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# Asymmetric responses to simulated global warming by populations of *Colobanthus quitensis* along a latitudinal gradient

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The increase in temperature as consequence of the recent global warming has been reported to generate new ice-free areas in the Antarctic continent, propitiating the colonization and spread of plant populations. Consequently, antarctic vascular plants have been observed extending their southern distribution. But as the environmental conditions toward southern localities are progressively far apart from these species' physiological optimum, the colonization of new sites and ecophysiological responses could be decreased. However, if processes of local adaptation are the main cause of the observed southern expansion, those populations could appear constrained to respond positively to the expected global warming. Using individuals from the southern tip of South America, the South Shetland Islands and the Antarctic Peninsula, we assess with a long term experiment (3 years) under controlled conditions if the responsiveness of *Colobanthus quitensis* populations to the expected global warming, is related with their different foliar traits and photoprotective mechanisms along their latitudinal gradient. In addition, we tested if the release of the stress condition by the global warming in theses cold environments increase the ecophysiological performance. For this, we describe the latitudinal pattern of net photosynthetic capacity, biomass accumulation, and number of flowers under current and future temperatures -by warming- respective to each site of origin after three growing seasons. Overall, was showed a clinal trend was found in the foliar traits and photoprotective mechanisms in the evaluated *C. quitensis* populations. On the other hand, an asymmetric response to warming was observed for southern populations in all ecophysiological traits evaluated, suggesting that low temperature is limiting the performance of *C. quitensis* populations, mainly in those from southern. Our results suggest that under a global warming scenario those plant populations that inhabiting cold zones at high latitudes could be improved in their ecophysiological

performance, enhancing the size of populations or their spread.

1 **Asymmetric responses to simulated global warming by populations of**  
2 ***Colobanthus quitensis* along a latitudinal gradient**

3

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21 **ABSTRACT**

22 The increase in temperature as consequence of the recent global warming has been reported to generate  
23 new ice-free areas in the Antarctic continent, propitiating the colonization and spread of plant  
24 populations. Consequently, Antarctic vascular plants have been observed extending their southern  
25 distribution. But, as the environmental conditions toward southern localities become progressively more  
26 departed from the species' physiological optimum, the ecophysiological responses and survival to the  
27 expected global warming could be reduced. However, if processes of local adaptation are the main cause  
28 of the observed southern expansion, those populations could appear constrained to respond positively to  
29 the expected global warming. Using individuals from the southern tip of South America, the South  
30 Shetland Islands and the Antarctic Peninsula, we assess with a long term experiment (3 years) under  
31 controlled conditions if the responsiveness of *Colobanthus quitensis* populations to the expected global  
32 warming, is related with their different foliar traits and photoprotective mechanisms along their latitudinal  
33 gradient. In addition, we tested if the release of the stress condition by the global warming in these cold  
34 environments increase the ecophysiological performance. For this, we describe the latitudinal pattern of  
35 net photosynthetic capacity, biomass accumulation, and number of flowers under current and future  
36 temperatures -by warming- respective to each site of origin after three growing seasons. Overall, was  
37 showed a clinal trend was found in the foliar traits and photoprotective mechanisms in the evaluated *C.*  
38 *quitensis* populations. On the other hand, an asymmetric response to warming was observed for southern  
39 populations in all ecophysiological traits evaluated, suggesting that low temperature is limiting the  
40 performance of *C. quitensis* populations, mainly in those from southern. Our results suggest that under a  
41 global warming scenario those plant populations that inhabiting cold zones at high latitudes could be  
42 improved in their ecophysiological performance, enhancing the size of populations or their spread.

43

## 45 INTRODUCTION

46 The Antarctic continent is among the most stressful environments for plant life worldwide (Robinson,  
47 Wasley & Tobin, 2003; Peck, Convey & Barnes, 2006); establishment and survival is limited by  
48 conditions such as low temperatures, desiccation, wind abrasion, high radiation and low water and  
49 nutrient availability (Alberdi et al., 2002; Robinson, Wasley & Tobin, 2003; Wasley et al., 2006; Convey,  
50 2011). Although it was recently indicated that warming has stopped in Antarctica (Turner et al. 2016),  
51 over the last few 50 years the mean annual temperature of the Antarctic Peninsula increased by almost 3  
52 °C (Vaughan et al., 2003; Turner et al., 2014). Although global warming is a major threat for biodiversity  
53 worldwide, the Antarctic region is particularly sensitive to small increases in temperature, showing  
54 changes long before they can be seen elsewhere in the world (Walther et al., 2002; IPCC, 2014).

55 Only two vascular plants (*Deschampsia antarctica* and *Colobanthus quitensis*) have been able to  
56 establish and survive in Antarctica. Although both species are present in the same spatial range in  
57 Antarctica (from 62°S to 68° S), *C. quitensis* is more restricted in its habitat distribution than *D.*  
58 *antarctica*. *C. quitensis* (Kunth) Barttl. (Caryophyllaceae), commonly known as the Antarctic pearlwort,  
59 is a small-sized cushion-like perennial herb, with self-compatible sexual reproduction (Kennedy, 1993;  
60 Convey, 1996). The Antarctic pearlwort has an extremely wide range of distribution spanning from  
61 Mexico (17°N) to the southern Antarctic Peninsula (69°S) (Smith, 2003; Convey, 2012). Recent warming  
62 during the last five decades has produced new summer ice-free areas, which have provided suitable  
63 habitats for plant colonization (Convey et al., 2014; Cannone et al., 2016). Consequently, increases in  
64 both the size and number of *C. quitensis* and *D. antarctica* populations have been reported (e.g., Smith,  
65 1994; Day et al., 1999; Torres-Mellado et al., 2011; Cannone et al., 2016), and southward population  
66 expansions can be projected for the next century. Although climate change is expected to have an overall  
67 positive impact on the growth, survival and fitness of *C. quitensis* (Convey, 2011; Day et al., 2009;  
68 Molina-Montenegro et al., 2012a; Torres-Díaz et al., 2016), the eco-physiological responses to the  
69 different components of climate change (e.g., warming) could differ among populations along the  
70 latitudinal gradient.

71 In species with widespread distribution ranges, peripheral populations such as those of *C. quitensis*  
72 from the Antarctic Peninsula (ca. 68°S) are expected to depart more from the species' physiological  
73 optimum than their central or northern counterparts (Gaston, 2009; Sexton, Hangartner & Hoffman,  
74 2014). This prediction finds support in previous studies showing that *C. quitensis* is limited by abiotic  
75 conditions (e.g., low temperatures); this limitation is more evident in the southern populations of its range  
76 (Gianoli et al., 2004; Sierra-Almeida et al., 2007; Torres-Diaz et al., 2016). For instance, Sierra-Almeida  
77 et al. (2007) found significantly higher net photosynthesis rates in Antarctic (62°S, King George Islands)  
78 than in Andean (33°S, La Parva) populations of *C. quitensis* at both low and high temperatures (4 and 15  
79 °C), suggesting that Antarctic populations of *C. quitensis* are physiologically adapted to colder habitats  
80 and that thermal stress release would produce increases in their performance. With respect to cold  
81 adaptation, Gianoli et al. (2004) found greater levels of freezing resistance after cold acclimation and  
82 shorter and wider leaves in Antarctic than Andean genotypes. The conjunction of high irradiance and low  
83 temperature may damage the photosynthetic apparatus, causing a reduction in photosynthesis known as  
84 photoinhibition (Demmig-Adams & Adams, 1992). Bascuñan-Godoy et al. (2010) showed that foliar  
85 microstructures as well as high levels of the xanthophyll cycle pool helped to maintain high physiological  
86 performance in *C. quitensis* from an Antarctic population more than an Andean population under high  
87 radiation and low temperature conditions. Thus, differential responses in morphology and/or physiology  
88 can be expected among populations of *C. quitensis* along the latitudinal distribution gradient, based on the  
89 most recent global warming predictions and models (IPCC, 2014; Turner et al., 2014).

90 Since Antarctic fieldwork can be complex and logistically demanding, most of the experimental  
91 studies of global warming have been carried out under controlled laboratory conditions using present and  
92 future climate scenarios (Molina-Montenegro et al., 2016, but see: Day et al., 2008 and Day et al., 2009).  
93 Most studies assessing the effects of warming on different plant species along a latitudinal gradient use a  
94 constant rise in temperature for all origins, although warming is specific to every place (IPCC, 2014).  
95 Thus it is common to observe several studies assessing the effects of global warming on Antarctic plant  
96 species that have used only one temperature to represent the current conditions of the Antarctic ecosystem

97 -Peninsula or Maritime Antarctica- as well as for the projected warming. But since a strong abiotic stress  
98 increase is present along the latitudinal gradient from the South Shetland Islands to the Antarctic  
99 Peninsula, it generates an important bias for the local conditions compared to the regional averages  
100 (Vaughan et al., 2003). For this reason, in order to make a more realistic analysis of the responses of  
101 Antarctic vascular plants to global warming, experimental designs should be performed considering their  
102 current and projected site-specific temperatures.

103 The main goals of this study were to determine whether populations of *C. quitensis* possess latitudinal  
104 variation in several traits (foliar anatomy and pigments) that avoids photoinhibition and to determine  
105 whether the ecophysiological response to simulated climate change will differ among populations  
106 distributed along a latitudinal gradient. We specifically addressed the following questions: (1) Does *C.*  
107 *quitensis* show signs of clinal variation in anatomical (foliar microstructures) or physiological  
108 (xanthophyll pigments) traits along a latitudinal gradient in which environmental stress (the combination  
109 of cold, aridity and photo-inhibitory radiation) increases with latitude? (2) Will southern populations of *C.*  
110 *quitensis* be more responsive to simulated global warming than more northern populations? To address  
111 these questions, we measured leaf anatomy and xanthophyll pigments in *C. quitensis* along a latitudinal  
112 gradient consisting of three locations from South America to the Antarctic Peninsula. In addition, we  
113 measured the change of the photosynthetic responses, total biomass and flower production in *C. quitensis*  
114 from all locations exposed for three years to simulated global warming.

115

## 116 MATERIALS AND METHODS

### 117 *Target species and study sites*

118 Commonly known as the Antarctic pearlwort, *Colobanthus quitensis* (Kunth) Bartl. (Caryophyllaceae), is  
119 a small-sized cushion-like perennial herb with an extremely wide distribution range spanning from  
120 Mexico (17° N) to the Antarctic continent (68° S); sporadic populations can be found in different islands  
121 of Maritime Antarctica, as well as along the coast of the Antarctic Peninsula (Smith, 2003). *C. quitensis*  
122 individuals in Antarctic ecosystems are mostly distributed near seashores which are frequently associated



123 with *D. antarctica* and mosses. Clonal reproduction is the more common means of propagation in the  
124 Antarctic populations of *C. quitensis*, but it is also capable of self-compatible sexual reproduction  
125 (Convey, 1996).

126 Individuals of *C. quitensis* were collected from three locations along a simple latitudinal transect:  
127 South America (SA), close to the city of Punta Arenas (53.1°S – 70.9°W); South Shetland Islands (SI),  
128 close to the Polish Antarctic Station in Admiralty Bay (62.1°S – 58.3°W), and the Antarctic Peninsula  
129 (AP), in Lagotellerie Island (67.5°S – 67.2°W) (Fig. 1). Sixty plants were dug out from each site during  
130 the 2014/2015 growing season with enough soil around the roots (ca. 250 g) and kept well-watered in a  
131 plastic box under natural conditions of light and temperature until their transportation to the growth  
132 chambers at the Universidad de Talca, Chile (35.2°S). All plants were collected under permission of the  
133 Chilean Antarctic Institute (INACH; authorization number: 1060/2014).

134

### 135 ***Latitudinal trait variation in pigments and microstructures***

136 Variations in anatomical (foliar microstructure) and physiological (photoprotective pigment) traits were  
137 assessed in individuals from all locations along the latitudinal gradient. Specifically, in 25 individuals  
138 from each location (one leaf per plant) we measured and compared five microstructure foliar traits:  
139 cuticle, mesophyll, palisade parenchyma and spongy mesophyll width [mm], and leaf transversal area  
140 [mm<sup>2</sup>]. In the laboratory, leaves were sectioned in 2–3 mm in length and dehydrated in a graded ethanol  
141 series. Thin fragments of 75-100 nm sections were prepared on an ultra-microtome. Sections were stained  
142 with toluidine blue and viewed with a light microscope to analyse morphological attributes of the leaf.  
143 Thin sections were cut with a diamond knife and were stained on grids with uranyl acetate and lead  
144 citrate, and then examined in transmission electron microscope.

145 In addition, in a subset of 15 individuals from each location (one leaf per plant), we estimated the  
146 xanthophyll-cycle pigment content (violaxanthin, antheraxanthin and zeaxanthin) and the de-epoxidation  
147 state of the xanthophyll cycle pigments (DEPS). Leaves were repeatedly extracted (3 times) with ice-cold

148 85% (v/v) acetone and 100% acetone using sonication for 45 minutes at 4° C. Pigments were separated on  
149 a Dupont non-end capped Zorbax ODS-5  $\mu$ m column at 30° C at a flow rate of 1 ml min<sup>-1</sup>. The solvents  
150 consisted of (A) acetonitrile/methanol (85:15, v/v) and (B) methanol/ethyl acetate (68:32, v/v). The HPLC  
151 gradient used was: 0-14 min 100% A, 14-16 min decreasing to 0% A, 16-28 min 0% A, 28-30 min  
152 increasing to 100% A, and 30-38 min 100% A. Detection was carried out at 445 nm. The de-epoxidation  
153 state (DEPS) of the pigments involved in the xanthophyll cycle was quantified as  $Z + (0.5 \times A) / (V + A +$   
154  $Z)$  (for more details see Molina-Montenegro et al., 2012).

155

### 156 *Latitudinal responses to simulated global warming experiment*

157 To evaluate whether different latitudinal origins of *C. quitensis* differ in the magnitude of their responses  
158 to global warming, we measured the ecophysiological performance of plants from each origin (South  
159 America, Shetland Islands and Antarctic Peninsula) under current and future temperature conditions  
160 (warming) predicted by climate change models (IPCC, 2014). Based on the available predictions, a 4 °C  
161 increase in temperature was applied as warming treatment for all populations. Thus, “current”  
162 temperatures were 10 °C, 5 °C and 3°C for SA, SI and AP, and “warming” temperatures were 14 °C, 9 °C  
163 and 7 °C for SA, SI and AP, respectively.

164 We established six experimental abiotic conditions using six automatic air-cooling growth chambers  
165 (model: LTJ300LY; Tianyi Cool, China) to simulate current and future environmental conditions during  
166 summer months of each latitudinal origin. The current conditions for each location were: South America  
167 (mean temperature: 10° C, photoperiod: 18/6 h light/dark), Shetland Islands (mean temperature: 5° C,  
168 photoperiod: 19/5 h light/dark) and Antarctic Peninsula (mean temperature: 3° C, photoperiod: 21/3 h  
169 light/dark). In addition, future conditions for each location were: South America (mean temperature: 14°  
170 C, photoperiod: 18/6 h light/dark), Shetland Islands (mean temperature: 9° C, photoperiod: 19/5 h  
171 light/dark) and Antarctic Peninsula (mean temperature: 7° C, photoperiod: 21/3 h light/dark). During all  
172 experimental time every chamber was maintained in the temperature and photoperiod indicated above,

173 with a constant intensity of the photosynthetic active radiation (PAR) of  $275 \mu\text{mol m}^{-2}\text{s}^{-1}$ . But PAR was  
174 lowered to  $20 \mu\text{mol m}^{-2}\text{s}^{-1}$  during seven months in order to mimic the natural variation in the solar  
175 radiation that affect at high latitude populations. A total of 30 plants per each latitudinal origin (SA, SI  
176 and AP) were randomly assigned to the current or warming conditions. Hence, in each growth chamber a  
177 total of 15 plants were maintained during three years, and once per year in January (middle of the  
178 growing season), photosynthetic rate was recorded on every individual in both current and warming  
179 conditions. The photosynthetic rate was recorded using an infra-red gas analyzer (IRGA, model Ciras-2,  
180 PP-System, USA) under the same temperature of each growth chamber. In addition, at the end of the third  
181 year two fitness-related traits were measured as response variables, total biomass accumulation and  
182 reproductive effort. Total plant growth was measured as the average individual total biomass increase  
183 (final biomass – initial biomass, g) during the three years of the experiment. At the beginning of the  
184 experiments, we selected similar size plants (from each origin). These plants were randomly assigned to  
185 current and warming treatments. There were no differences in the initial weight of plants between current  
186 and warming treatments for any latitude (one-way ANOVA,  $F_{2, 87} = 29,4$ ;  $p < 0.001$ ). At the end of the  
187 experiments, whole plants were harvested (root plus shoot), and individually weighed using a digital  
188 balance. Reproductive effort was measured by counting the number of flowers produced by each plant  
189 during the last year of the experiment. Since there were no differences in initial plant biomass (fresh  
190 weight) between current and future thermal regimes, all individuals were weighed before the start of the  
191 experiment. The magnitude of the responses of each latitudinal origin of *C. quitensis* to experimental  
192 warming was estimated as the average difference between future and current thermal conditions (*i.e.*,  
193  $\Delta = \text{future} - \text{current values}$ ).

194

### 195 ***Statistical analysis***

196 We used independent one-way ANOVAs to assess the significance of the observed differences between  
197 origins for all microstructural traits, pigment content and the DEPS state of foliar samples of *C. quitensis*.

198 The magnitude of the responses of *C. quitensis* to experimental warming on the delta values (future –  
199 current conditions) for each trait (photosynthetic rate, total biomass accumulation, and reproductive  
200 effort) in different populations along of the latitudinal gradient was tested using one-way ANOVAs. In all  
201 analyses, significant differences between treatments were estimated using Tukey tests (HSD) as *post-hoc*  
202 comparisons. Due to the number of multiple comparisons the sequential Bonferroni correction was  
203 applied to all *a posteriori* contrasts. All statistical tests were made using R v.3.1.3 (R-Core Team, 2015).

204

## 205 RESULTS

### 206 *Latitudinal trait variation in pigments and microstructures*

207 As predicted, pigment contents (xanthophyll-cycle pigments), de-epoxidation state of pigments (DEPS)  
208 and micro-structural foliar traits showed a clinal pattern of variation (Table 1 and Table S1). With the  
209 exception of antheraxanthin that did not have a clear relationship with latitude, concentration of the other  
210 pigments and the DEPS significantly increased with latitude (Table 1). Leaves became significantly  
211 thicker and more cylindrical towards higher latitudes (Table 1 and Table S1). This pattern of clinal  
212 variation is consistent with the increase in the photo-inhibitory conditions (lower temperatures and  
213 moisture and longer daylight exposition) at higher latitudes.

214

### 215 *Latitudinal responses to simulated global warming experiment*

216 The photosynthetic rates of *C. quitensis* exposed to experimental warming were significantly different  
217 among latitudinal origins (Fig. 2A-C; Table S2, S3). The greatest response to experimental warming was  
218 found in individuals from the southernmost population (AP), while individuals from South America  
219 showed the lowest response to experimental warming (Fig. 2; Table S2, S3).

220 At the end of third year, experimental warming also had a greater positive and significant effect on  
221 total biomass accumulation and reproductive effort of Antarctic Peninsula *C. quitensis* individuals than  
222 those from South America or even from the Shetland Islands (Fig. 3; Table S2, S3), suggesting that the

223 observed differences in the photosynthetic response are also effectively translated into important fitness-  
224 related traits.

225

## 226 **DISCUSSION**

227 Our results indicate that in the widely distributed *C. quitensis*, morphological and physiological traits  
228 reflect an asymmetric response associated with increasing environmental stress induced by a combination  
229 of increasingly colder, arid and photo-inhibitory conditions with latitude. Moreover, photosynthetic  
230 performance and fitness-related traits were increased with warming in all populations. The prediction that  
231 responses to experimental warming would differ over latitude was supported by the greater responses in  
232 photosynthesis, biomass and reproductive effort found in the southernmost population of *C. quitensis*.  
233 Together, our findings suggest that the direction and magnitude of the responses of *C. quitensis* to global  
234 warming will be positive and specific to latitude.

235

### 236 *Latitudinal trait variation in pigments and microstructures*

237 The prediction of a progressive latitudinal change in both physiological and morphological traits was  
238 supported by seven of the eight traits measured in *C. quitensis*. The direction of the trait variation was  
239 consistent with the functional physiological responses expected to cope with increasingly stressful abiotic  
240 conditions such as cold temperatures, low water availability and longer daylight periods found in the  
241 Antarctic continent (Alberdi et al., 2002; Convey, 2006). Despite the clear clinal variation in functional  
242 traits shown by *C. quitensis* that cope with photoinhibitory conditions, the biological performance  
243 (biomass and flower production) was lower in the southern margin. This result seems to agree with the  
244 core of the “spatial ecology theory” (Gaston, 2009; Sexton, Hangartner & Hoffman, 2014), which states  
245 that peripheral populations reduce their biological performance as a consequence of the reductions in  
246 habitat suitability and increased isolation (see, Sagarin & Gaines, 2002; Vaupel & Matthies, 2012).

247 Several studies have documented that high levels of the xanthophyll cycle pool could be considered as  
248 a pivotal mechanisms to avoid photoinhibition under high radiation and/or low temperature (Demmig-

249 Adams & Adams, 1996; García-Plazaola et al., 2007; Molina-Montenegro et al., 2012b). In addition, high  
250 levels of the xanthophyll cycle pool have been correlated with thermal dissipation of excess energy, being  
251 a dynamic and reversible mechanism in plants that inhabit cold environments (Bravo et al., 2007;  
252 Bascuñan-Godoy et al., 2010; Molina-Montenegro et al., 2012b; Míguez et al., 2015). In our study, those  
253 individuals of *C. quitensis* living in the south edge of distribution showed a significantly higher  
254 xanthophyll cycle pool, suggesting that in this population the capacity to avoid photoinhibition and to  
255 maintain its growth rate could be explained -at least in part- by the presence of this mechanism. The de-  
256 epoxidation state was also higher in the southern populations, where environmental stress is greater. The  
257 high de-epoxidation state found in all *C. quitensis* populations may be related to the capacity to dissipate  
258 excess energy, avoiding photoinhibition; this was more evident in the southern population where a  
259 combination of environmental stress conditions (colder, dryer, and photo-inhibitory) is found.

260 Morphological adaptations have been documented as one of the main mechanisms in plants to cope  
261 with environments (Mooney et al., 1991; and references therein). Foliar modifications in *C. quitensis*  
262 exposed to different abiotic conditions have been previously reported (Bascuñan-Godoy et al., 2010;  
263 Cavieres et al., 2016). We found that toward higher latitudes, *C. quitensis* individuals showed lower leaf  
264 transversal area and greater mesophyll thickness. It has been reported that increases in leaf thickness  
265 under cold acclimation may be beneficial for leaf survival under frost-induced cell dehydration, reducing  
266 the mechanical stress experienced during thawing (Stefanowska et al., 1999). The thicker palisade  
267 parenchyma shown by the southern population is likely to be associated with the higher photosynthesis  
268 values, since this foliar adaptation can influence CO<sub>2</sub> diffusion and assimilation (Vieira & Mantovani,  
269 1995). These variations in foliar micro-structures seem to be a constitutive adaptation, since trait  
270 differences between populations were partially maintained in a common garden under controlled  
271 laboratory condition, suggesting that these functional adaptations could have a genetic basis.

272

273 ***Latitudinal responses to global warming***

274 Altitudinal and latitudinal shifts in distribution are among the earlier impacts of global warming observed  
275 in plants (e.g., Menzel et al., 2006; Kelly & Goulden, 2008; Kopp et al., 2014). Nonetheless, there are still  
276 few studies focusing on the potential adaptive responses of plant species to climate change (but see  
277 Nicotra et al., 2010; Merilä & Hendry, 2014). If increased temperature associated with climate change  
278 exceeds the thermal tolerance of a plant species, the species may either: (1) adjust to the new  
279 environmental conditions through acclimation (through phenotypic plasticity) or evolve (ecotype  
280 differentiation due to natural selection) (Bellard et al., 2012), or (2) track suitable environmental  
281 conditions in space (changing their geographical distribution) and/or time (adjusting their phenology and  
282 physiology). In contrast, if increased temperatures do not exceed the thermal tolerance, plastic responses  
283 rather than ecotype differentiation should be expected. Overall, our results indicate that *C. quitensis* will  
284 mainly respond to future warming through plastic adjustment and probably through range shifts after local  
285 scale population expansions in response to global change. However, biotic interactions (mostly  
286 competitive) will be also relevant to predict how this species will deal with future climate change. In a  
287 recent study, Torres-Díaz et al. (2016) showed that responses of *C. quitensis* to future climate change will  
288 be not only modulated by abiotic factors such as temperature and soil moisture, but also by biotic  
289 interactions with fungal endophytes. Moreover, plant-plant interactions between *C. quitensis* and the  
290 native and invasive plants could be even more critical to forecast the impacts of climate change on  
291 Antarctic vegetation. As shown by Molina-Montenegro et al. (2016) the alien *P. annua* shows high  
292 adaptive plasticity and greater competitive ability than the native *D. antarctica*. Therefore future studies  
293 should address how climate change will affect the interactions between the native species and also  
294 between the native *C. quitensis* and the alien *P. annua*.

295 Although environmental stress releasing due to future warming may promote anatomical changes that  
296 would increase traits such as light absorption, photosynthesis, growth and reproductive effort, warming  
297 may also compromise plant freezing tolerance and photoprotection. Warming has been reported to reduce  
298 the ability of perennial plants to resist freezing events through cold de-acclimation (reviewed in Pagter &  
299 Arora, 2013). Similar effects have been found in Andean plants exposed to experimental warming (e.g.,

300 Sierra-Almeida & Cavieres, 2010). Thus, future studies should address these potentially negative effects  
301 of stress releasing on Antarctic vascular plants.

302 Antarctic vascular plants are distributed along one of the most stressful gradients of the world, being  
303 affected by extreme environmental pressures that often limit their individual performance and population  
304 dynamics (Peck, Convey & Barnes, 2006). Nevertheless, recent warming during the last decades has  
305 already increased their frequency and distribution (Cannone et al., 2016). In a recent review, Valladares et  
306 al. (2014) showed how plastic responses are highly variable between populations of the same species, and  
307 how the spatial distribution of these responses are key to cope with rapid anthropogenic climate change.  
308 Understanding the adaptive response landscape of both plastic and selective processes would greatly  
309 improve the forecasting of the local and regional effects of global warming on plant species, particularly  
310 those with widespread ranges of distribution such Antarctic vascular plants.

311 It is important to mention that future climate change will not only raise temperature but will also  
312 increase liquid precipitation. For instance, Turner *et al.*, (2009) documented increases in precipitation in  
313 the Antarctic Peninsula. It is important to acknowledge that in our experimental design plants we only  
314 evaluated the response of plants to warming, maintaining irrigation similar for both treatments. As shown  
315 in Torres-Díaz *et al.*, (2016) warming tend have lower effects than watering or combined warming plus  
316 watering on *C. quitensis* fitness. Therefore, our experimental design might have underestimated the  
317 effects of future climate change on *C. quitensis* net photosynthesis, growth and reproductive effort.

318

### 319 **Final remarks**

320 It is important to note that our study is not free of limitations. Natural environmental conditions are  
321 almost impossible to reproduce in growth chambers, thus our estimations of plant performance could  
322 differ from those we would find in the field. Natural conditions were not fully mimicked in our  
323 experimental setup and future experimental research under field conditions could provide more accurate  
324 predictions of the effects of warming on *C. quitensis* performance. Field experiments using open top  
325 chambers (OTCs) would have been the more realistic way to study the future responses of *C. quitensis* to



326 environmental warming. Nonetheless, as shown by Torres-Díaz et al. (2016) the responses of *C. quitensis*  
327 to future climate change can be complex, modulated by abiotic and biotic interactions, and additive and  
328 even antagonistic effects may affect the results of laboratory experiments.

329

### 330 **ACKNOWLEDGEMENTS**

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334 Resilience and Adaptation" (AnT-ERA) and "State of the Antarctic Ecosystem" (Ant-Eco).

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501 **Table 1.** Leaf microstructure characteristics and mean pigment concentrations in foliar tissues of  
 502 *Colobanthus quitensis* from three origins along a sub-Antarctic – Antarctic latitudinal gradient.  
 503 Values are means  $\pm$  2 SE. Different lowercase letters indicate significant differences between  
 504 populations (Tukey HSD tests,  $\alpha = 0.05$ ) Letters were ordered from higher to lower trait values  
 505 (from a to c).

506

Trait	South America (53.5°S)	Shetland Islands (62.1°S)	Antarctic Peninsula (67.5°S)
<i>Microstructure</i>			
Cuticle width ( $\mu\text{m}$ )	19.54 $\pm$ 2.48 <sup>a</sup>	16.16 $\pm$ 1.59 <sup>b</sup>	11.52 $\pm$ 1.68 <sup>c</sup>
Mesophyll width ( $\mu\text{m}$ )	358.28 $\pm$ 23.99 <sup>c</sup>	408.96 $\pm$ 7.62 <sup>b</sup>	454.01 $\pm$ 11.28 <sup>a</sup>
Palisade Parenchyma width ( $\mu\text{m}$ )	91.72 $\pm$ 1.48 <sup>c</sup>	95.92 $\pm$ 1.52 <sup>b</sup>	107.56 $\pm$ 5.09 <sup>a</sup>
Spongy Mesophyll width ( $\mu\text{m}$ )	246.92 $\pm$ 24.68 <sup>c</sup>	296.88 $\pm$ 8.41 <sup>b</sup>	334.92 $\pm$ 12.52 <sup>a</sup>
Leaf transversal area ( $\text{mm}^2$ )	0.434 $\pm$ 0.026 <sup>a</sup>	0.327 $\pm$ 0.015 <sup>b</sup>	0.245 $\pm$ 0.020 <sup>c</sup>
<i>Pigment contents</i>			
Anteraxanthin ( $\mu\text{g g}^{-1}$ DW)	73.73 $\pm$ 6.98 <sup>ab</sup>	77.06 $\pm$ 2.21 <sup>a</sup>	71.73 $\pm$ 3.03 <sup>b</sup>
Violaxanthin ( $\mu\text{g g}^{-1}$ DW)	16.86 $\pm$ 2.64 <sup>b</sup>	18.13 $\pm$ 2.13 <sup>ba</sup>	19.46 $\pm$ 1.18 <sup>a</sup>
Zeaxanthin ( $\mu\text{g g}^{-1}$ DW)	12.00 $\pm$ 3.29 <sup>c</sup>	24.46 $\pm$ 6.64 <sup>b</sup>	32.33 $\pm$ 5.89 <sup>a</sup>
DEPS	0.476 $\pm$ 0.021 <sup>c</sup>	0.524 $\pm$ 0.27 <sup>b</sup>	0.551 $\pm$ 0.024 <sup>a</sup>

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516 **Figure legend**

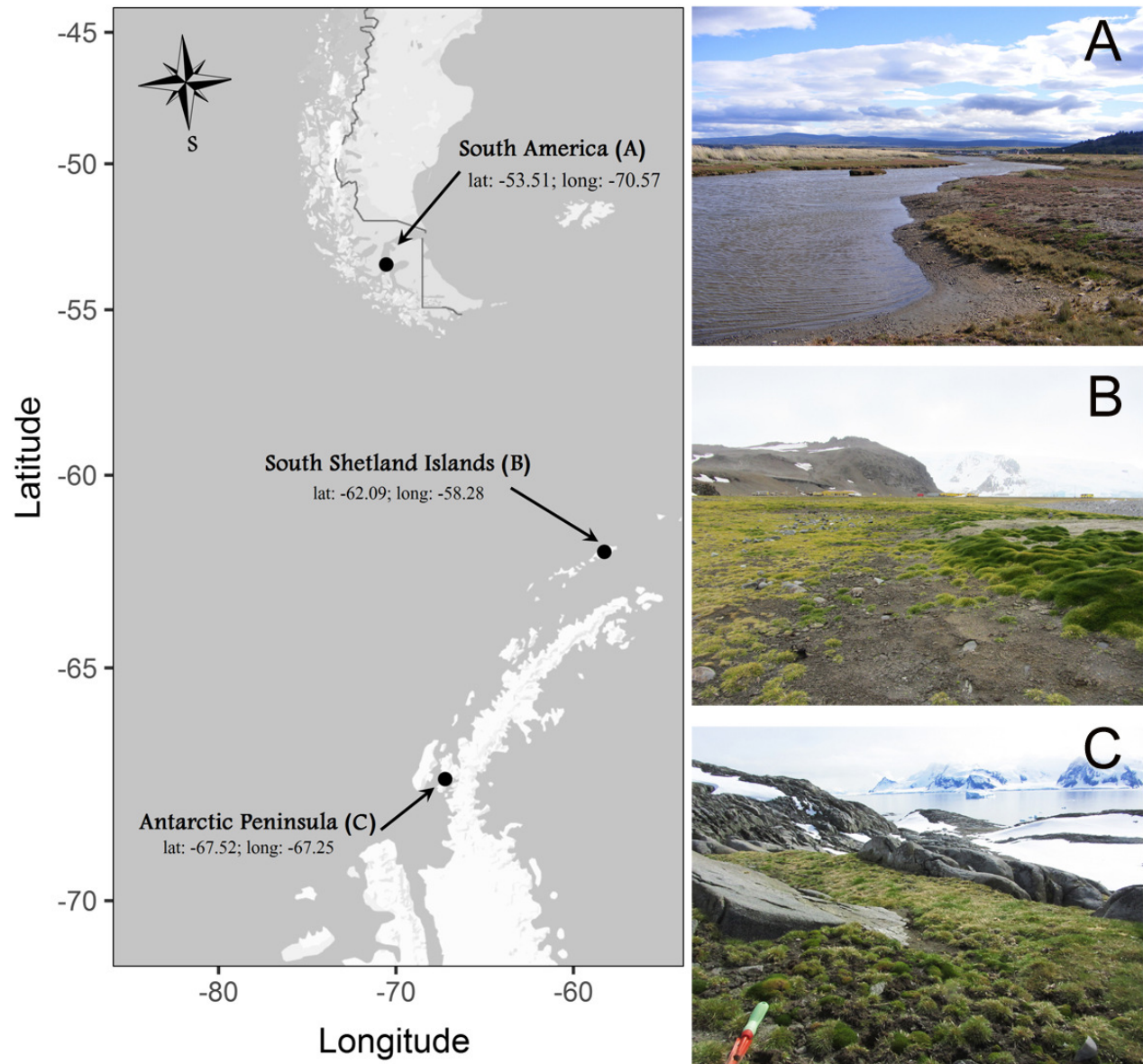
517 **Figure 1.** Sites where individuals of *Colobanthus quitensis* were collected: (A) South America (SA:  
518 53.5°S), (B) Shetland Islands (SI: 62.1°S) and (C) Antarctic Peninsula (AP: 67.5°S). Locations  
519 photographed by Marco A. Molina-Montenegro on 2012-2013 growing season.

520 **Figure 2:** Frequency distribution of the photosynthetic response of *Colobanthus quitensis* individuals  
521 from three different origins (South America 53.5° S, Shetland Islands 62.1° S and Antarctic Peninsula  
522 67.5° S). Estimations were performed under both the current thermal conditions of each site ( $t_0$ ), and  
523 during three consecutive simulated growing seasons ( $t_1$ : $t_3$ ), where all individuals experienced their  
524 respective projected temperatures. The extent of the mean temporal response for each population is  
525 expressed as the mean delta value ( $\pm$ SD) between the photosynthetic responses at the last simulated  
526 warming season ( $t_3$ ) and their values under the current thermal conditions ( $t_0$ ). Different letters between  
527 these values refer to significant differences (Tukey HSD tests,  $\alpha = 0.05$ ) between populations. Bonferroni  
528 correction was applied due to multiple comparisons.

529 **Figure 3:** Violin plot for the average response of *Colobanthus quitensis* from three different latitudinal  
530 origins: South America (SA: 53.5°S), Shetland Islands (SI: 62.1°S) and Antarctic Peninsula (AP: 67.5°S)  
531 to experimental warming. The effects of warming (+ 4 °C) were estimated as the absolute difference (i.e.,  
532 delta) between plant performance under warming (simulated future conditions) and current thermal  
533 conditions in two fitness-related traits: aboveground biomass accumulation delta in grams (A) and  
534 reproductive effort delta estimated as the number of produced flowers (B). The mean delta value for each  
535 population in both traits was obtained after averaging the mean differences of each individual against all  
536 other plants from the same population. The box and whisker plot inside the violins represent the  
537 interquartile distribution of the data around the median (box inner line). Black dots correspond to outlier  
538 values. Different letters indicate significant differences (Tukey HSD tests,  $\alpha = 0.05$ ) between populations.

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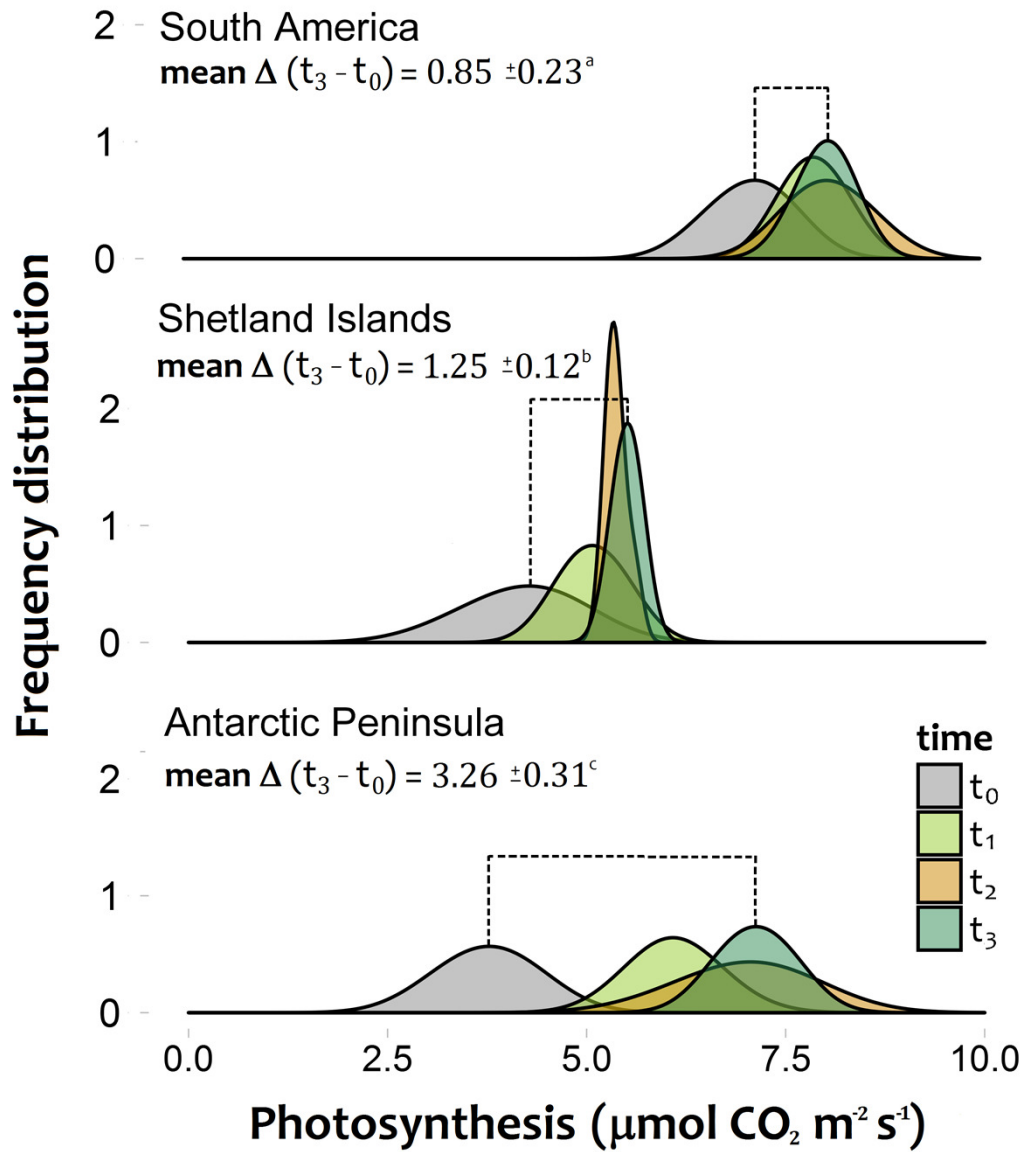
542 **Figure 1**

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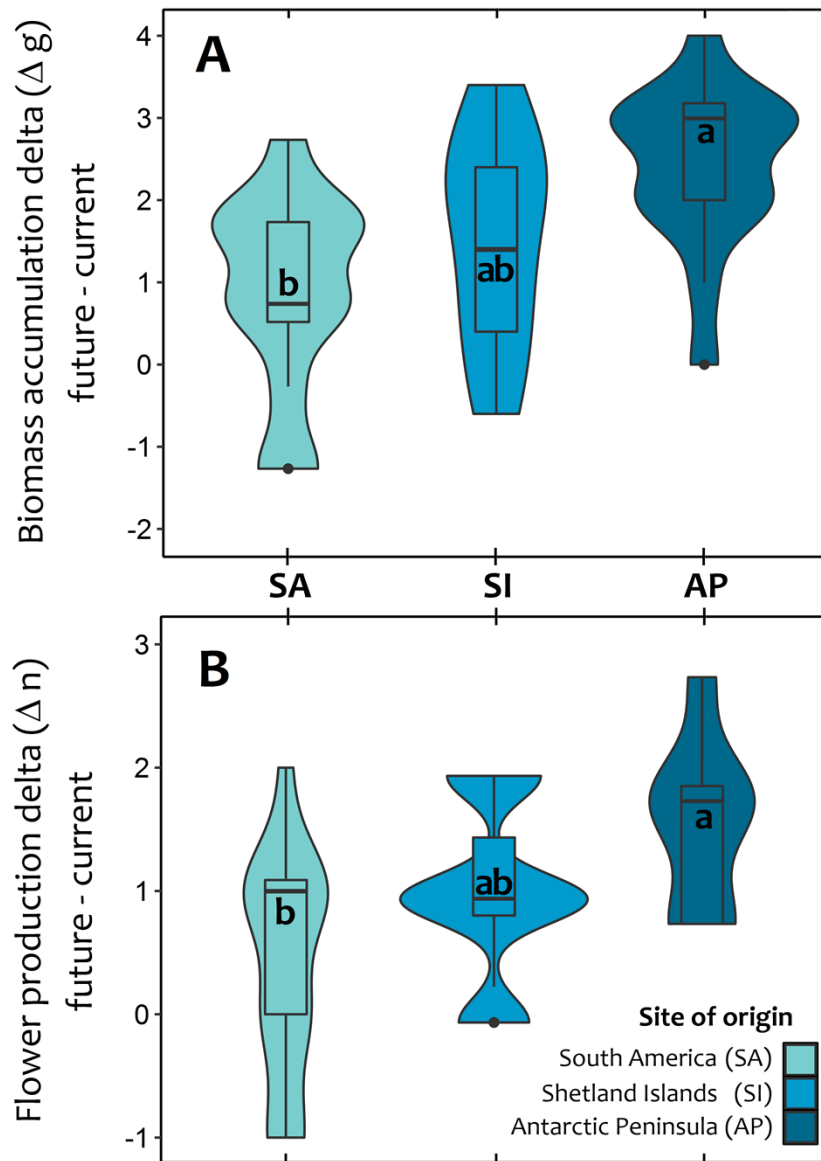
546 **Figure 2**

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551 **Figure 3**

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