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Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1528087> since 2016-02-24T10:28:40Z

Published version:

DOI:10.1007/s10584-015-1551-7

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This is an author version of the contribution published on:

Questa è la versione dell'autore dell'opera:

Climatic Change, 134, 2016, 10.1007/s10584-015-1551-7

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pagg.651-665

The definitive version is available at:

La versione definitiva è disponibile alla URL:

<http://link.springer.com/article/10.1007/s10584-015-1551-7>

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15

16 **VASCULAR PLANT CHANGES IN EXTREME ENVIRONMENTS: EFFECTS OF**
17 **MULTIPLE DRIVERS**

18

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33

34 **Abstract**

35 The Antarctic Peninsula is one of three regions of the planet that have experienced the
36 highest rates of climate warming over recent decades. Based on a comprehensive large-scale
37 resurvey, allowing comparison of new (2009) and historical data (1960s), we show that the
38 two native Antarctic vascular plant species have exhibited significant increases in number of
39 occupied sites and percent cover since the 1960s: *Deschampsia antarctica* increasing in
40 coverage by 191% and in number of sites by 104%. *Colobanthus quitensis* increasing in
41 coverage by 208% and number of sites by 35%. These changes likely occurred in response to
42 increases of 1.2°C in summer air temperature over the same time period. Both species
43 exhibited changes with elevation due to the interaction of multiple drivers (climatic factors
44 and animal disturbance), producing heterogeneity of responses across an elevation gradient.
45 Below an elevation of 20 m fur seal activity exerted negative impacts. Between 20 and 60 m,
46 both plant species underwent considerable increases in the number of sites and percent cover,
47 likely influenced by both climate warming and nutrient input from seals. Above an elevation
48 threshold of 60 m the maximum elevation of the sites occupied decreased for both species,
49 perhaps as a consequence of physical disturbance at higher elevations due to the permafrost
50 conditions and/or the snow cover thickness and persistence. Understanding the role of
51 disturbance drivers for vegetation change in cold regions may become a research priority to
52 enable improved forecasting of biological responses and feedbacks of climate warming on
53 ecosystems in these globally influential regions.

54

55 **Keywords:** Antarctica; Climate Warming; Fur Seals; Permafrost; Upwards Migration;
56 Disturbance.

57

58

59 **1. Introduction**

60 Climate change has been particularly evident in recent decades along the Antarctic Peninsula,
61 one of three regions of the planet recording the most rapid atmospheric warming over the last
62 50 years (Turner et al 2009). Impacts are clearly evident on both abiotic (e.g. glacier retreat)
63 and biotic components of ecosystems (Convey and Smith 2006; Convey 2011). Among the
64 globally-recognized effects of rapid atmospheric warming on angiosperms are accelerated
65 growth and biomass allocation (Elmendorf et al 2012), improved metabolic performance and
66 changes in phenology, range shifts and upwards distributional migration (Walther et al 2002).
67 Studies in the Arctic have highlighted that recent vegetation changes over multiple decades
68 may include apparently contrasting responses (increase, decrease, stability). These result
69 from the impacts and interactions of multiple drivers (climate, permafrost, biotic
70 interactions), complex processes (competition, facilitation) and, in some instances, spatial
71 heterogeneity of species responses (Callaghan et al 2013). In the Antarctic, observed changes
72 have been primarily interpreted as climate warming resulting in a vegetation increase
73 (Fowbert and Smith 1994; Convey 1996a; le Roux and McGeoch 2008; Parnikoza et al 2009;
74 Torres Mellado et al 2011), or to the generally negative impacts of recent rapid recovery of
75 Antarctic fur seal populations following historical over-exploitation (Smith 1988, 2003;
76 Favero-Longo et al 2011), with only one case of facilitation reported only for selected exotic
77 plant species in the sub-Antarctic (Hausmann et al 2013).

78 In the maritime Antarctic, the two species of native vascular plant (*Deschampsia antarctica*
79 Desv. and *Colobanthus quitensis* (Kunth) Bartl.) have exhibited significant expansions in
80 local range and population numbers over up to the last 50 years at several locations (Fowbert
81 and Smith 1994; Convey 1996a; Parnikoza et al 2009; Torres Mellado et al 2011).

82 Both species are pioneer colonists with wide ecological amplitude, occurring in habitats
83 ranging from mineral to organic soils, although neither colonizes active patterned ground and

84 unstable surfaces (Edwards 1972; Smith 2003). *Deschampsia antarctica* occasionally forms
85 extensive stands within its Antarctic distribution. Environmental manipulation experiments
86 have shown that both species respond positively to warming, with increased above-ground
87 biomass, growth rate, water use efficiency, flower and seed production (Day et al 2008;
88 Ruhland and Krna 2010), but that water or nutrient additions had few detectable effects (Day
89 et al 2008). Hill et al (2011), however, demonstrated that *D. antarctica* is a particularly
90 effective competitor for available nitrogen in the soil, and its efficient acquisition of the N
91 released in decomposition of soil organic matter may give it an advantage over competing
92 mosses.

93 Signy Island (South Orkney Islands) lies within the Antarctic Peninsula region that has
94 experienced the most rapid atmospheric warming over the past 50 years (Smith 1990; Royles
95 et al 2012). It is also one of the few high latitude locations in the Southern Hemisphere where
96 detailed and extensive vegetation surveys were made around 50 years ago, with the spatial
97 distribution and abundance of *D. antarctica* and *C. quitensis* carefully documented across the
98 island during the 1960s (1961-1970; Edwards 1972).

99 Here we assess: 1) whether these native vascular plant species have undergone any change in
100 number of sites occupied and percent cover since the 1960s, 2) how different environmental
101 drivers (climate warming, animal and human disturbance) have affected them, producing
102 heterogeneity of responses across an elevational gradient.

103

104 **2. Materials and Methods**

105 *2.1 Study area*

106 Signy Island (60°43'S, 45°38'W) is located in the South Orkney Islands (Maritime Antarctic).
107 It is characterised by a cold oceanic climate, with mean annual air temperature of -3.5°C and
108 annual precipitation of 400 mm, primarily as summer rain (Smith 1990; Royles et al 2012).

109 An ice cap covers about half of the island's area, although this is currently shrinking rapidly
110 (Favero-Longo et al 2012). Ice-free ground is underlain by continuous permafrost, with an
111 active layer depth ranging between 40 cm and 2 m (Cannone et al 2006; Guglielmin et al
112 2008, 2012). Soils are mainly Gelisols and Fibristels (Guglielmin et al 2012).

113 Two major vegetation formations are dominant, the Antarctic herb tundra formation
114 (characterized by the two native vascular plants *D. antarctica* and *C. quitensis*) and the more
115 widespread Antarctic non-vascular cryptogam tundra formation (Smith 1972). Most of the
116 ice-free area of the island is covered by cryptogamic vegetation.

117 A notable environmental change on the island since the late 1970s has been the large increase
118 in the numbers of resting and moulting Antarctic fur seals (*Arctocephalus gazella* Peters
119 1875) present during the summer months (Waluda et al 2010) due to recent rapid recovery
120 following historical over-exploitation. This species' breeding populations are centred
121 primarily on South Georgia, and non-breeding fur seals were first seen on Signy Island in the
122 late 1970s, with numbers then increasing rapidly to 10-20,000 individuals being present
123 during the 1990s, and this number remaining relatively stable to the present day. Fur seal
124 activity has drastically impacted vegetation on the island, both through trampling/crushing
125 (Smith 1988), and polluting levels of nitrogen release in faeces/urine (Favero-Longo et al
126 2011).

127

128 *2.2 Methods*

129 A detailed survey of *D. antarctica* and *C. quitensis* across Signy Island was carried out
130 during the 1960s (Edwards 1972). All sites colonized by these two species were mapped with
131 a resolution of 20-25 m, with the size of the population at each site also being documented.
132 Population sizes were classified as follows (Edwards 1972):

133 a) *D. antarctica*: populations of discrete plants containing 1 (s1 - smallest), 2-20 (s2 - small),
134 or >20 discrete plants or few clumped plants (s3 - intermediate); plants forming coalesced
135 swards < 10m² (s4 – large) or >10m² in area (s5 – largest);

136 b) *C. quitensis*: populations of discrete plant sites containing 1 (s1 - smallest), 2-10 (s2 -
137 small), 10-30 (s3 - intermediate), 30-50 (s4 – large), or >50 cushions (s5 – largest).

138 During January and February 2009, we carried out a field survey of both species across Signy
139 Island following the criteria adopted by Edwards (1972) for comparison with the previous
140 detailed surveys carried out in the 1960s.

141 The maps provided by Edwards (1972) were geo-referenced, included in a GIS system and
142 re-drawn using ArcGIS 9.2. The data recorded in 2009 were mapped using the same
143 software. Each colonized site was characterized in terms of elevation (m a.s.l.), slope (°) and
144 aspect (divided into 8 sectors: N; NE; E; SE; S; SW; W; NW), using the most recent digital
145 elevation model of Signy Island. For each site occupied by either species, distance (m) from
146 trails used by humans and proximity to penguin colonies were also estimated. For each plant
147 occurrence site identified during the field survey we assessed the occurrence/absence of fur
148 seal disturbance on the basis of the visible health and indication of impacts on the
149 surrounding bryophyte communities (e.g. crushing/flattening, colour changes due to urine
150 deposition, etc). Both the new and previously-published survey data were spatially referenced
151 to topographic features (elevation, slope, aspect), anthropogenic influence (trails) and biotic
152 (fur seal, penguin) disturbance.

153

154 To assess any changes of the two species with respect to elevation, we performed non
155 parametric statistics (maximum and minimum elevations; median, 25% and 75% quartiles,
156 providing the core of the species distribution) (Maggini et al 2011). We compared the
157 elevation of the sites occupied in the 1960s and 2009 data. These analyses were applied to the

158 entire dataset as well as to each population size class separately (s1-s5, from smallest to
159 largest) of each species. Differences with respect to elevation, slope and aspect were tested
160 using the Wilcoxon test. These analyses were performed using Statistica®.

161

162 Relationships between the occupied sites topography, climate and disturbance were analyzed
163 using multivariate approaches. Canonical Correspondence Analyses (CCA, using biplot
164 scaling for inter-species distances, Hill's scaling for inter-sample distances; choosing the
165 forward selection of variables option; performing the Monte Carlo permutation test on the
166 first and all ordination axes) were performed using CANOCO 4.5 (Ter Braak and
167 Verdonschot 1995) to analyse the patterns present in the different population size classes of
168 both plant species and to evaluate all the environmental factors affecting them in the 1960s
169 vs. 2009 and in 2009. Comparing the two surveys, as increasing precipitation acted as an
170 inflation factor autocorrelated with air temperature warming, we deleted it from the analysis.
171 The factor "fur seal disturbance" was converted in a dummy variable (1 = presence, 0 =
172 absence) (Lepš and Smilauer 2003).

173

174 There are no specific long-term climatic data currently being collected on Signy Island. We
175 therefore quantified the rate of climate change in this region of maritime Antarctica by
176 analyzing the trends in climate using the century-long data record provided from
177 neighbouring Orcadas AWS (Orcadas Station, Laurie Island, c. 50 km from Signy Island).
178 This is the nearest WMO (World Meteorological Observation) long-term monitoring station
179 to our study area, and its temperature record is very closely correlated ($p < 0.01$, $r^2 = 98\%$, as
180 tested by linear regression) to the 47 year (1948-1995) record available from Signy Island
181 (Royles et al 2012). We computed the mean annual and seasonal (spring = September,
182 October, November; summer = December, January, February; autumn = March, April, May;

183 winter = June, July, August) air temperatures (°C) and precipitation (mm) over the period
184 1960–2009. Air temperature and precipitation trends over time were obtained by linear
185 regression using Statistica®.

186

187 **3. Results**

188 *3.1 Climate*

189 Over the period 1960-2009, atmospheric temperature showed an increasing trend of +0.9°C
190 in mean annual air temperature ($p < 0.05$) and in the seasonal data, especially in summer which
191 showed an increase of +1.2°C ($p < 0.01$) (Fig. 1). Analyzing the changes of seasonal and mean
192 annual air temperature at the decadal scale, while the 1970s were a cold period (except for
193 summer), since the early 1980s there has been an almost continuous warming trend (with the
194 exception of winter in the last decade). Summer and autumn exhibited the largest air
195 temperature changes (Table 1 Supplementary Materials), with the summer increase
196 commencing in the 1970s, and that in autumn only in the last decade.

197 Since 1960 total annual precipitation has also increased by c. 72 mm (Royles et al 2012). The
198 strongest precipitation increase has occurred since 1993, with the recent trend being almost
199 double that between 1960 and 1993 (+28 mm/y vs. +14.5 mm/y) (Fig. 1). At the decadal
200 scale precipitation exhibited a decrease during the 1970s while, since the 1990s, both
201 seasonal and mean annual values continued to increase (as some precipitation data were
202 absent between 1983 and 1992, changes in means of seasonal and annual precipitation from
203 the 1980s were not statistically significant) (Table 1 Supplementary Materials). As with air
204 temperature, the largest precipitation increases were observed in summer (Table 1
205 Supplementary Materials), and there was also increased occurrence (more than twofold) of
206 intense precipitation events (> 30 mm water equivalent per day). Summer precipitation also
207 now falls mainly as rain and is therefore immediately available to terrestrial organisms.

208

209 3.2 *Deschampsia antarctica*

210 Fifty years after Edward's (1972) survey, *D. antarctica* and *C. quitensis* have both undergone
211 large increases in number of sites occupied, and percent cover (Table 1). The total number of
212 sites occupied by *D. antarctica* increased by 104%, and many areas previously occupied by
213 scattered populations are now characterized by patches of continuous sward. Newly
214 colonized sites were predominantly adjacent to those which hosted the grass in the 1960s. A
215 simple estimate of total percent cover suggests a 191% increase between the two surveys
216 (Table 1). There was no evidence for any upwards migration at higher elevations (Fig. 2A)
217 and, indeed, the highest elevation recorded decreased from 137 to 91 m (Fig. 2A). Almost
218 95% of *D. antarctica* records were located below 60 m both in the 1960s and 2009 (Fig. 2A),
219 this elevation acting apparently as a threshold.

220 Considering all data, there was a maximum elevation decrease ('All' in Fig. 3A) of *D.*
221 *antarctica*, although this integrated different patterns apparent in the separate population size
222 classes (Fig. 3A). There was a maximum elevation decrease in the small (S2) and
223 intermediate (S3) populations, and the opposite pattern for the smallest (S1), large (S4) and
224 largest (S5) populations. Only the largest population (S5) exhibited an increase of +10% over
225 the 50 year period above 60 m. The differences in elevation of sites occupied were
226 statistically significant (Wilcoxon test) in the entire dataset (All) as well as in separate
227 population size classes other than S2 (Fig. 3A).

228 The changes with slope were not statistically significant ($p > 0.05$, Wilcoxon test) (data not
229 shown).

230 There were statistically significant changes with respect to aspect for the entire dataset
231 ($p < 0.01$, Wilcoxon test) (Fig. 2B), with a decrease of the proportion of the overall population
232 occurring in north-exposed sites in favour of the west, south-east and south-west sectors.

233 However, among the different population sizes, only the small (S2) exhibited statistically
234 significant differences ($p=0.01$, Wilcoxon test) with respect to aspect (data not shown).

235 Fur seal damage (expressed as the percent of *D. Antarctica* sites measured that had fur seal
236 damage) was mainly observed below 60 m, decreased with increasing elevation, and was
237 highest from sea level up to 20 m (0-20 m = 64.6%; 21-40 m = 49.3%; 41-60 m = 22.2%;
238 above 61 m <20%).

239 The multivariate analyses (CCA) showed that the different population size classes (s1-s5,
240 smallest to largest) underwent changes between the 1960s and 2009 (Fig. 4A). The most
241 important environmental factor responsible for these changes was air warming ($p<0.01$, $F =$
242 53.8), affecting all the size classes. Topographic parameters acted as secondary factors
243 (slope: $p<0.01$, $F = 3.2$; elevation: $p<0.01$, $F = 2.9$; aspect: $p<0.01$, $F = 2.7$). The biotic
244 disturbance factors exerted a limited influence ($F<0.6$) when compared to that of air
245 warming. Among them, fur seal disturbance ($F = 0.57$) exhibited a direct relationship with the
246 dominant climate factor and was correlated to the observed population changes since the
247 1960s, but with low conditional effects (Table 2 Supplementary Materials) and, among the
248 2009 populations, a tighter association to the smallest and small populations (S1, S2).

249 With reference to the contemporary influence of biotic and anthropogenic disturbance factors
250 on *D. antarctica* (2009 data, Fig. 4B), of the potential biotic and anthropogenic disturbance
251 factors, evidence for fur seal disturbance was apparent in the smallest, small and intermediate
252 (S1, S2, S3) rather than the large and largest (S4, S5) population size classes ($p<0.01$, $F =$
253 7.47) (Fig. 4B). Penguins ($F = 0.33$) and trails ($F = 0.94$) exerted an extremely limited
254 influence.

255

256 *3.3 Colobanthus quitensis*

257 In both surveys, *C. quitensis* was considerably less common than *D. antarctica*, but it again
258 showed a clear increase of 35% in the number of sites occupied across the island (Table 1).
259 New colonization again occurred adjacent to sites which were already occupied in the 1960s.
260 Total estimated percent cover increased by 208% between the two surveys (Table 1). There
261 was again no evidence of upwards migration, with a decrease of the maximum elevation of
262 sites occupied recorded from 116 to 88 m, and areas of local decrease generally at altitudes
263 below 20 m (see bars in Fig. 2C). The maximum elevation decrease was attributable to the
264 smallest (S1) and intermediate (S3) population size classes (which decreased the maximum
265 elevation of their sites of 75 m and c. 60 m, respectively) (Fig. 3B), while the small (S2),
266 large (S4) and largest (S5) classes increased their maximum elevation by between c. 20 and
267 65 m. Overall, the core distribution of the entire dataset of *C. quitensis* suffered a range
268 contraction over the last 50 years (Fig. 3B). Changes were also detected with respect to
269 aspect (Fig. 2D), with increases in the north- and north-west facing sites and decreases in the
270 other aspects, contrasting with the decrease in north-facing slopes documented for *D.*
271 *antarctica*. However, the changes with slope (data not shown) and aspect (Fig. 2D) were not
272 statistically significant ($p > 0.05$, Wilcoxon test).

273 Fur seal damage (expressed as the percent of sites measured that had fur seal damage) on *C.*
274 *quitensis* was observed only below 60 m (0-20 m = 21.4%; 21-40 m = 21.4%; 41-60 m =
275 37.5%).

276 The multivariate analysis (CCA) did not provide statistically significant results for *C.*
277 *quitensis*, probably due to the smaller number of records available.

278

279 **4. Discussion**

280 *Number of sites colonized and percent cover changes*

281 Our data show that both species exhibited large increases in the number of sites occupied and
282 percent cover, across Signy Island in the last 50 years. These results confirm the trends of
283 these two species reported at some more restricted locations in the maritime Antarctic.
284 According to Smith (1994) the large rates of increase recorded here for these two species
285 (Table 1) are greater than would be expected either in a state of climatic equilibrium (where
286 establishment of new plants should compensate loss of old plants) or during the colonization
287 of recently deglaciated sites (where the increase rate is relatively low). In the context of other
288 recent studies (Smith 1994; Fowbert and Smith 1994; Parnikoza et al 2009; Torres-Mellado
289 et al 2011; Vera 2011), it is likely that the changes observed in *D. antarctica* at Signy Island
290 have been promoted by recent climate warming (Fig. 4A). The available studies have covered
291 different time spans, smaller physical areas and overall population sizes than those described
292 here: 1960s-1990s by Fowbert and Smith (1994) and subsequently to 2007/08 by Parnikoza
293 et al (2009) in the Argentine Islands; 1980s-2009 by Torres Mellado et al (2011) for areas of
294 King George and Robert Islands. Furthermore, some of these studies have indicated that
295 trends may not be continuous (Parnikoza et al 2009), or spatially uniform, with some
296 locations showing contrasting patterns (Torres Mellado et al 2011).

297 Of the studies available, our data are most comparable with those of Parnikoza et al (2009),
298 with both studies covering a similar time period (1960s-2008/9). However, the extremely
299 small population of *C. quitensis* in the Argentine Islands means that comparisons can only be
300 made for *D. antarctica*. Over this period, in both studies this species showed similar overall
301 increases in the number of occupied sites (+136% in Parnikoza et al. (2009), compared with
302 +104% in this study), even though the rate of summer warming was greater at Signy Island (β
303 = 0.0224, $p < 0.01$) than at the Argentine Islands ($\beta = 0.0128$, $p < 0.01$) (as tested by linear
304 regression).

305

306 *Environmental drivers and mechanisms of change*

307 Among the factors likely to underlie the increase in populations, environmental manipulation
308 experiments have suggested that atmospheric warming is more influential than water or
309 nutrient addition (Day et al 2008). However, air warming could also improve nutrient
310 availability due to the potential increase in the rate of soil organic matter decomposition
311 (Mack et al., 2004). The spring and autumn warming experienced at the Argentine Islands
312 may also have extended the growing season length and improved seed maturation,
313 germination and establishment (Convey 1996a), thereby enhancing the reproductive success
314 and recruitment of *D. antarctica*. As well as air warming, the strong increase in summer
315 precipitation at Signy Island (Fig. 1, Table 1 Supplementary Materials) is likely to have
316 enhanced water availability.

317 Relating to the processes of spatial colonization and development, both species adopted
318 similar strategies through recruitment primarily taking place from neighbouring pre-existing
319 populations and the formation of coalesced aggregates of individuals, as new colonization for
320 both species predominantly occurred adjacent or very close to sites which were already
321 occupied in the 1960s. This has been noted elsewhere for *D. antarctica* in Antarctica (Vera et
322 al 2013), and for other species in the colonization of open and disturbed alpine and polar
323 environments, such as at the treeline (Gehrig-Fasel et al 2007) and in shrub expansion and the
324 re-colonization of active layer detachment slides (Cannone et al 2010).

325

326 Warming temperatures have led ecologists to predict that vegetation gradients will “march up
327 the hill” as climate envelopes shift with elevation (Walther et al 2002; Breshears 2008). Such
328 shifts in elevation can be understood as the result of enhanced growth and new establishment
329 at higher elevations. However, our data are not consistent with this general prediction, with
330 both species showing a decrease of their maximum elevation below the 1960s values. Above

331 the 60 m elevation threshold, despite a small increase in the number of occupied sites, both
332 species suffered a range contraction, as their maximum elevation decreased from that
333 recorded in the 1960s', although this integrated different patterns in the separate population
334 size classes (Fig. 2A,C; Fig. 3A,B).

335 Further, more than 90% of the individuals of both species were located below an elevation
336 threshold of 60 m (Fig. 2A, C; Fig. 3A,B). Notably, this threshold coincides with the upper
337 boundary of fur seal occurrence confirmed by direct observations of the occurrence of seal
338 trampling/crushing of the surrounding bryophyte communities. The island's annual fur seal
339 census also covers those parts of the island from sea level up to 60 m (Favero-Longo,
340 personal communication), with the most intense fur seal impacts occurring between sea level
341 and 20 m, then decreasing progressively with elevation.

342 *D. antarctica* and *C. quitensis* are relatively tolerant (the former more so) to physical impacts
343 caused by trampling and compaction by the increased fur seal numbers now present in
344 summer at many maritime Antarctic sites (Smith 2003). Through its roots *D. antarctica* is
345 able to acquire N as short peptides (i.e. at an early stage of protein decomposition) faster than
346 amino acids, nitrate or ammonium, giving a significant advantage over competing mosses
347 (Hill et al 2011). Coastal bird and seal colonies are known to influence vegetation in their
348 vicinity through increased nitrogen deposition (Lindeboom 1984). At Signy Island, fur seal
349 occurrence is associated with a large increase in soil N stock; in sites influenced by fur seals
350 C:N ratio ranges between 7.5 and 9.9, while in areas where fur seals are absent the ratio is
351 much higher (13.1) (Favero-Longo et al 2011).

352 We therefore hypothesize that the large increases in fur seals numbers recorded at Signy
353 Island since the 1970s, may have induced a facilitation process at elevations between 20 and
354 60 m, which has promoted the increase of both *D. antarctica* (the number of sites where *D.*
355 *antarctica* occurs increased, see squares in Fig. 2A) and of *C. quitensis* (the % of population

356 and the number of occupied sites increased, see bars and squares in Fig. 2C), at least at
357 locations where this effect was not outweighed by the damage of physical trampling.

358 Between 20 and 60 m, it is likely that the combination of climate warming and fur seal
359 nutrient input interacted to produce convergent positive impacts. Indeed, the large/largest (S4,
360 S5) populations of both species (and the intermediate S3 of *C. quitensis*) increased the
361 elevation of their core distribution (75% increased for all, the median increased only for S3
362 and S4 of *C. quitensis*, Fig. 3A, B), although remaining well below the maximum elevation
363 recorded in the 1960s dataset.

364 The presence of seabirds and marine mammals provides effective predictors for the
365 distribution of *D. antarctica* in the South Shetland Islands (Park et al 2012), due to the
366 preference of this species for fertilized soils, although soil fertility alone is not enough to
367 promote success, which depends on a combination of soil fertility, drainage and snow
368 patterns (Park et al 2012). A manipulation experiment involving fertilization carried out on
369 *D. antarctica* over a decade at Signy Island (Smith 1994) demonstrated that the success of
370 fertilization depends on soil chemical characteristics: at a high elevation site deficient in soil
371 nitrogen *D. antarctica* responded positively to nutrient addition, while there was no
372 significant change at a low elevation site with optimal soil nutrient status.

373 Facilitation of plant establishment by fur seals has been reported recently for some exotic
374 species occurring on Marion Island (Hausmann et al 2013). In this instance their physical
375 trampling damaged the native vegetation and provided new niches for the exotic species, as
376 trampling had greater impact on less resilient native species, and the soil nutrient enrichment
377 gave them a competitive advantage (Hausmann et al 2013).

378

379 Climate warming is expected to interact with the environmental envelopes of terrestrial plants
380 and animals, leading to alterations in ranges upwards or towards higher latitudes mainly in

381 response to increases in air temperature (Walther et al 2002). At sub-Antarctic Marion Island,
382 vascular plant distributions have increased their maximum elevation by around 70 ± 30 m over
383 a 40 y period (1966-2006) in response to a warming of $+1.2^{\circ}\text{C}$ (le Roux and McGeoch 2008).
384 Most of the species analyzed on Marion Island were habitat generalists, as are *D. antarctica*
385 and *C. quitensis* in the current study. Therefore, the heterogeneity of responses with elevation
386 observed at Signy Island may depend on the effect of other environmental drivers.

387 Disturbance can affect ecosystems and physical disturbance has been recognized to be a
388 potentially effective factor in shaping species distributions (le Roux et al 2013). At high
389 latitudes and elevations disturbance related to geomorphological processes (frost creep, frost
390 heave, cryoturbation, landslides, solifluction, gelifluction, erosion, etc.) is frequent,
391 widespread and often intense, and affects the fine-scale distribution and dynamics of many
392 biological communities (Convey 1996b; Cannone and Gerdol 2003; Walker et al 2004;
393 Engelen et al 2008; Lantz et al 2009; Cannone et al 2010; Virtanen et al 2010). The effect of
394 such physical disturbance may explain some idiosyncratic and unexpected species responses
395 to climate warming, such as instances of downslope migration or lack of upward migration,
396 that have been described worldwide in high elevation and high latitude sites (Walther et al
397 2005; Cannone et al 2007). At Signy Island the observed decreases in maximum elevation
398 since the 1960s may be related to changes in the permafrost conditions on the island, and/or
399 disturbance related to the active layer thickness and dynamics, frost heave and freeze-thaw
400 cycles. At higher elevations the depth of frost action coincides with the root depth zone of
401 vascular plants (c. 10-20 cm, direct field observation) and this could limit plant colonization
402 and persistence through gelifluction, cryoturbation and/or ice segregation in the soil
403 (Guglielmin et al 2012). Manipulation experiments performed at Signy Island demonstrated
404 that at a high elevation site (Jane Col, 140 m), the survival of *D. antarctica* was reduced due
405 to the exposure to low temperatures combined with freeze-thaw cycles and the uprooting

406 effect on plants of needle ice formation (occurring in the upper 1-2 cm of the soil), while the
407 same type of manipulation did not exert negative impacts on the survival of this species at a
408 low elevation site (Factory Cove, 5 m) (Smith, 1994), where these physical disturbances did
409 not occur.

410 Snow cover thickness and persistence may also be a potential driver: snow cover is likely to
411 be thicker and spring melt occur later at higher elevations, hence reducing the growing season
412 length. An indirect confirmation of this hypothesis is provided by the distribution patterns of
413 *D. antarctica* and *C. quitensis* at Livingston Island, where at the highest altitudes both species
414 only occur at restricted sites that are frequently snow-free in the early austral summer (Vera
415 2011). Park et al (2013) reported that heavy snowfall may affect the survival of *D. antarctica*
416 and that the amount of snowfall could be an important factor limiting the species' distribution,
417 its density being higher where snow melts earlier.

418 Therefore, the recent increase in number of occupied sites and percent cover of *D. antarctica*
419 and *C. quintensis* at Signy Island is likely to be underlain by the interaction of multiple
420 drivers. These changes also indicate that the ecological processes occurring in maritime
421 Antarctica are similar to those in the Arctic (Callaghan et al 2013). Understanding the role of
422 disturbance drivers for vegetation change in cold regions may become a research priority to
423 enable improved forecasting of biological responses and feedbacks between climate warming
424 and ecosystems in these globally influential regions.

425

426 **Acknowledgements**

427 The authors thank PNRA (Progetto Nazionale di Ricerca in Antartide, Project 2013/C1.01;
428 Project PDR2009/A2.12) for providing funding and BAS (British Antarctic Survey) for
429 logistical support. The study contributes to the BAS 'Polar Science for Planet Earth' and
430 SCAR 'State of the Antarctic Ecosystem' and 'Antarctic Thresholds - Ecosystem Resilience

431 and Adaptation' (AnT-ERA) research programmes. Climatic data were provided by the
432 Servicio Meteorologico Nacional, Centro de Informacion Meteorologica de Buenos Aires
433 (Argentina), and we thank Lic. Ana Teresa Gomez. We thank three anonymous reviewers and
434 the Editor for their comments and suggestions, allowing significant improvement of this work.
435
436

Figure legends

437

438

439 **Figure 1.** Annual and summer air temperature (Temp) and precipitation (Prec) at Orcadas in
440 the period 1960-2010 .

441

442 **Figure 2.** Percentage of population (columns) and number of sites (squares) occurring at
443 different ranges of elevation (0-20; 21-40; 61-80; 81-100; 101-120; 121-140 m a.s.l.) and
444 aspect (sectors, see Materials and Methods) for *Deschampsia antarctica* (A: elevation, B:
445 aspect) and *Colobanthus quitensis* (C: elevation, D: aspect). Legend: * = statistically
446 significant differences between 1960s and 2009 ($p < 0.05$); + = occurrence at one site at an
447 elevation between 121 and 140 m in 1960.

448

449 **Figure 3.** Relation of the occupied sites with elevation (m) of A) *D. antarctica* and B) *C.*
450 *quitensis*, for the entire populations (All) and the single population size classes (S1-S5, from
451 smallest to largest) with changes of minimum, median, 25° and 75° percentile and maximum
452 elevation. Legend: statistically significant differences between 1960s and 2009 (according to
453 the Wilcoxon test) * = $p < 0.05$; ** = $p < 0.01$.

454

455 **Figure 4.** Biplots of the canonical correspondence analysis (CCA) showing the position of
456 the different sized populations (s1-s5, smallest to largest, represented by quadrats of
457 increasing size) of *D. antarctica* with respect to the environmental factors (represented by
458 vectors) in: A) 1960s vs. 2009 (cumulative percentage of variance of species-environmental
459 relation: Axis 1 = 84.0%; Axis 2 = 11.2%); B) 2009 (cumulative percentage of variance of
460 species-environmental relation: Axis 1 = 72.7%; Axis 2 = 15.9%). Each biplot shows the
461 correlation between quadrats and vectors. The product of the vector length and the cosine of

462 its angle with each biplot axis (axis1, axis2) is proportional to the correlation of each vector
463 with each axis (e.g. in 1960s vs. 2009 ‘air warming’ is the most important factor correlated
464 with axis 1 while ‘aspect’ and ‘slope’ correlate with axis 2; in 2009 ‘fur seals’ is the most
465 important factor correlated with axis 1, while ‘elevation’ and ‘slope’ correlate with axis 2).
466 Ranking of each quadrat along a vector is inferred by projecting the quadrat onto the vector
467 (e.g. in 1960s vs. 2009, the 1960s populations show negative correlations with air warming,
468 while the 2009 populations show positive correlations with this factor; in 2009 the smallest
469 and small populations - S1, S2 - are more strongly correlated to fur seals than the large and
470 largest - S4, S5 - populations). In both analyses, the direction of the vector labelled as
471 “aspect” indicated south. Scores of the CCA are reported in Supplementary Materials Table
472 2.
473

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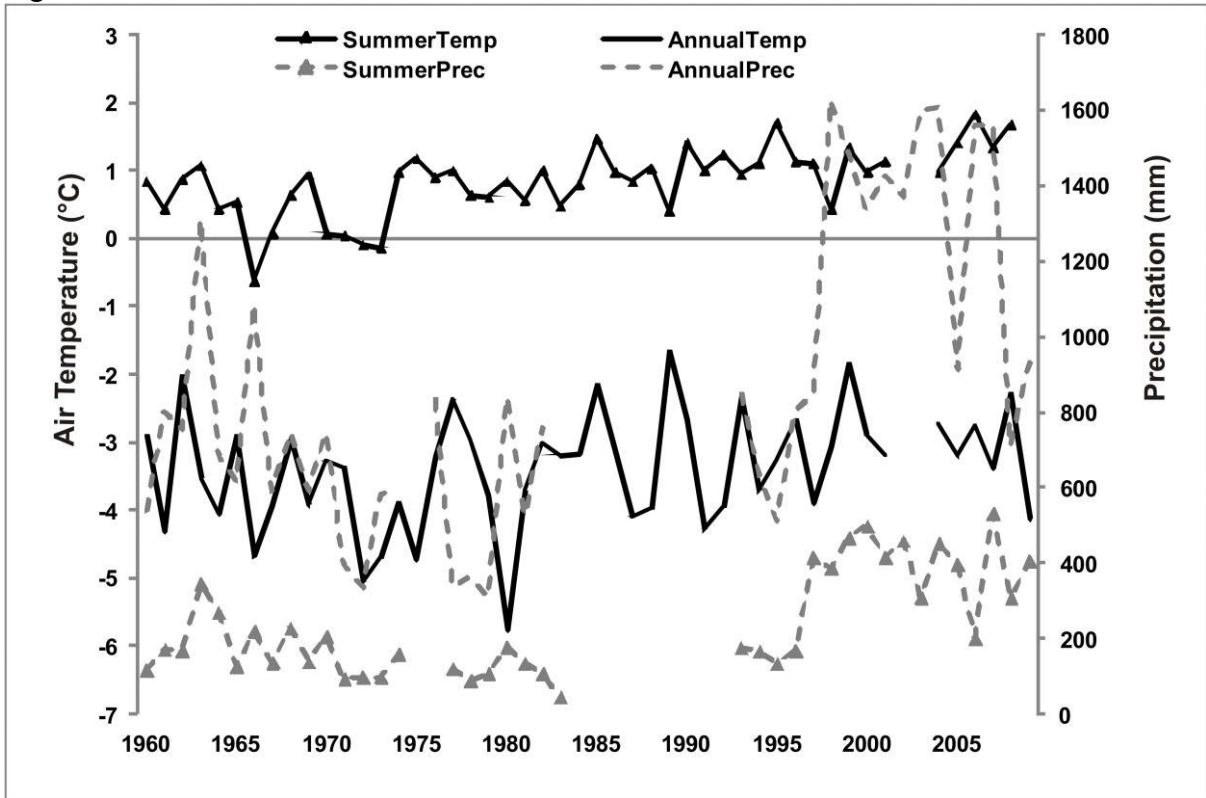
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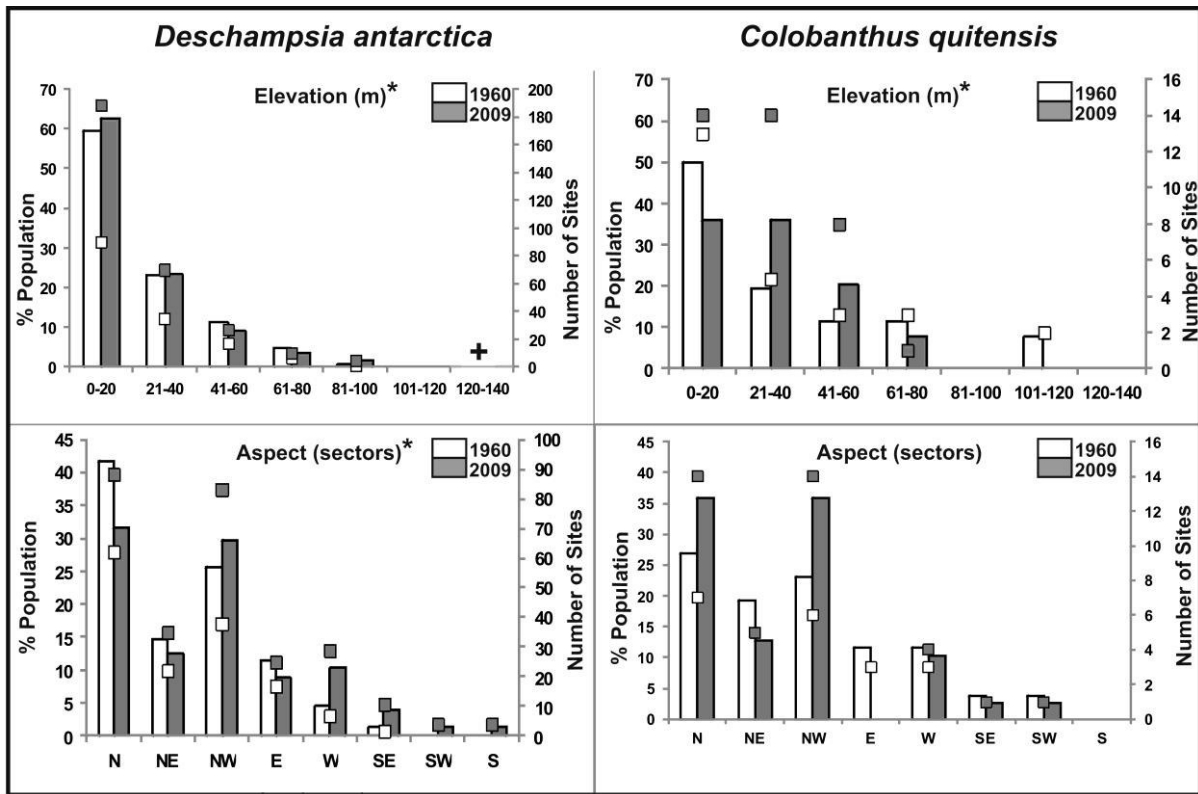
587 Fig. 1



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589

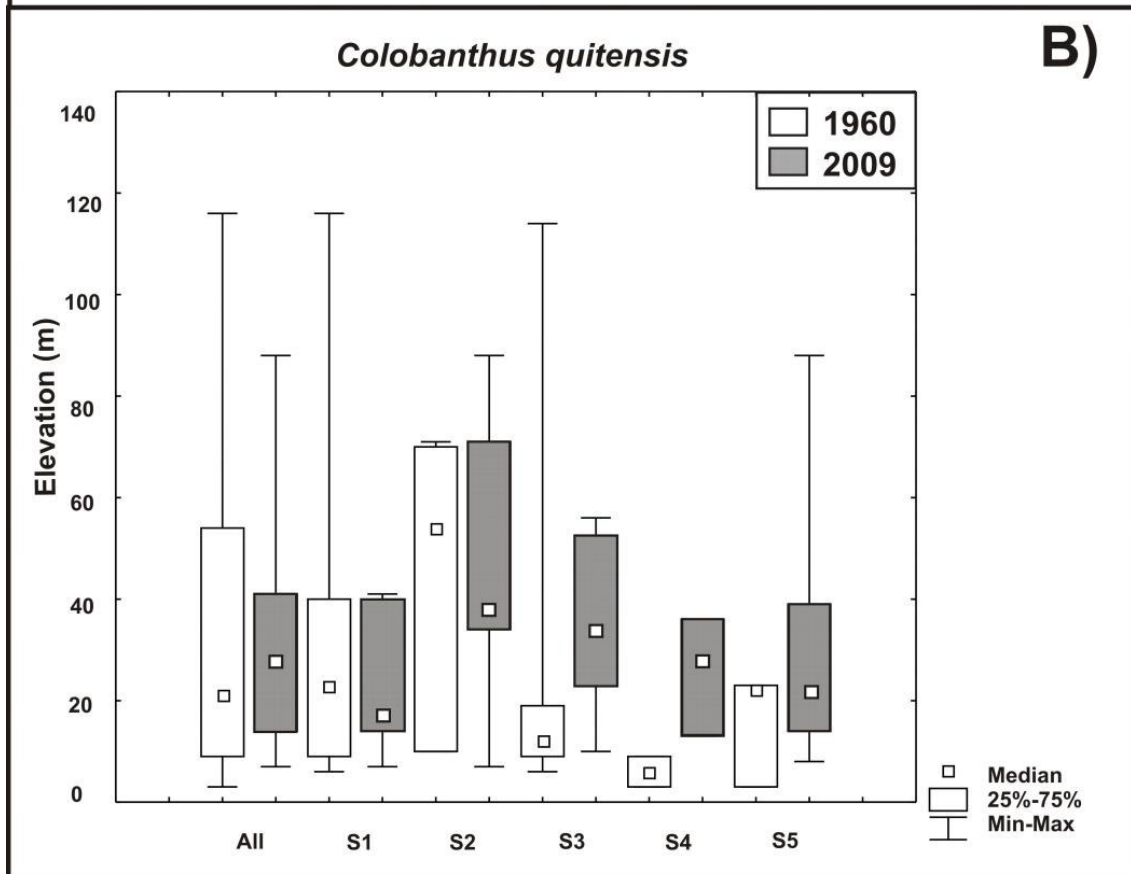
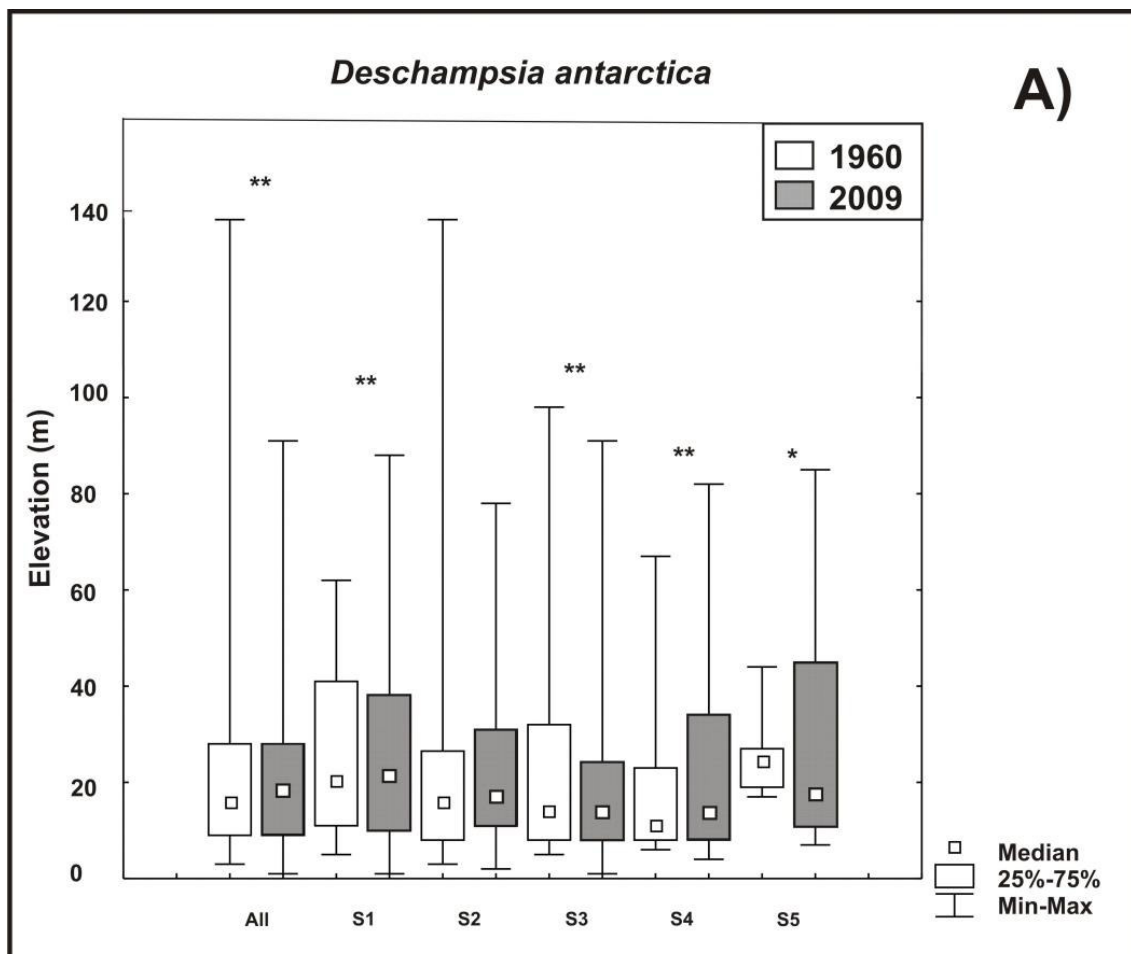
590 Fig. 2



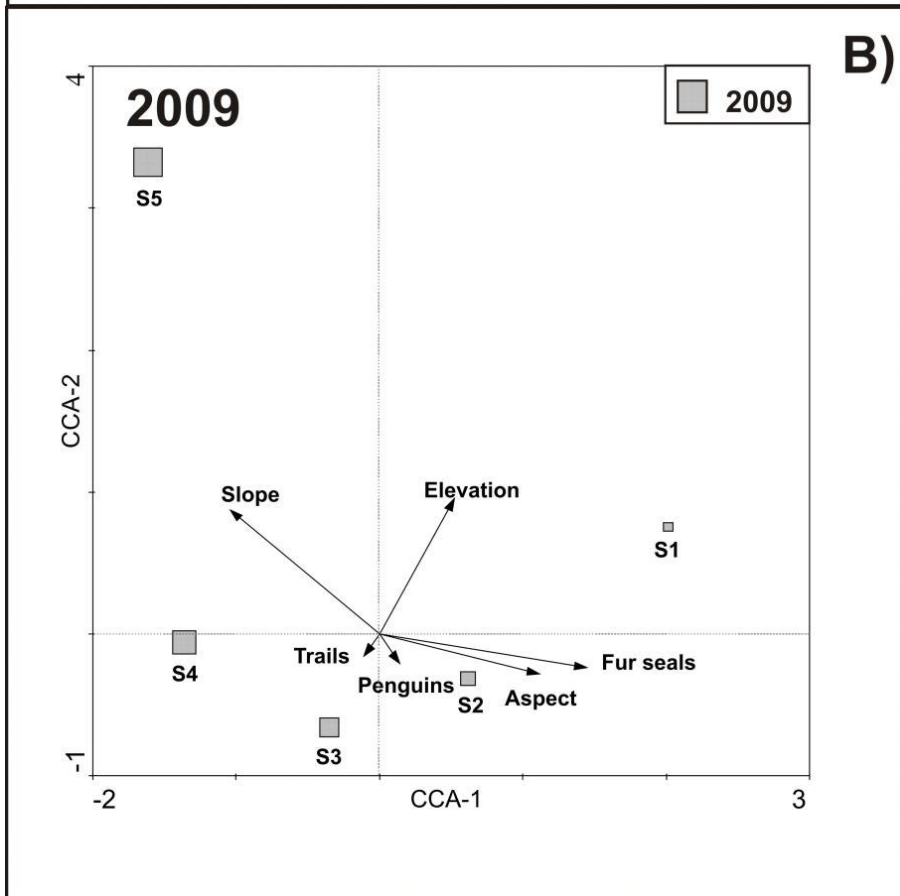
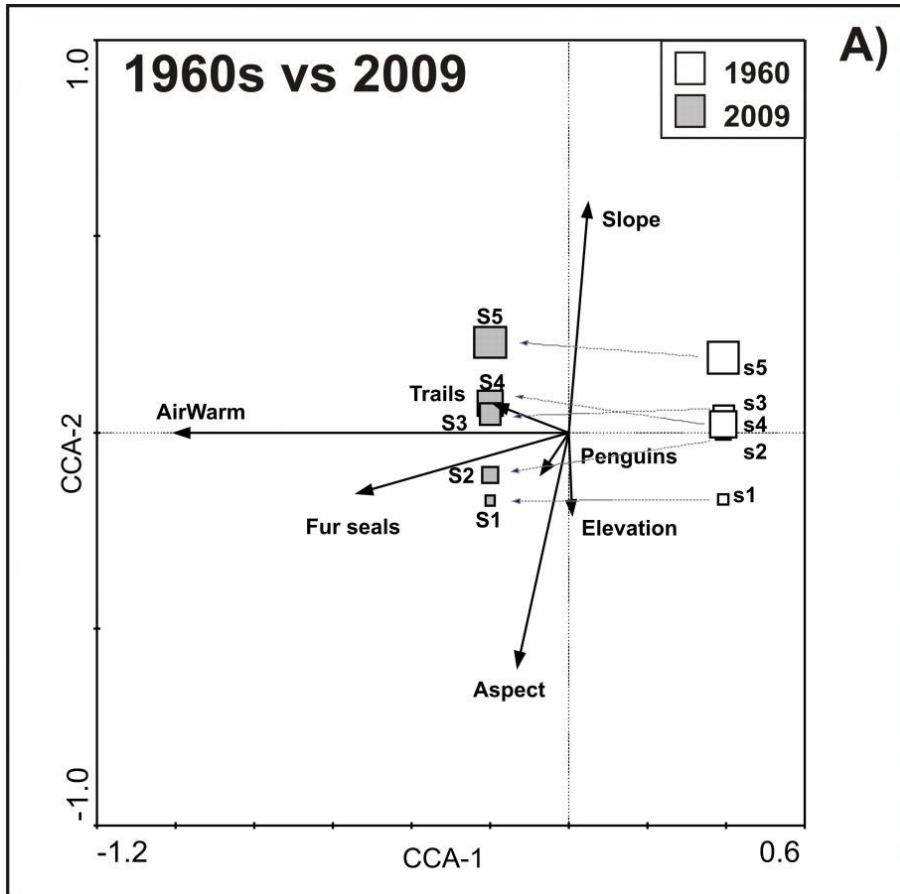
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593 Fig. 3



596 Fig. 4



597

598

599 **Table 1.** Number of sites, percent cover (m²) and % change 1 (Δ %) in the period 1960s-2009
 600 2 of *Deschampsia antarctica* and *Colobanthus quitensis* at Signy Island. Values are
 601 3 recalculated on the basis of field observations of the mean surface area (m²) occupied by
 602 the
 603 4 distinct populations (1 individual \cong 0.01 m² for *Deschampsia antarctica* and 0.005 m² for
 604 5 *Colobanthus quitensis* based on mean plant diameter measured in the field).

605
 606 ***Deschampsia antarctica***

607 **1960s 2009 Δ % 1960s 2009 Δ %**

608 **Site size Number**

609 **of sites**

610 **Number**

611 **of sites**

612 **Number**

613 **of sites**

614 **m² m² m²**

615 **1 plant (s1)** 21 52 +148 0.21 0.52 +147

616 **2-20 plants (s2)** 56 49 -13 5.6 4.9 -12.5

617 **>20 plants (s3)** 45 139 +209 22.5 69.5 +209

618 **< 10m² (s4)** 19 41 +116 95 205 +116

619 **> 10m² (s5)** 6 19 +217 300 950 +216

620 **Total** 147 300 +104 423.31 1229.92 +191

621

622 ***Colobanthus quitensis***

623 **1960s 2009 Δ % 1960s 2009 Δ %**

624 **Site size Number**

625 **of sites**

626 **Number**

627 **of sites**

628 **Number**

629 **of sites**

630 **m² m² m²**

631 **1 cushion (s1)** 8 5 -38 0.04 0.025 -38

632 **2-10 cushions (s2)** 8 6 -25 0.16 0.12 -25

633 **10-30 cushions (s3)** 5 7 +40 0.5 0.7 +40

634 **30-50 cushions (s4)** 2 2 0 0.4 0.4 0

635 **>50 cushions (s5)** 3 15 +398 1.125 5.6 +398

636 **Total** 26 35 +35 2.225 6.845 +208

637