

Competition between native Antarctic vascular plants and invasive *Poa annua* changes with temperature and soil nitrogen availability

Lohengrin A. Cavieres  · Ana Karen Sanhueza · Gustavo Torres-Mellado ·
Angélica Casanova-Katny

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Abstract Over the last decades human have introduced non-native organisms to Antarctica, including the grass species *Poa annua*. This non-native grass under constant growth temperatures has been shown negatively affect the growth of the only two native Antarctic vascular plants, *Deschampsia antarctica* and *Colobanthus quitensis*, under constant growth temperatures. However, whether there are changes in the interaction between these species under warmer conditions is an important question. In cold ecosystems, soil nutrient status directly affects plant responses to increases in temperature and Antarctic soils are highly variable in nutrient supply. Thus, in this study we experimentally assessed the interaction between the non-native *Poa* with the two native Antarctic vascular plant species at two different temperatures and levels of nutrient availability.

Individual mats of the study species were collected in King George Island, and then transported to Concepcion where we conducted competition experiments. In the first experiment we used soil similar to that of Antarctica and plants in competition were grown at two temperatures: 5°/2° and 11°/5 °C (day/night temperature). In a second experiment plants were grown in these two temperature regimes, but we varied nitrogen (N) availability by irrigating plants with Hoagland solutions that contained 8000 or 300 μM of N. Overall, *Poa* exerted a competitive effect on *Deschampsia* but only at the higher temperature and higher N availability. At 5°/11 °C the competitive response of *Deschampsia* to *Poa* was of similar magnitude to the competitive effect of *P. Deschampsia*, and the competitive effect was greater with at low N. The competitive effect of *Poa* was similar to the competitive response of *Colobanthus* to *Poa* at both temperatures and N levels. Thus, at low temperatures and N soil content the native Antarctic species might withstand *Poa* invasion, but this might change with climate warming.

L. A. Cavieres (✉) · A. K. Sanhueza ·
G. Torres-Mellado
Departamento de Botánica, Facultad de Ciencias
Naturales y Oceanográficas, Universidad de Concepción,
Concepción, Chile
e-mail: lcaviere@udec.cl

L. A. Cavieres · A. K. Sanhueza
Instituto de Ecología y Biodiversidad (IEB), Santiago,
Chile

A. Casanova-Katny
Núcleo de Estudios Ambientales (NEA), Facultad de
Recursos Naturales, Universidad Católica de Temuco,
Temuco, Chile

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Introduction

Climate change and biological invasions are key components of the global changes induced by human activities on the world biota (Sala et al. 2000). Although both processes negatively affect diversity (Vilà et al. 2011; Bellard et al. 2012; Pyšek et al. 2012), their effects were usually considered separately (Dukes and Mooney 1999; Walther et al. 2002, 2009). However, it is now understood that climate change and biological invasions are linked, with climate change influencing the rate and extent of biological invasions (e.g. Hellmann et al. 2008; Sorte et al. 2013; Blumenthal et al. 2016).

There are good reasons to expect that the rate and extent of biological invasions can be influenced by climate change (Dukes and Mooney 1999; Walther et al. 2009; Ziska and Dukes 2014). For example, in warmer conditions, alien species originating from warmer regions could spread to historically cold areas (Walther et al. 2009) or increase their negative impacts if they are already there (Hellmann et al. 2008). Verlinden and Nijs (2010) conducted a field study in Belgium where they exposed native and invasive species to warmer conditions and found that while invasive species showed no response, native species became less productive, suggesting that warmer conditions represent an indirect advantage for invasive species through the negative effects of warming on natives. Recently, Blumenthal et al. (2016) reported that artificial warming increased the growth and reproduction of the invasive grass *Bromus tectorum* in semi-arid grasslands of North America, independent of the presence of native competitors or the fact that warming decreased soil moisture. Thus, synergistic interactions between invasion and climate change can increase the problems created by the presence of non-native organisms (Bradley et al. 2010; Compagnoni and Adler 2014; Ziska and Dukes 2014). However, synergistic effects between climate change and invasion are not the rule (see Sorte et al. 2013 for a review), and a deeper understanding of where and how they might occur is important.

Until recently the Antarctic continent was quite pristine with regard to invasive organisms, but the increase in human activities in the last decades have increased the arrival of non-native organisms (Frenot et al. 2005; Hughes and Convey 2010; Chown et al. 2012; Hughes et al. 2015). The low species richness

and the relatively simple community structure of Antarctic ecosystems suggest that they might be particularly sensitive to the colonization and spread of non-native species (Frenot et al. 2005). These include some non-native vascular plants which have colonized the Antarctic region (Chwedorzewska 2008; Olech and Chwedorzewska 2011; Pertierra et al. 2013). This has been attributed to increase in human activities and accelerated climate change (Hughes and Convey 2010). However, it is not clear if increases in temperature in Antarctica can have synergistic effects on the success of non-native invasive species already present in this continent. In addition, it has been suggested that warmer conditions may favor the performance of the native species (e.g. Gerighausen et al. 2003; Cannone et al. 2016), challenging the potential advantage of non-native species over natives. Thus, the interaction between native and non-native Antarctic vascular plants is a good model for evaluating synergistic effects between climate change and invasion potential.

Poa annua L. (Poaceae) has been reported in several locations along the Antarctic Peninsula and adjacent islands, but the only large and permanent population has been observed in King George Island in the vicinity of the Polish Antarctic Station Henry Arctowsky (Chwedorzewska et al. 2015). The species was initially recorded in the austral summer of 1985/86 in front of the entrance of the main building of the Arctowsky station (in metal grids used to clean shoes, Olech 1996). Since this first record, *P. annua* has increased in density and abundance (Chwedorzewska 2008; Olech and Chwedorzewska 2011) around the Arctowski station, where human activities have damaged the natural substrate (Olech 1996; Chwedorzewska et al. 2015). Eradication actions for this species have been initiated (Galera et al. 2016), but they are not complete and removal is not a guarantee of eradication as seeds may remain viable in the soil (Wódkiewicz et al. 2014). *Poa annua* is native to regions with cold-temperate climate (Pertierra et al. 2017); suggesting that its spread and impact may increase as climate warms (Chown et al. 2012; Duffy et al. 2017). The Antarctic Peninsula warmed rapidly (about 3.7 °C) in the last part of the past century (Turner 2013). However, Turner et al. (2016) reported that warming in the Antarctic Peninsula (AP) has stopped in the last decade, but warned that warming episodes are likely to occur in the future. Ludescher

et al. (2017) applying new analytical approaches to long-term temperature records along the AP indicated while in some places there was no evidence of significant warming (e.g. Rothera station 1978–2013) there were others where warming has been significant (e.g. Faraday–Verdnasky 1951–2013). Lee et al. (2017) pointed out that the recently paused warming observed in the AP is a consequence of short-term natural climate variability and that new warming phase will be observed across the AP.

There is concern that *P. annua* may transform into a much more aggressive invasive species in Antarctica. Studies with young and small individuals (0.6–2.0 mg fresh weight) under controlled conditions have evaluated the interaction among *P. annua* and the only two Antarctic vascular plants (*Deschampsia antarctica* (Poaceae) and *Colobanthus quitensis* (Caryophyllaceae)), showing that *P. annua* negatively influences the biomass accumulation of both Antarctic species under a constant growth temperature (Molina-Montenegro et al. 2012). In other experiments young and small individuals of *P. annua* are more phenotypically plastic than the native *D. antarctica*, and in an experiment where soil moisture was varied, the invasive species exerted a competitive effect on the native, with this effect being greater with higher soil moisture (Molina-Montenegro et al. 2016). Nonetheless, these experiments were conducted at a single temperature, and beg the question what might happen to the interaction among these plants under warmer conditions.

Soil nutrient status in cold ecosystems is important because it directly affects plant responses to increases in temperature (Klanderud 2005). Antarctic soils are highly variable in nutrient supply (Campbell and Claridge 1987; Beyer 2000). Recently exposed soils (after ice retreat) have a high content of coarse mineral particles and low nutrients, whereas older soil are very rich in nutrients due to the accumulation of organic matter by debris from mosses, lichens and algae additional nitrogen (N) input from seabirds (Beyer 2000; Bölter 2011). In addition, future warming of cold habitats may increase nutrients availability, especially N due to the positive effect of warmer temperatures on nitrogen fixing and/or decomposer microorganisms in the soil (Convey et al. 2012). Thus, it is prudent to assess the likely synergistic effects

between warming and invasion success of *P. annua* under different soil nutrient conditions.

We experimentally assessed the intensity of competition and the competitive response of the interaction between the non-native invasive *P. annua* with the two Antarctic native vascular plant species *C. quitensis* and *D. antarctica* at two different temperatures and nutrient availabilities. As *P. annua* is a highly competitive species of temperate origin (Holm 1997), we hypothesized that the competitive effect of *P. annua* on the Antarctic natives will be higher with the increase in temperature. Also, as this invasive species prefers nutrient rich soils, this synergistic effect between higher temperature and invasive negative effect on native is expected to be particularly evident at high N. At lower nitrogen availabilities the invasive species may be disadvantaged relative to the native species that can grow naturally in poor soils (Greene and Holtom 1971; Park et al. 2012).

Methods

Study species

Poa annua is a perennial creeping grass, native to Eurasia and is one of the five most widely distributed plants in the world (Holm 1997). It can be found in every zone of the world, including Antarctica (Chwedorzewska et al. 2015). This species easily invades and persists in irrigated, closely mown, fertilized turfgrass stands. The competitive potential of *P. annua* has only been studied in agricultural contexts, and indicate that this species is more competitive in the spring and fall and that once it invades and becomes established, it quickly becomes the dominant species (Beard et al. 1978).

Deschampsia antarctica is distributed in southern South America (Argentina and Chile) including Tierra del Fuego and Falkland Is. (Los Malvinas), and on different Subantarctic Islands and the maritime Antarctica. It is also present along the western coasts of the Antarctic Peninsula and other islands on the adjacent Archipelagos (Komárková et al. 1985, 1990; Torres-Mellado et al. 2011). This native grass species is able to colonize a wide range of soil-types, ranging from mineral and nutrient-poor to highly organic (i.e. ornithogenic soil) (Komárková et al. 1985; Smith 2003).

Colobanthus quitensis is a perennial herb forming loosely compact small cushions of 0.5–10 cm diameter. It occurs from Mexico to the northern continental edge of Antarctica Antarctic Peninsula, as well as in several Antarctic and sub-Antarctic islands (Moore 1970). The distribution of *C. quitensis* is more limited in Antarctica than *D. antarctica*. It prefers drier, mineral rich soil and occurs alone only in 3% of all localities where vascular plant has been described (Komárková et al. 1985).

Competition experiments

Mats of *P. annua*, *D. antarctica* and *C. quitensis* were collected in the surroundings of the Polish Antarctic base Henry Arctowski (62°09'S 58°28'W), located in King George Island, South Shetland Islands, Maritime Antarctic. We transported plants in well-watered plastic boxes to Concepcion (Chile), where we conducted the competition experiments.

From the mats of *P. annua* and *D. antarctica* we separated rooted tillers of similar size and development (3–4 leaves per tiller). For *C. quitensis*, we selected individuals of similar size (ca. 2 cm diameter). Thus, the initial size of the experimental individuals was similar within each species.

To assess the effect of growing temperature and nitrogen availability on the interaction among the native vascular plant species and the invasive *P. annua* we conducted two competition experiments. In the first experiment, 480 plastic pots of 300 cm³ of volume each were filled with soil taken from the central Chilean Andes at 3600 m elevation. These soils have similar level of nutrients as those reported for Antarctic soils with some cover of mosses and lichens (N: 9 ppm, P: 98 ppm, K: 230 ppm). Soils were autoclaved to avoid the presence of mycorrhizae or any other micro-organisms that could affect the experiment. To evaluate the sign and intensity of interactions between established individuals, we planted individuals of each of the native species in the following conditions (hereafter competition series): (1) a single individual with no other individuals in the pot (control), (2) an individual with presence of one *Poa annua* individual (interspecific competition), and (3) presence of one co-specific individual (intraspecific competition). Additionally, *P. annua* individuals were grown: (4) in absence of other individuals and (5) in presence of one co-specific

individual. This last treatment (intraspecific interaction) was added to distinguish inter-specific effects from density dependant effects. We generated two set of the competition series, where each condition was replicated 30 times (240 pots). One of these replicated competition series was transferred to a walk-in growth chamber (pi-Tec, Santiago, Chile) that was set-up with a thermoperiod of at 5°/2 °C (day/night) with 18 h light and 6 h dark photoperiods and a light intensity inside the growth chambers at 350 μmol m⁻² s⁻¹. The other replicated competition series was transferred to an identical walk-in growth chamber to the former but with a thermoperiod of 11°/5 °C (day/night). We selected these thermoperiods because the lower (5°/2 °C) represents the mean air temperature during the daylight hours during summer in King George Island (Sáez et al. in press), while the 11°/5 °C was selected based on pessimistic climate change scenarios (i.e. A1 family). In this scenario temperature increases as high as those observed in the last century are expected for the next century (Bracegirdle and Stephenson 2012; DeConto and Pollard 2016). Soil in the pots was kept moist to field capacity. The duration of the experiment was 3.5 months (June–September), corresponding to the growing season length in the Antarctic Peninsula (December–March). After this period, all individuals of each species were collected and dried in an electric drying oven at 60 °C for 4 days, and then weighted with an analytical balance (Boeco, Germany) for biomass.

In the second experiment we assessed the interactions among the invasive and each of the two natives at the two growing temperatures used in the previous experiment and two levels of nitrogen availability in the soil. For this, we prepared 800 plastic pots of 300 cm³ of volume each that were filled with an inert substrate comprised of a mixture of perlite and vermiculite 1:1. In addition, two Hoagland-type solutions were prepared where we varied the content of nitrogen (see “Appendix” section for details of the Hoagland solutions). One of the solutions contained 8000 μM of nitrogen, corresponding approximately to 56 ppm of nitrogen in the soil. This corresponds to soils enriched in nitrogen similar to those found near abandoned penguin rookeries where the more luxuriant growth of *D. antarctica* has been described (Lindsay 1971; Tatur et al. 1997). The other solution contained 300 μM of nitrogen, which corresponds to 4.2 ppm in soil, typical of bare fellfields or recently

exposed soils after glacier retreat (Kozeretka et al. 2010). We refer to these treatments as high-N and low-N availability. As for the former experiment, we generated four competition series where each of the native species were planted: (1) as a single individual with no other individuals in the pot (control), (2) an individual with presence of one *P. annua* individual (interspecific competition), (3) presence of one co-specific individual, for *P. annua*, there were also individuals growing (4) in absence of other individuals (control) and (v) in presence of one co-specific individual) with 25 replicate each. Two competition series were transferred to a growth chamber that was set-up with a thermoperiod of 5°/2 °C (day/night) and a photoperiod of 18 h light and 6 h dark. The other two competition series were transferred to a growth chamber with a similar photoperiod but a thermoperiod of 11°/5 °C (day/night). Light intensity inside both growth chambers was 550 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In each growth chamber, twice a week one of the competition series was irrigated with the high-N solution while the other series was irrigated with the low-N solution. Thus, in this experiment we had two growing temperatures and two levels of nitrogen availability. The duration of the experiment was also 3.5 months (June–September), and after this period all individuals of every species were collected and dried in an electric drying oven at 60 °C for 4 days, and then weighed with an analytical balance (Boeco, Germany) for biomass.

Data analyses

In the first experiment, biomass in the experimental conditions was assessed with two-way ANOVAs, where growing temperature (two levels: 5°/2 °C and 11°/5 °C), neighbor presence (three levels: no-neighbors, co-specific and inter-specific neighbor) and the interaction among these factors were the independent variables. To achieve normality, biomass data were square-root transformed. In the second experiment, biomass among experimental conditions was assessed with a three-way ANOVA, where growing temperature (two levels: 5°/2 °C and 11°/5 °C), nitrogen availability (two levels: low and high), neighbor presence (three levels: no-neighbors, co-specific and inter-specific neighbor) and the interaction among these factors were the independent variables. Again, to achieve normality, biomass data were square-root

transformed. A posteriori Tukey's HSD tests were performed after ANOVAs.

We determined the intensity of the interaction between *P. annua* and the native Antarctic species at different growing temperatures as a function of biomass. We used the relative interaction index, RII (Armas et al. 2004) as a metric of interaction intensity, which is defined as:

$$\text{RII} = \text{Bw} - \text{Bo} / \text{Bw} + \text{Bo}$$

where Bw is the mass of an individual growing with another plant and Bo is the mean value of control plants of the same species (growing alone). RII has defined limits $[-1, +1]$, being negative when competition prevails, positive for prevalence of facilitation and 0 when the net balance of the interaction is neutral. Significant departures from zero were assessed with t tests. All analyses were performed in R (R Core Team 2013).

Results

First experiment

For the interaction between *Deschampsia* and *Poa*, growing temperature, the presence of neighbors, and the interaction among these two factors affected the biomass of *D. antarctica* (hereafter we refer to genus; Table 1). The biomass of *Deschampsia* was greater with higher temperature, but not in the presence of *Poa*; at both temperatures the biomass of *Deschampsia* significantly decreased when growing with *Poa* (Fig. 1). RII values also indicated that regardless of the growing temperature, *Poa* exerted a strong competitive effect on *Deschampsia* (Fig. 2). The competitive effect of *Poa* on *Deschampsia* was not affected by temperature (Fig. 2). The presence of conspecific individuals did not show any effect (Fig. 2). Interestingly, the competitive response of *Deschampsia* to *Poa* was of similar magnitude to the competitive effect of *Poa* on *Deschampsia* at 5 °C. At higher temperature there was no competitive response of *Deschampsia* to *Poa* (Fig. 2). Thus, while at lower temperature these species might co-exist (similar magnitude of the competitive effect and response), at higher temperature *Poa* might outcompete *Deschampsia*.

Regarding the interaction *Colobanthus* and *Poa*, only temperature and the interaction temperature and

Table 1 ANOVA results for biomass accumulation after 3 months in the Antarctic vascular plants *D. antarctica* and *C. quitensis* when growing in a competition experiment with the invasive species *P. annua* at two growing temperatures (5°/2° and 11°/5 °C day/night)

Factor	SS	df	MS	F	<i>p</i>
<i>Deschampsia antarctica</i>					
Intercept	20.11	1	20.11	2310.62	< 0.001
Neighbor	0.64	2	0.32	36.61	< 0.001
Temperature	1.07	1	1.07	122.57	< 0.001
Neighbor × Temperature	0.11	2	0.06	6.51	0.002
Error	1.5	174	0.01		
<i>Colobanthus quitensis</i>					
Intercept	10.11	1	10.11	2118.95	< 0.001
Neighbor	0.02	2	0.01	2.22	0.111
Temperature	0.23	1	0.23	47.42	< 0.001
Neighbor × Temperature	0.09	2	0.05	9.45	< 0.001
Error	0.83	174	0.005		
<i>Poa annua</i>					
Intercept	91.25	1	91.25	4050.97	< 0.001
Neighbor	1.86	3	0.62	27.48	< 0.001
Temperature	1.80	1	1.80	79.77	< 0.001
Neighbor × Temperature	0.39	3	0.13	5.76	< 0.001
Error	5.23	232	0.02		

neighbors affected the biomass of *Colobanthus* (Table 1). The presence of neighbors per se did not affect *Colobanthus* biomass (Table 1), although there was a trend towards greater biomass with either a conspecific or inter-specific neighbor (Fig. 1). Higher growing temperature increased biomass of *Colobanthus* regardless of the presence of a conspecific or inter-specific neighbor (Fig. 1). Although changes in biomass were of little magnitude, RII values indicated that *Poa* competed with *Colobanthus* only at the lower temperature (Fig. 2). Surprisingly, the presence of *Poa* had positive effects on *Colobanthus* at the higher temperature (Fig. 2). Similar effects can be observed with the presence of a conspecific individual, where at the lower temperature we observed competition, but facilitation at the higher temperature (Fig. 2). The effect of *Poa* was of similar sign and magnitude to the competitive response of *Colobanthus* at both temperatures. Thus, these species may coexist regardless of growing temperature.

The biomass of *Poa* individuals was significantly affected by temperature, the presence of neighbors and the interaction between these two factors (Table 1). *Poa* biomass was not affected by growing temperature when growing without neighbors, the presence of conspecific neighbors strongly decreased biomass at both temperatures (Fig. 1). The presence of both

Deschampsia and *Colobanthus* decreased *Poa* biomass only at the low temperature (Fig. 1).

Second experiment

In this experiment, *Deschampsia* biomass was affected by N availability and the interaction between N and temperature (Table 2). At low N, *Deschampsia* biomass was not affected by growing temperature nor the presence of *Poa* (Fig. 3). However, at high N, plants growing at higher temperatures were larger. *Poa* did not affect *Deschampsia* growth at the lower temperature, but it reduced *Deschampsia* biomass at the higher temperature (Fig. 3). RIIs indicated that at low N there were neutral effects among species at both temperatures, but at high N *Poa* had a negative effect on *Deschampsia* at the higher temperature. The effect of *Deschampsia* on *Poa* growth (competitive response) was neutral at both growing temperatures, it was significantly negative at low N and low temperature (Fig. 4).

At both N levels, only the presence of *Poa* negatively affected *Colobanthus* growth but only at the high temperature (Fig. 3). Nonetheless, there was no effect of *Colobanthus* on *Poa* (competitive response of *Colobanthus*) lower temperature at both N levels, but negative at higher temperature and high

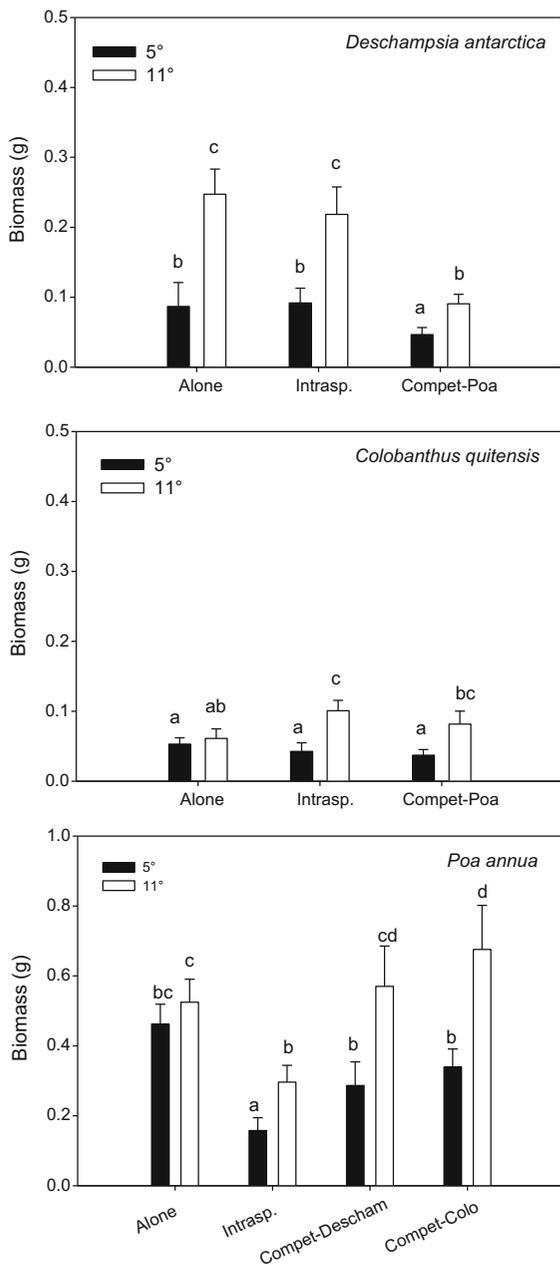


Fig. 1 Biomass accumulated after 3 months by individuals of the native Antarctic vascular plants *D. antarctica* and *C. quitensis*, and the exotic *P. annua*, when growing alone, in intraspecific and interspecific competition, at two growing temperatures (5°/2° and 11°/5 °C day/night). Different letters indicate significant differences according to a Tukey a posteriori test. Please note the change in scale in *P. annua* compared to the Antarctic vascular plants

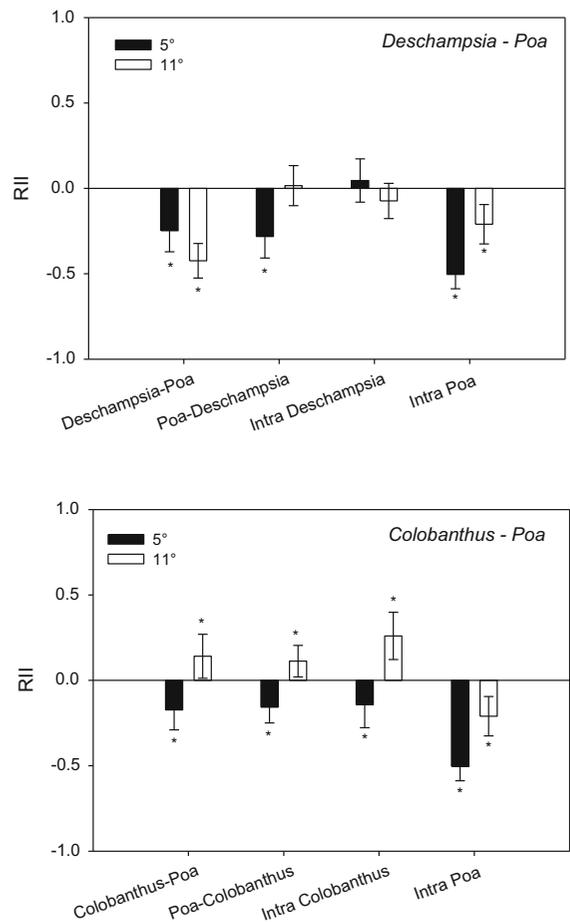


Fig. 2 Relative interactions index (RII) between individuals of the Antarctic vascular plants *D. antarctica* and *C. quitensis* at the intraspecific level and in competition with the invasive species *P. annua* at two growing temperatures (5°/2° and 11°/5 °C day/night). Asterisks indicated significant different from zero (i.e. neutral interaction)

N (Fig. 4). As in the first experiment we found a positive effect of *Colobanthus* on *Poa* when N was low at the high temperature.

At low N, *Poa* biomass was not affected by temperature or the presence of a neighbor, either intra- or interspecific. However, at high N, biomass was greater at the higher temperature (Fig. 3). The higher RII observed for *Poa* corresponded to those where *Poa* individuals were growing with co-specifics (Fig. 4). As noted, both *Deschampsia* and *Colobanthus* exerted competitive effects on *Poa* at the lower temperature and low N (Figs. 3 and 4).

Table 2 ANOVA results for biomass accumulation after 3.5 months for the Antarctic vascular plants *D. antarctica* and *C. quitensis* when growing in a competition experiment with the invasive species *P. annua*, and for *P. annua* growing with the natives, at two growing temperatures (5°/2° and 11°/5 °C day/night) and two levels of nitrogen availability (300 and 8000 μmolN)

Factor	SS	df	MS	F	<i>p</i>
<i>Deschampsia antarctica</i>					
Neighbor	0.05	2	0.02	8.77	< 0.001
Temperature	0.08	1	0.08	29.25	< 0.001
Nitrogen	0.10	1	0.10	39.50	< 0.001
Neighbor:temperature	0.02	2	0.01	2.91	0.057
Neighbor \times nitrogen	0.02	2	0.01	4.78	< 0.001
Temperature \times nitrogen	0.08	1	0.08	31.62	< 0.001
Neighbor \times temperature \times nitrogen	0.05	2	0.02	9.35	< 0.001
Error	0.46	180	0.002		
<i>Colobanthus quitensis</i>					
Neighbor	0.18	2	0.09	38.82	< 0.001
Temperature	0.001	1	0.002	0.75	0.387
Nitrogen	0.044	1	0.04	19.06	< 0.001
Neighbor \times temperature	0.067	2	0.03	14.27	< 0.001
Neighbor \times nitrogen	0.005	2	0.002	1.00	0.369
Temperature \times nitrogen	0.004	1	0.004	1.59	0.209
Neighbor \times temperature \times nitrogen	0.021	2	0.01	4.59	< 0.001
Error	0.39	168	0.002		
<i>Poa annua</i>					
Neighbor	0.28	3	0.09	9.58	< 0.001
Temperature	1.34	1	1.34	136.15	< 0.001
Nitrogen	1.62	1	1.62	164.41	< 0.001
Neighbor \times temperature	0.18	3	0.06	6.22	< 0.001
Neighbor \times nitrogen	0.21	3	0.07	6.97	< 0.001
Temperature \times nitrogen	1.79	1	1.79	181.89	< 0.001
Neighbor \times temperature \times nitrogen	0.31	3	0.10	10.52	< 0.001
Error	2.88	292	0.01		

Discussion

If rapid climate change returns to the Antarctic Peninsula, greater numbers of successful dispersal and establishment events of non-native species are likely (Chown et al. 2012; Duffy et al. 2017). Thus, it is important to experimentally assess the potential of synergistic effects between the presence of invasive species and climate change on the Antarctic native species.

We found that the invasive grass species *P. annua* exerted different effects on the two native vascular plant species in Antarctica (*D. antarctica* and *C. quitensis*) depending on the growing temperature and N availability. In particular, for the interaction between *Poa* and *Deschampsia*, we found that at the temperature reflecting current conditions (5 °C) both

the native and the invasive species might co-exist as indicated by the similar magnitude of the competitive effect and response at low and high N levels in the soil. In other words, with the current climate conditions the native grass may withstand invasion by the exotic grass *Poa annua*. Interestingly, at the low temperature and low N, the native *Deschampsia* outcompeted the exotic *Poa*. Our results contrast with the finding of negative effects of the non-native *P. annua* on both native vascular plant species (Molina-Montenegro et al. 2012, 2016). They reported an asymmetry of competitive effects between *P. annua* and native plants, and suggested that the future spread of this non-native species across Antarctica may result in decreased growth of both native species. These different might be related to differences in the soil nutrient availability in the different experiments.

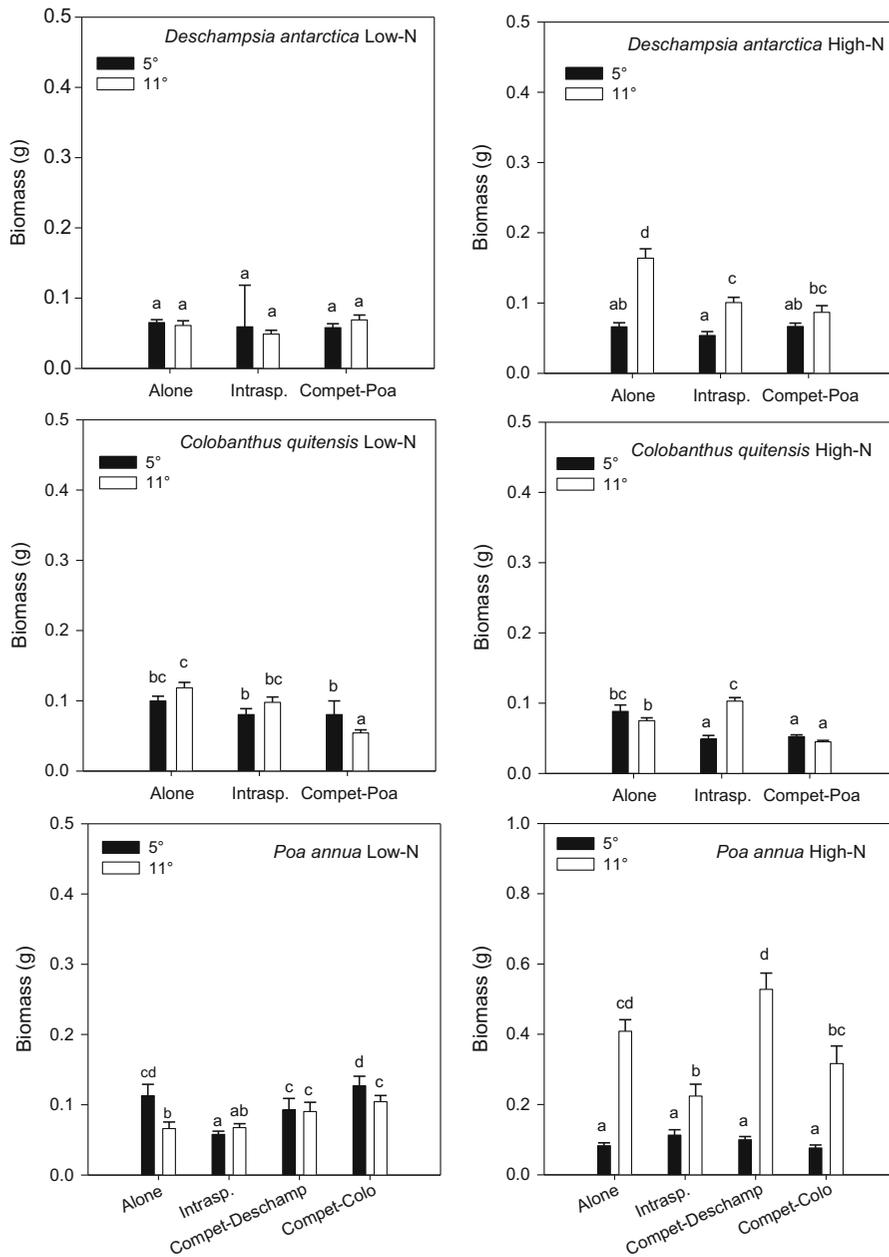


Fig. 3 Mean biomass (\pm 2SE) accumulated after 3 months by individuals of the native Antarctic vascular plants *D. antarctica* and *C. quitensis* and the exotic *P. annua* when growing alone, in intraspecific competition and in interspecific competition at two

growing temperatures (5°/2° and 11°/5 °C day/night) and two levels of nitrogen availability (low = 300 and high = 8000 - μ mol N). Different letters indicate significant differences according to a Tukey a posteriori test

Additionally, the use of young, small individuals of all the Antarctic plant species by Molina-Montenegro et al. (2012, 2016) versus adult plants in our study is not trivial; as the sign and intensity of interactions

among plants change with ontogeny (Miriti 2006; LeRoux et al. 2013).

Our study highlights the greater ability of *Deschampsia* perform better than *Poa* at low temperatures and low soil N. Several anatomical and

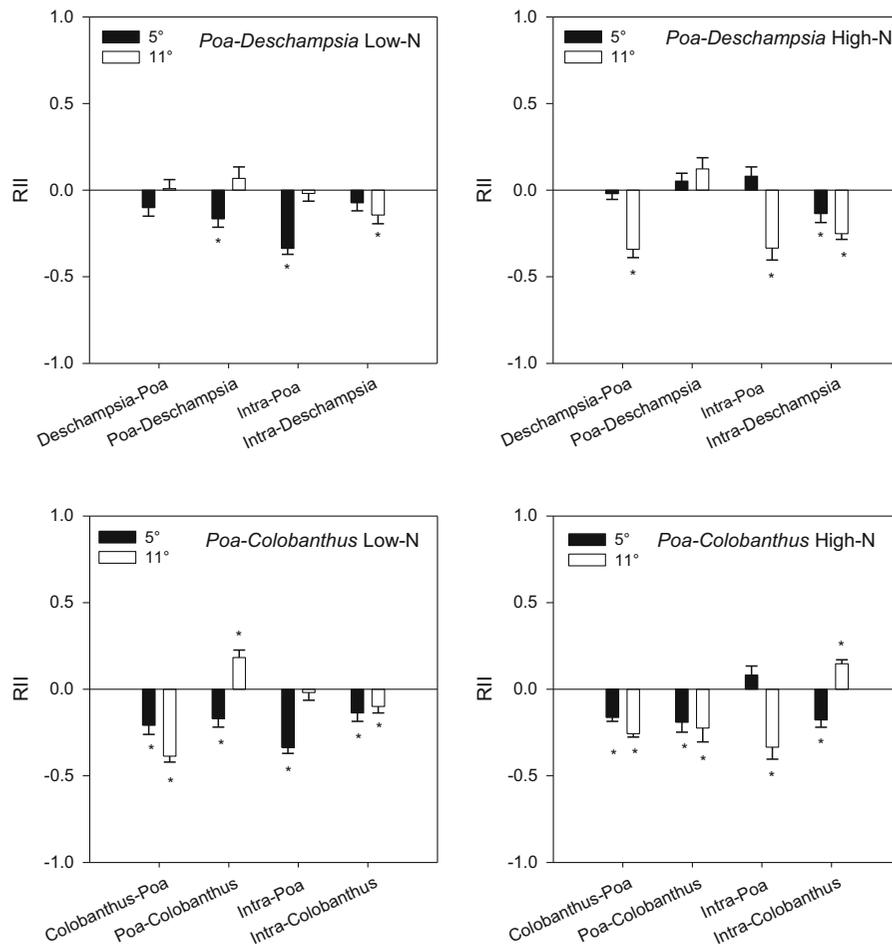


Fig. 4 Relative interactions index (RII) between individuals of the Antarctic vascular plants *D. antarctica* and *C. quitensis* at the intraspecific level and in competition with the invasive species *P. annua* at two growing temperatures (5°/2° and 11°

5 °C day/night) and two levels of nitrogen availability (low = 300 and high = 8000 μmolN). Asterisks indicated significant different from zero (i.e., neutral interaction)

physiological adaptations to withstand the severe environmental conditions of the Antarctica have been highlighted in *Deschampsia* (see Cavieres et al. 2016 for a recent review). Among them, Hill et al. (2011) demonstrated that *Deschampsia* has the ability to avoid N limitation from slow N mineralization in the soil by directly using N from free amino acids and short-chain peptides present in the soil. In addition, Upson et al. (2009) have shown the presence of dark septate endophytes fungi that might act as root mutualists playing an important role in plant nutrition. *Poa annua* does not host any mycorrhiza or non dark septate endophytes in individuals growing in Admiralty bay, Antarctica (Casanova-Katny, personal observation). Despite its worldwide distribution in

several climate types (Pertierra et al. 2017), *P. annua* is a temperate species that behaves as weedy species in crops and cultivars indicating a high demands for nutrients (Warwick 1979). Molina-Montenegro et al. (2014) has recently shown that in the Antarctica *P. annua* grows better in soils with higher availability of nutrients as those associated with disturbance. Thus, *Deschampsia* might be resilient to *Poa* under the current cold temperature conditions of the Antarctica, especially in nutrient poor soils (see also Chwedorzewska et al. 2015).

However, at higher temperatures, *Poa* might out-compete *Deschampsia*, although not at low N. This interpretation corresponds with other studies where invasive species perform better than native with

warmer conditions in cold habitats (Compagnoni and Adler 2014; Blumenthal et al. 2016). Many of the non-native species invading cold habitats are originally from temperate zones (Frenot et al. 2005; Pauchard et al. 2009; Walther et al. 2009), and the low environmental temperature that characterizes cold habitats is an important limiting factor for their success. Thus, it is not surprising that in these habitats warmer conditions promote the success of non-native species over natives (Walther et al. 2009; Blumenthal et al. 2016) as we observed in the interaction between *Poa* and *Deschampsia*.

Antarctic plants have positively responded to the climate warming observed in the Peninsula during the last decades (e.g., Fowbert and Smith 1994; Torres-Mellado et al. 2011; Cannone et al. 2016), but further increases in temperature could be detrimental for these plants, especially for *Deschampsia* (Day et al. 1999; Bokhorst et al. 2007a). Also, warmer conditions in the Antarctic may increase nutrient availability, especially N due to the positive effect of warmer temperatures on nitrogen fixing and/or decomposer microorganisms in the soil (Bokhorst et al. 2007b; Convey et al. 2012). Therefore, climate warming might put the native Antarctic grass at a competitive disadvantage.

For *Colobanthus* we found that with low and high N, the effect of *Poa* was of a similar sign and magnitude to the competitive response of *Colobanthus* at both temperatures. Thus, with these conditions both species might coexist regardless of temperature. Therefore, for *Colobanthus* we did not observe synergistic effects between warming and invasion success, which supports the suggestion that synergistic effects between warming and invasion are context-dependent and species-specific (Sorte et al. 2013; Blumenthal et al. 2016). In contrast to *D. antarctica* that grows at low elevations and lower latitudes (e.g., in the Patagonian steppe), at low latitudes *C. quitensis* only grows at high-elevations and descends to sea level at very high latitudes. Thus, *Colobanthus* is a species that typically grows in sites exposed to low temperatures during the growing season. Species in these habitat-types are typically very conservative in terms of their requirements and uses of nutrients, where even high availability of nutrients these species do not show luxury growth (Chapin et al. 1995; Körner 2003). Indeed, Greene and Holtom (1971) mentioned that across its distribution in Antarctica the N status of

the substrate does not correlate with the abundance of *C. quitensis*. Thus, in the classic CSR scheme of Grime (1979), *Colobanthus* fits the stress-tolerant species syndrome, and it is known that these species are not highly affected by the presence of neighbors (Grime 2002). Here it is important to note that across its entire distribution (except Antarctica), *Colobanthus* is a subordinate species that grow within huge carpets formed by other vascular species with prominent clonal growth such as *Oxychloe andina* or *Patosia clandenstina* (Ruthsatz 1993; Ginocchio et al. 2008) indicating the capacity of *Colobanthus* to tolerate competition. Regardless, *Colobanthus* might be more resilient to the presence of *Poa* under some environmental scenarios.

In summary, we have found that at a low temperature and low N soil content the two native Antarctic species might withstand the invasion of *Poa annua*. As the invasive grass species prefers and performs better on human-disturbed sites (Molina-Montenegro et al. 2014), simply avoiding the arrival of propagules and the disturbance of natural communities could protect the Antarctic vascular plant species. However, our evidence indicates that future climate warming is likely to enhance the competitive effect of the non-native invasive grass on the native grass, posing a menace to the simple but fragile Antarctic terrestrial ecosystems where *D. antarctica* is a major component. Recently, Duffy et al. (2017) reported that future climate warming along the Antarctic Peninsula will provide more suitable sites for the colonization of *P. annua*. Thus, active monitoring is needed for the success of the eradication programs (Galera et al. 2016; Pertierra et al. 2017) and report new arrivals.

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Appendix

See Tables 3 and 4.

Table 3 Hoagland solutions: 4000 μmN

	Volume (ml)
Macronutrients	
KNO ₃	9
NH ₄ H ₂ PO ₄	11
MgSO ₄ × 7H ₂ O	2.5
Ca (H ₂ PO ₄) ₂ × H ₂ O	200
K ₂ SO ₄	2.5
KH ₂ PO ₄	5
Ca (OH) ₂	500
Micronutrients	
KCL	5
H ₃ BO ₃	5
MnSO ₄ × H ₂ O	5
ZnSO ₄ × 7H ₂ O	5
CuSO ₄ × 5H ₂ O	5
H ₂ MoO ₄	5
FeEDTA	2.5

Table 4 Hoagland solutions: 300 μmN

	Volume (ml)
Macronutrients	
KNO ₃	0.15
NH ₄ H ₂ PO ₄	0.6
MgSO ₄ × 7H ₂ O	2.5
Ca (H ₂ PO ₄) ₂ × H ₂ O	200
K ₂ SO ₄	7.5
KH ₂ PO ₄	10
Ca (OH) ₂	500
Micronutrients	
KCL	5
H ₃ BO ₃	5
MnSO ₄ × H ₂ O	5
ZnSO ₄ × 7H ₂ O	5
CuSO ₄ × 5H ₂ O	5
H ₂ MoO ₄	5
FeEDTA	2.5

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