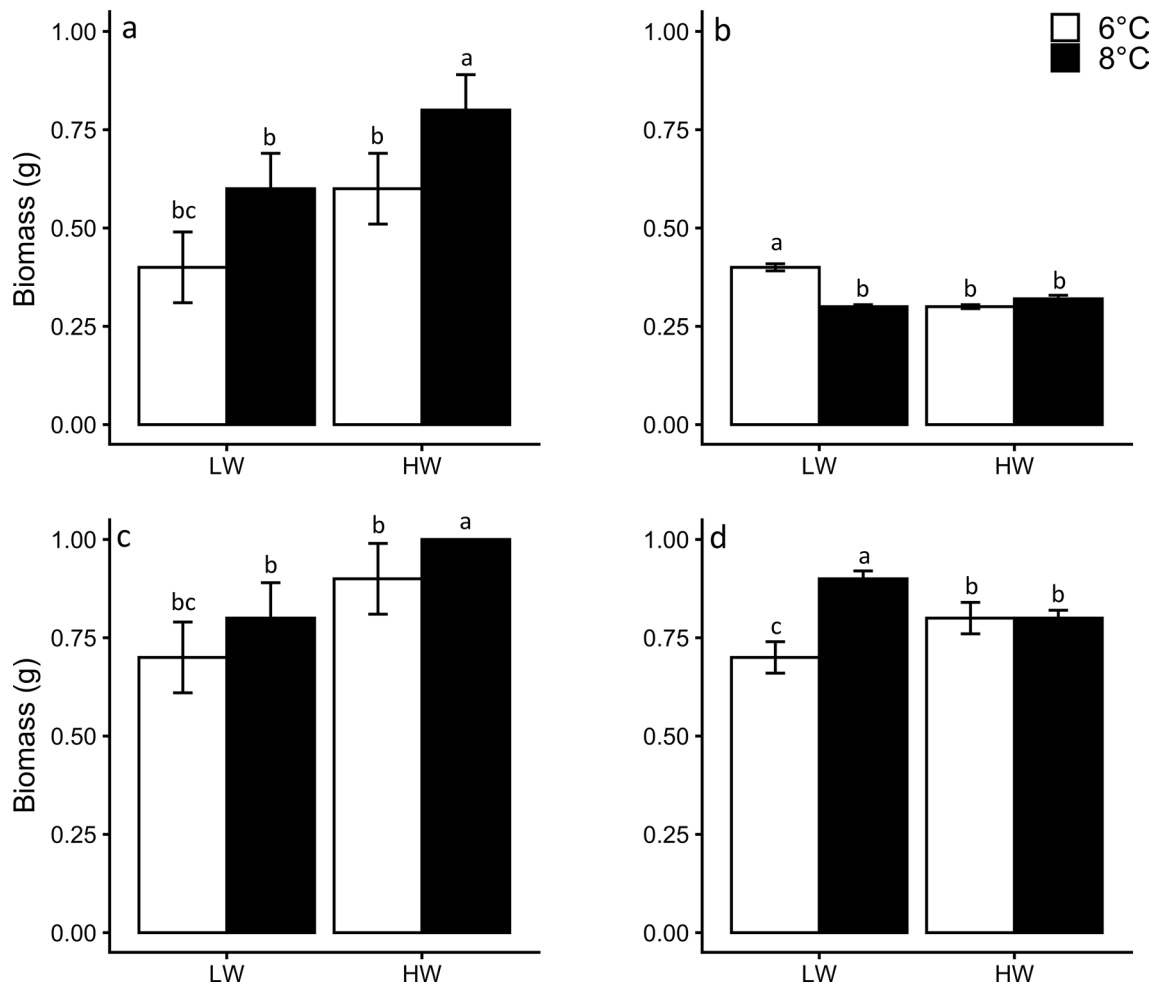
Fig. 1 Biomass accumulation of native *Colobanthus quitensis* (**a**) and *Deschampsia antarctica* (**b**) and non-native *Juncus bufonius* (**c**) and *Poa annua* (**d**) Antarctic vascular plants under different conditions of temperature (6 °C-colorless and 8 °C-orange) and water availability (low-LW and high-HW). error bars represent SE and different letters show significant differences with a p-value < 0.001

Discussion

Growth response and mortality percentage of native and non-native species under a climate change scenario (Experiment 1)

The results indicated that, except *D. antarctica*, increased temperature had a significant effect on the biomass production of the species under study. The effect was more intense with higher water availability for *C. quitensis* and *J. bufonius*. For *D. antarctica* and *P. annua* an effect of water availability on biomass production was not observed. These results coincide with the general trends of the eco-physiological response (photosynthetic performance) and growth (biomass accumulation) of native species. Several studies have determined that the increase in temperature above 7 °C generates a significant increase in biomass production, modifying the relative growth rate, increasing photosynthetic

performance, and decreasing the mortality percentage in *C. quitensis* (Day et al. 1999; Torres-Díaz et al. 2016; Acuña-Rodríguez et al. 2017; Fuentes-Lillo et al. 2017a). Additionally, our results highlight the importance of the increase in water availability (about ~ 30%) on the general performance of *C. quitensis*. Water availability has been determined as one of the most significant variables for increases in the accumulation of biomass and the photosynthetic performance of native Antarctic species (Molina-Montenegro et al. 2012b; Torrez-Díaz et al. 2016; Fuentes-Lillo et al. 2017a). In addition, it has been identified as one of the main drivers of biodiversity in Antarctic terrestrial ecosystems (Convey et al. 2014). In contrast, *D. antarctica* exhibited a decline in biomass accumulation with rising temperature and water availability. Such divergent responses in the two native Antarctic species have been observed in previous experiments. *D. antarctica* showed no changes in carbon gain or growth, and its anatomical characteristics remained

Table 2 Two-way ANOVAs the effects of temperature (6 °C or 8 °C) and water availability (LW or HW) on percentage of mortality of native (*Colobanthus quitensis* and *Deschampsia antarctica*) and non-native (*Juncus bufonius* and *Poa annua*) Antarctic vascular plants

Species	Variables effects on mortality	Statistical parameters			
		df	SS	F	*p-value*
C. quitensis	Temperature (T)	2	0.200	0.188	0.671
	Water Condition (WC)	2	394.8	333.4	**< 0.001***
	T × WC	2	0.200	0.150	0.704
	Error	14	16.6		
D. antarctica	Temperature (T)	2	0.405	42.76	**< 0.001***
	Water Condition (WC)	2	0.428	45.17	**< 0.001***
	T × WC	2	0.238	25.10	**< 0.001***
	Error	14	0.009		
J. bufonius	Temperature (T)	2	0.008	0.292	0.597
	Water Condition (WC)	2	0.406	13.381	**0.002***
	T × WC	2	0.003	0.111	0.744
	Error	14	0.034		
P. annua	Temperature (T)	2	0.205	13.482	**0.002***
	Water Condition (WC)	2	0.105	0.658	0.430
	T × WC	2	0.046	2.509	0.135
	Error	14	0.260		

df degree of freedom; *SS* sum of squares; *F* test F

**p-value* with significant differences

unaltered when subjected to in situ warming using open-top chambers, exhibiting no significant differences compared to plants grown in the open field. Conversely, *C. quitensis* exhibited higher leaf carbon gain and plant growth due to specific photosynthetic adjustments during warming in the same study (Sáez et al. 2018).The observed decline in biomass in *D. antarctica* may be attributed to its limited ability to adapt its photosynthetic and metabolic processes, as suggested by other studies conducted in both in situ and ex situ conditions (Xiong et al. 1999; Day et al. 1999; Sáez et al. 2018). Different reactions of *C. quitensis* may be related to its greater phenotypic and functional plasticity (Xiong et al. 1999; Gianoli et al. 2004; Molina-Montenegro et al. 2012b; Cuba-Díaz et al. 2017; Sáez et al. 2018).

Regarding non-native species, our findings align with previous studies, demonstrating that biomass production and the photosynthetic response of *J. bufonius* significantly increase with the combined effect of elevated temperature and water availability (Fuentes-Lillo et al. 2017a). These results are consistent with the findings of Cavieres et al. (2018), who observed that biomass accumulation in non-native species was favored by temperature increases up to 11 °C. Additionally, we found that water availability does not influence the biomass production of *P. annua*. However, previous research by Molina-Montenegro et al. (2019) has shown that increased water availability (by approximately 25% under current conditions in Antarctica) is the most critical factor explaining the enhanced biomass production of *P. annua*. The higher biomass production observed in both native and non-native species in response to climate

change can be attributed to an increased net photosynthesis rate driven by higher temperatures (Xiong et al. 1999; 2000; Dusenge et al. 2019). Similarly, in extreme climate ecosystems, the combined effect of temperature and precipitation has been found to significantly enhance primary production in herbaceous plants and grasses (Ma et al. 2017). Our results support the general patterns indicating that there are no differential responses between native and non-native species to climate change effects (Sorte et al. 2013), except for the biomass decrease observed in *D. antarctica*. Therefore, it is conceivable that both native species, particularly *C. quitensis*, and the non-native species analyzed in this study could expand their distribution ranges and colonize ice-free areas in the maritime Antarctic as environmental conditions improve. It is noteworthy that both native species are distributed in both Antarctic and South American ecosystems, such as the Andes and the Patagonian steppe (Parnikoza et al. 2007; Chen et al. 2016; Lee et al. 2017).

In this context, in situ monitoring has determined that global warming has had implications for the increased abundance, coverage, and changes in the distribution range of *C. quitensis* and *D. antarctica* (Torres-Mellado et al. 2011; Cannone et al. 2016; 2022). However, our results indicate that *D. antarctica* is not favoured in terms of biomass accumulation under the influence of climate change, despite in situ studies by Torres-Mellado et al. (2011) showing an increase in coverage (~20%) associated with rising temperatures in the maritime Antarctic Peninsula. Similarly, Cannone et al. (2016) observed an increase in coverage and distribution but limited growth over 49 years on Signy Island.

Table 3 Three-ways ANOVAs the effects of temperature, the water conditions, and non-native species competition (*Poa annua* and *Juncus bufonius*) on biomass accumulation in native Antarctic vascular plants (*Deschampsia antarctica* and *Colobanthus quitensis*)

Competition and variables effects on biomass	Statistical parameters			
	df	SS	F	p-value
C. quitensis—J. bufonius				
Competition (C)	1	0.209	4.795	**0.033***
Temperature (T)	1	0.551	12.622	**< 0.001***
Water condition (WC)	1	0.245	5.617	**0.021***
C×T	1	0.013	0.305	0.582
C×WC	1	0.008	0.019	0.890
T×WC	1	0.014	0.324	0.571
C×T×WC	1	0.008	0.183	0.670
Error	51	0.043		
C. quitensis—P. annua				
Competition (C)	1	0.054	2.427	**0.001***
Temperature (T)	1	0.214	9.501	**0.003***
Water condition (WC)	1	0.273	12.154	**0.001***
C×T	1	0.001	0.006	0.940
C×WC	1	0.304	13.507	**0.005***
T×WC	1	0.018	0.800	0.375
C×T×WC	1	0.012	0.555	0.459
Error	51	1.148		
D. antarctica—J. bufonius				
Competition (C)	1	1.156	61.188	**< 0.001***
Temperature (T)	1	0.360	19.097	**< 0.001***
Water condition (WC)	1	0.006	0.031	0.861
C×T	1	0.265	14.059	**< 0.001***
C×WC	1	0.042	2.233	0.141
T×WC	1	0.043	2.323	0.133
C×T×WC	1	0.002	0.145	0.705
Error	51	0.963		
D. antarctica—P. annua				
Competition (C)	1	0.179	23.070	**< 0.001***
Temperature (T)	1	0.040	5.203	**0.026***
Water condition (WC)	1	0.168	21.704	**< 0.001***
C×T	1	0.004	0.602	0.441
C×WC	1	0.032	4.127	**0.041***
T×WC	1	0.002	0.379	0.540
C×T×WC	1	0.001	0.007	0.931
Error	51	0.395		

df degree of freedom; *SS* sum of squares; *F* test F

**p-value* with significant differences

Distribution models suggest that non-native species like *P. annua* could significantly expand their area in the maritime Antarctic due to climate change and increased anthropogenic pressure (Pertierra et al. 2017; Duffy et al. 2017). While there are no distribution models specifically addressing the effect of climate change on *J. bufonius* in this region.

Some studies have evaluated its expansion on sub-Antarctic islands, where its occurrence probability increases when the mean temperature exceeds 4 °C (Bazzichetto et al. 2021). Based on the significant biomass accumulation observed in this study and the high relative growth rates of *J. bufonius* under climate change conditions (Fuentes-Lillo et al. 2017a, b), it is reasonable to suggest that *J. bufonius* has the potential to compete with native Antarctic plants. This competitive advantage may be attributed to its superior water acquisition capabilities and higher relative growth rates compared to native Antarctic plants (Fuentes-Lillo et al. 2017a, b).

Although climate change may benefit the range patterns of both native and non-native species, this expansion could have implications for future interactions between them, such as increased competition (Corlett and Westcott 2013; Lancaster et al. 2017), as demonstrated by observations from Molina-Montenegro et al. (2016, 2019).

Competition experiments (Experiment 2)

In recent studies, it has been determined that the interaction between climate change and the intensity of interactions between native and non-native species varies depending on the context and the specific species involved (Diez et al. 2012; Sorte et al. 2013; Dainese et al. 2017; Zettlemoyer et al. 2019). In line with these findings, our results support the conclusion that the biomass production of *C. quitensis* is reduced in the presence of both non-native plants. However, we did not observe significant differences in this interaction under current conditions (6 °C/LW) and "climate change" conditions (8 °C/HW), compared to the control group where species grew without competition. The reduction in biomass in the presence of non-native species led to a significant increase in the mortality of *C. quitensis*.

The Relative Interaction Intensity analysis between *C. quitensis*/*J. bufonius* and *C. quitensis*/*P. annua* indicates that when water availability is limited (LW) at 6 °C, competition is the predominant interaction. However, if water availability increases, the presence of *J. bufonius* generates a competitive interaction at 8 °C, while the interaction between *C. quitensis*/*P. annua* remains facilitation, regardless of temperature.

Our findings align with experimental field studies that have shown the impact of *P. annua* individuals, under increased water availability (− 20 kPa), on the biomass accumulation of *C. quitensis* and *D. antarctica*. These studies also indicate asymmetric competition, favouring the growth and survival of *P. annua* (Molina-Montenegro et al. 2016, 2019). However, it is important to exercise caution when interpreting these results, as other abiotic variables may influence the competitive interactions between *C. quitensis* and *P. annua*. For instance, studies by Cavieres et al. (2018) suggest the presence of a certain type of resistance in some
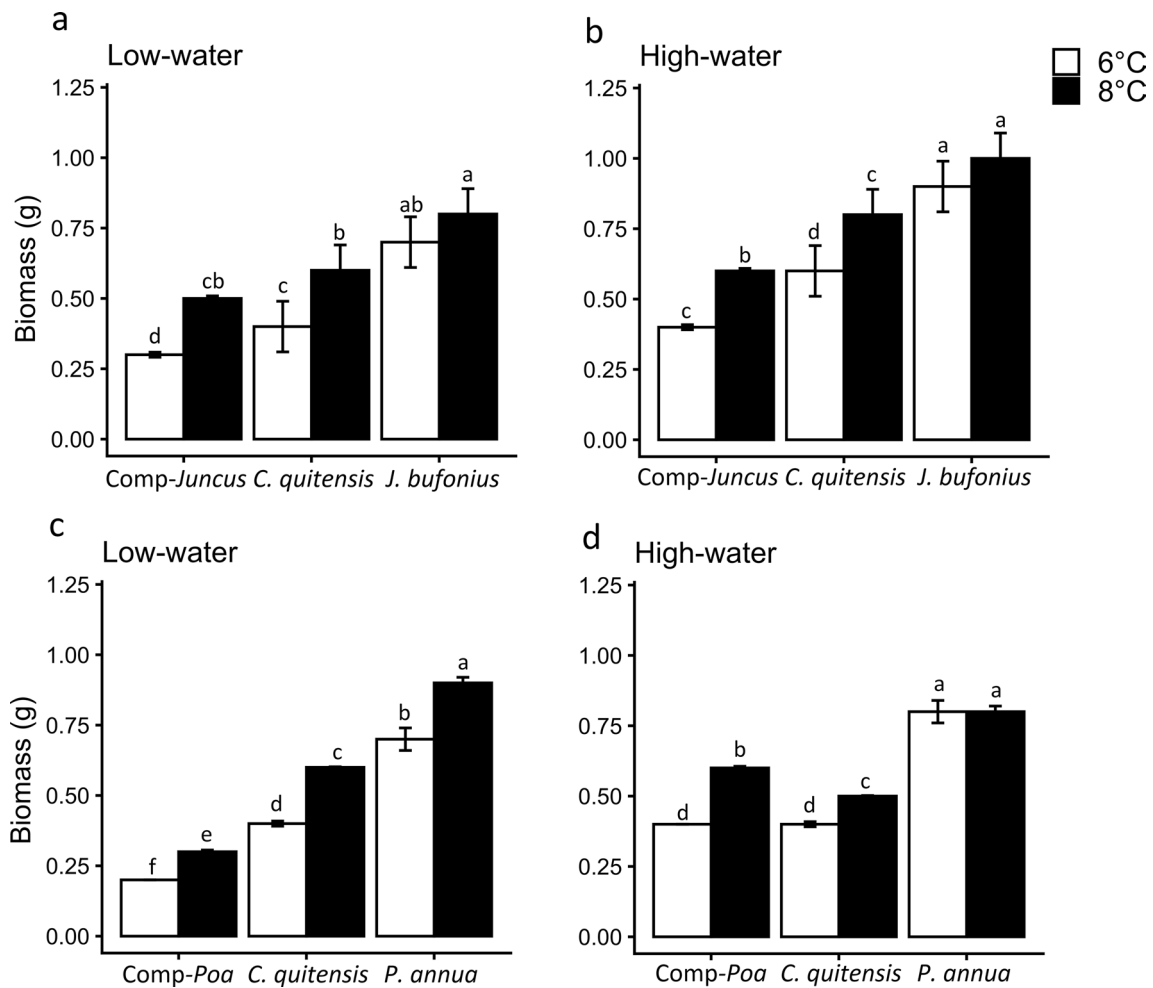
Fig. 2 Biomass accumulation of *Colobanthus quitensis* under different temperature conditions (6 °C-colorless and 8 °C-orange) and water availability (low-LW and high-HW), and in presence of non-native species *Juncus bufonius* (**a** and **b**) and *Poa annua* (**c** and **d**).

Comp-Juncus: interaction with *J. bufonius*. Comp-Poa: interaction with *P. annua*., error bars represent SE and different letters show significant differences with a p-value < 0.001

C. quitensis individuals to *P. annua* at different temperatures (5 and 11 °C) and nitrogen concentrations. They found that the effect of *P. annua* on *C. quitensis* was similar in magnitude, indicating no synergistic effect between warming and invasion. While *C. quitensis* typically grows in the presence of other vascular species, forming large mats throughout its distribution except in Antarctica (Ginocchio et al. 2008), it is important to consider that future climate warming and increased human activity in Antarctica may increase the vulnerability of native plant communities.

The presence of the non-native species *J. bufonius* and *P. annua* reduces the biomass of *D. antarctica* under both current and future climate change conditions compared to the growth of the species without non-native species. This reduction in biomass results in a significant increase in mortality (approximately 30%) of *D. antarctica* individuals. The RII analysis indicates that the presence of *J. bufonius*

generates competition under both water availability conditions, with greater intensity observed at 8 °C. Similarly, the presence of *P. annua* leads to more intense competition under LW at 6 °C and under HW at 8 °C. Our results are consistent with previous studies that have indicated the susceptibility of *D. antarctica* to the presence of *P. annua* individuals, which is associated with increased water availability and temperature (Molina-Montenegro et al. 2016), the density of *P. annua* individuals (Molina-Montenegro et al. 2012a, 2019), and decreased nitrogen content in the soil (Cavieres et al. 2018).

This greater susceptibility of *D. antarctica* may be attributed to the phylogenetic and functional similarities between *D. antarctica* and both non-native species. Several studies have shown that ecological, phylogenetic, and functional trait similarities tend to intensify competition for resources (Cahill et al. 2008; Dostál 2011; Burns and Strauss 2012;
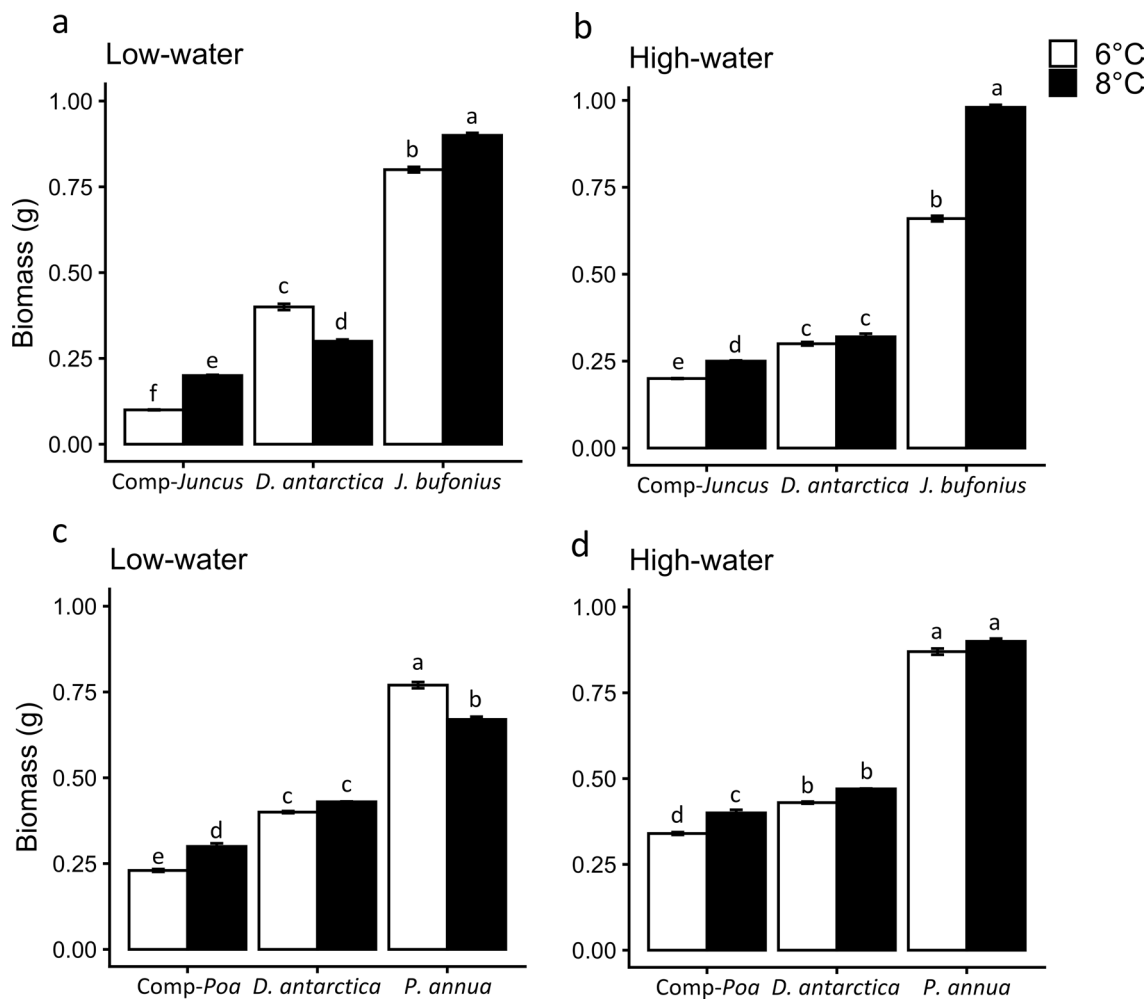
Fig. 3 Biomass accumulation of *Deschampsia antarctica* under different temperature conditions (6 °C-colorless and 8 °C-orange) and water availability (low-LW and high-HW), and in presence of non-native species *Juncus bufonius* (**a** and **b**) and *Poa annua* (**c** and **d**).

Comp-Juncus: interaction with *J. bufonius*. Comp-Poa: interaction with *P. annua*. error bars represent SE and different letters show significant differences with a p-value < 0.001

Kunstler et al. 2012). Additionally, these results support previous conclusions indicating that *D. antarctica* could be the species most vulnerable to the expansion of *P. annua* and other non-native species that may invade the maritime Antarctic (Molina-Montenegro et al. 2012a, 2016, 2019).

Final Remarks

Currently, the low abundance of non-native species in Antarctic ecosystems can be explained by abiotic conditions and low anthropogenic pressure. However, the global change process, characterized by increased temperature and greater anthropogenic pressure, will lead to an increase in the presence of non-native species, particularly in the maritime Antarctic (Duffy et al. 2017; Hughes et al. 2020). Human activities have been identified as a significant means of propagules

transport of non-native species including seeds of the genus *Juncus* sp. (Chown et al. 2012; Huiskes et al.2014; Fuentes-Lillo et al. 2017a). Germination studies involving 16 species of different growth forms have shown that a significant percentage of these non-native species can germinate and grow under the current abiotic conditions prevailing in the maritime Antarctic (Bokhorst et al. 2021). Therefore, our results, in particular on the influence of *J. bufonius* on *D. antarctica*, provide an approximation of the competitive response that non-native species arriving at the maritime Antarctic might exhibit.

Conducting future studies to assess the potential interactions between potential non-native species (species more likely to arrive on the peninsula, as identified by Hughes et al. 2020) and native Antarctic species would help evaluate the possible impacts of these new species on the native flora. This research would provide an opportunity to focus
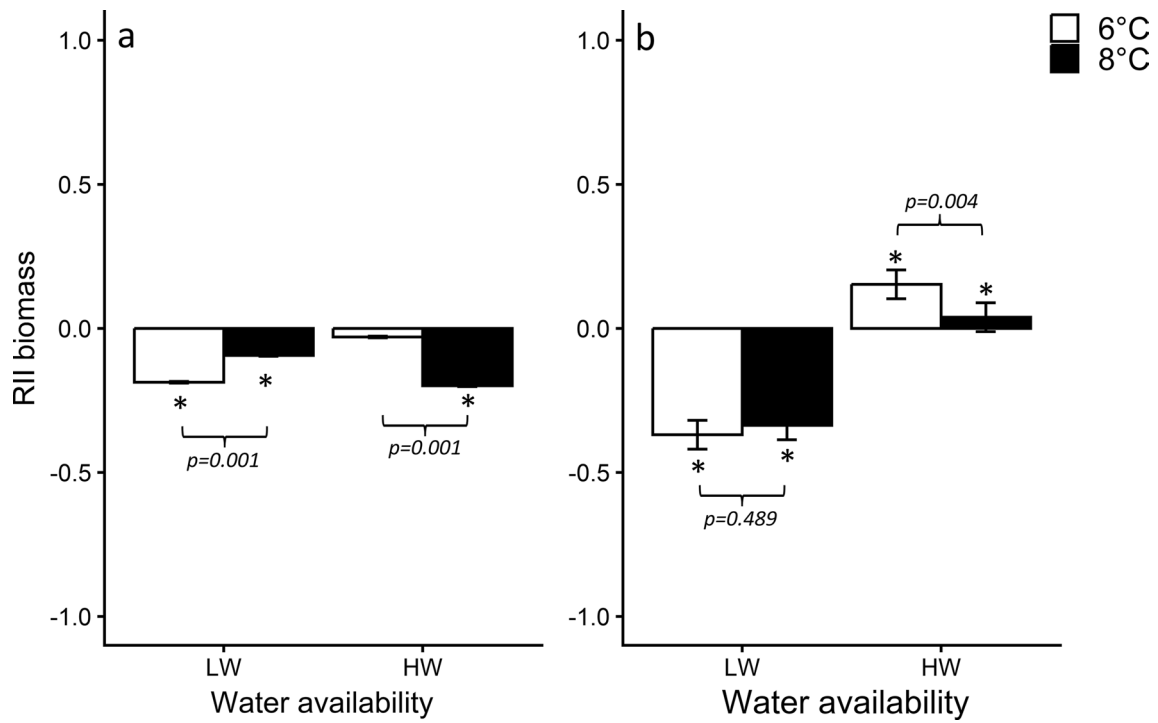
Fig. 4 Relative interaction index (RII) of the biomass in *Colobanthus quitensis* in presence of individuals of the non-native species *Juncus bufonius* (**a**) and *Poa annua* (**b**) error bars represent SE and the asterisks are the result of the t-test, indicating significant differences depending on whether they are different from 0, while the p-values show significant differences between temperatures (6 °C and 8 °C)
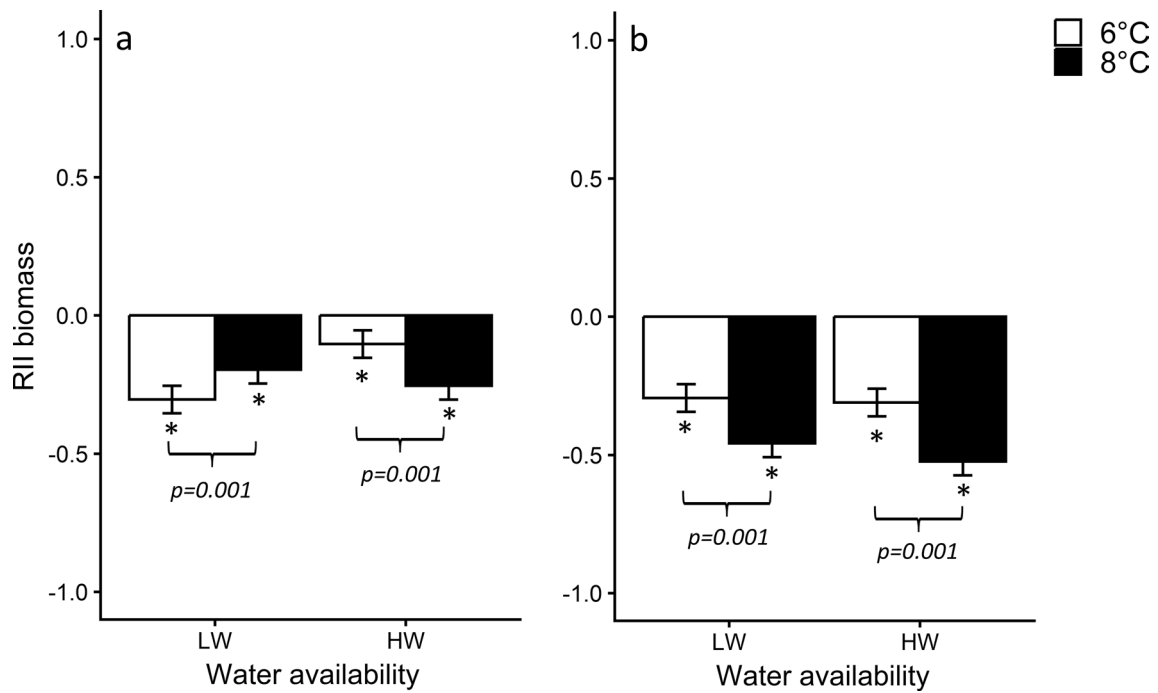

Fig. 5 Relative interaction index (RII) of the biomass in *Deschampsia antarctica* in presence of individuals of the non-native species *Juncus bufonius* (**a**) and *Poa annua* (**b**). error bars represent SE and the asterisks are the result of the t-test, indicating significant differences depending on whether they are different from 0, while the p-values show significant differences between temperatures (6 °C and 8 °C)

Table 4 Three-ways ANOVAs the effects of temperature, the water conditions, and non-native species competition (*Poa annua* and *Juncus bufonius*) on mortality in native Antarctic vascular plants (*Deschampsia antarctica* and *Colobanthus quitensis*)

Competition and variables effects on mortality	Statistical parameters			
	df	SS	F	*p-value*
C. quitensis—J. bufonius				
Competition (C)	1	4557	700.930	**< 0.001***
Temperature (T)	1	303	46.630	**< 0.001***
Water condition (WC)	1	646	99.319	**< 0.001***
C×T	1	179	27.490	**< 0.001***
C×WC	1	59	9.134	**0.003***
T×WC	1	6	0.898	0.347
C×T×WC	1	2	0.233	0.631
Error	51	332		
C. quitensis—P. annua				
Competition (C)	1	2718.9	365.237	**< 0.001***
Temperature (T)	1	20.9	2.811	**0.049***
Water condition (WC)	1	998.3	134.113	**< 0.001***
C×T	1	19.1	2.566	0.115
C×WC	1	10.9	1.460	0.232
T×WC	1	103.5	13.905	**< 0.001***
C×T×WC	1	54.9	7.370	**< 0.001***
Error	51	379.6		
D. antarctica—J.bufonius				
Competition (C)	1	4821	733.963	**< 0.001***
Temperature (T)	1	1401	213.281	**< 0.001***
Water condition (WC)	1	306	46.611	**< 0.001***
C×T	1	719	109.399	**< 0.001***
C×WC	1	178	27.149	**< 0.001***
T×WC	1	13	2.033	0.160
C×T×WC	1	9	1.362	0.249
Error	51	328		
D. antarctica—P. annua				
Competition (C)	1	1243	4.511	**0.038***
Temperature (T)	1	22	0.080	0.779
Water condition (WC)	1	53	0.194	0.661
C×T	1	1404	5.094	**0.028***
C×WC	1	1288	4.674	**0.035***
T×WC	1	387	1.405	0.241
C×T×WC	1	1354	4.912	**0.031***
Error	51	14,058		

df degree of freedom; *SS* sum of squares; *F* test F

*p-value with significant differences

efforts on preventing the arrival of the most problematic non-native species.

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Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors. The plant species used in this research have been maintained and propagated for years in the collection of Antarctic vascular plants of the Laboratorio de Biotecnología y Estudios Ambientales of the Universidad de Concepción. Previously the samples have been collected in different Antarctic campaigns under the permits granted by the Chilean Antarctic Institute that are listed below (Online resource 2): 1) For income and sampling in protected areas: N° 410/509–2009, N° 8/2011, N° 61/2015, N°72/2015; 2) For scientific sample collection: N° 410/506–2009, N° 7/2011; N° 71/2015; and 3) Certificates of transfers of scientific samples: N°410/530–2009, N° 33/2011.

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