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3 **VASCULAR PLANT CHANGES IN EXTREME ENVIRONMENTS: EFFECTS OF**
4 **MULTIPLE DRIVERS**

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21 **Abstract**

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

42

43 **Keywords:** Antarctica; Climate Warming; Fur Seals; Permafrost; Upwards Migration;
44 Disturbance.

45

46 **1. Introduction**

47 Climate change has been particularly evident in recent decades along the Antarctic Peninsula,
48 one of three regions of the planet recording the most rapid atmospheric warming over the last
49 50 years (Turner et al 2009). Impacts are clearly evident on both abiotic (e.g. glacier retreat)
50 and biotic components of ecosystems (Convey and Smith 2006; Convey 2011). Among the
51 globally-recognized effects of rapid atmospheric warming on angiosperms are accelerated
52 growth and biomass allocation (Elmendorf et al 2012), improved metabolic performance and
53 changes in phenology, range shifts and upwards distributional migration (Walther et al 2002).
54 Studies in the Arctic have highlighted that recent vegetation changes over multiple decades
55 may include apparently contrasting responses (increase, decrease, stability). These result
56 from the impacts and interactions of multiple drivers (climate, permafrost, biotic
57 interactions), complex processes (competition, facilitation) and, in some instances, spatial
58 heterogeneity of species responses (Callaghan et al 2013). In the Antarctic, observed changes
59 have been primarily interpreted as climate warming resulting in vegetation increase (Fowbert
60 and Smith 1994; Convey 1996a; le Roux and McGeoch 2008; Parnikoza et al 2009; Torres
61 Mellado et al 2011), or to the generally negative impacts of recent rapid recovery of Antarctic
62 fur seal populations following historical over-exploitation (Smith 1988, 2003; Favero-Longo
63 et al 2011), with only one case of facilitation reported only for selected exotic plant species in
64 the sub-Antarctic (Hausmann et al 2013).

65 In the maritime Antarctic, the two species of native vascular plant (*Deschampsia antarctica*
66 Desv. and *Colobanthus quitensis* (Kunth) Bartl.) have exhibited significant expansions in
67 local range and population numbers over up to the last 50 years at several locations (Fowbert
68 and Smith 1994; Convey 1996a; Parnikoza et al 2009; Torres Mellado et al 2011). Both
69 species are pioneer colonists with wide ecological amplitude, occurring in habitats ranging
70 from mineral to organic soils, although neither colonizes active patterned ground and

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

80 Signy Island (South Orkney Islands) lies within the Antarctic Peninsula region that has
81 experienced the most rapid atmospheric warming over the past 50 years (Smith 1990; Royles
82 et al 2012). It is also one of the few high latitude locations in the Southern Hemisphere where
83 detailed and extensive vegetation surveys were made around 50 years ago, with the spatial
84 distribution and abundance of *D. antarctica* and *C. quitensis* carefully documented across the
85 island during the 1960s (1961-1970; Edwards 1972). Here we assess: 1) whether these native
86 vascular plant species have undergone any change in number of sites occupied and percent
87 cover since the 1960s, 2) how different environmental drivers (climate warming, animal and
88 human disturbance) have affected them, producing heterogeneity of responses across an
89 elevational gradient.

90

91 **2. Materials and Methods**

92 *2.1 Study area*

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

96 An ice cap covers about half of the island's area, although this is currently shrinking rapidly
97 (Favero-Longo et al 2012). Ice-free ground is underlain by continuous permafrost, with an
98 active layer depth ranging between 40 cm and 2 m (Cannone et al 2006; Guglielmin et al
99 2008, 2012). Soils are mainly Gelisols and Fibristels (Guglielmin et al 2012). Two major
100 vegetation formations are dominant, the Antarctic herb tundra formation (characterized by the
101 two native vascular plants *D. antarctica* and *C. quitensis*) and the more widespread Antarctic
102 non-vascular cryptogam tundra formation (Smith 1972). Most of the ice-free area of the
103 island is covered by cryptogamic vegetation.

104 A notable environmental change on the island since the late 1970s has been the large increase
105 in the numbers of resting and moulting Antarctic fur seals (*Arctocephalus gazella* Peters
106 1875) present during the summer months (Waluda et al 2010) due to recent rapid recovery
107 following historical over-exploitation. This species' breeding populations are centred
108 primarily on South Georgia, and non-breeding fur seals were first seen on Signy Island in the
109 late 1970s, with numbers then increasing rapidly to 10-20,000 individuals being present
110 during the 1990s, and this number remaining relatively stable to the present day. Fur seal
111 activity has drastically impacted vegetation on the island, both through trampling/crushing
112 (Smith 1988), and polluting levels of nitrogen release in faeces/urine (Favero-Longo et al
113 2011).

114

115 *2.2 Methods*

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

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

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

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

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

140

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

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

148

149 Relationships between the occupied sites topography, climate and disturbance were analyzed
150 using multivariate approaches. Canonical Correspondence Analyses (CCA, using biplot
151 scaling for inter-species distances, Hill's scaling for inter-sample distances; choosing the
152 forward selection of variables option; performing the Monte Carlo permutation test on the
153 first and all ordination axes) were performed using CANOCO 4.5 (Ter Braak and
154 Verdonschot 1995) to analyse the patterns present in the different population size classes of
155 both plant species, to evaluate all the environmental factors affecting them in the 1960s and
156 2009. Comparing the two surveys, as increasing precipitation acted as an inflation factor
157 autocorrelated with air temperature warming, we deleted it from the analysis. The factor "fur
158 seal disturbance" was converted in a dummy variable. In both analyses, the direction of the
159 vector labelled as "aspect" indicates south.

160

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

170 winter = June, July, August) air temperatures ($^{\circ}\text{C}$) and precipitation (mm) over the period
171 1960-2009. Air temperature and precipitation trends over time were obtained by linear
172 regression using Statistica®.

173

174 **3. Results**

175 *3.1 Climate*

176 Over the period 1960-2009, atmospheric temperature showed an increasing trend of $+0.9^{\circ}\text{C}$
177 in mean annual air temperature ($p < 0.05$) and in the seasonal data, especially in summer which
178 showed an increase of $+1.2^{\circ}\text{C}$ ($p < 0.01$) (Fig. 1). Analyzing the changes of seasonal and mean
179 annual air temperature at the decadal scale, while the 1970s were a cold period (except for
180 summer), since the early 1980s there has been an almost continuous warming trend (with the
181 exception of winter in the last decade). Summer and autumn exhibited the largest air
182 temperature changes (Table 1 Supplementary Materials), with the summer increase
183 commencing in the 1970s, and that in autumn only in the last decade.

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

195

196 3.2 *Deschampsia antarctica*

197 Fifty years after Edward's (1972) survey, *D. antarctica* and *C. quitensis* have both undergone
198 large increases in number of sites occupied, and percent cover (Table 1). The total number of
199 sites occupied by *D. antarctica* increased by 104%, and many areas previously occupied by
200 scattered populations are now characterized by patches of continuous sward. Newly
201 colonized sites were predominantly adjacent to those which hosted the grass in the 1960s. A
202 simple estimate of total percent cover suggests a 191% increase between the two surveys
203 (Table 1). There was no evidence for any upwards migration at higher elevations (Fig. 2A)
204 and, indeed, the highest elevation recorded decreased from 137 to 91 m (Fig. 2A). Almost
205 95% of *D. antarctica* records were located below 60 m both in the 1960s and 2009 (Fig. 2A),
206 this elevation acting apparently as a threshold.

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

215 The changes with slope (Fig. 2B) were not statistically significant ($p > 0.05$, Wilcoxon test).

216 There were statistically significant changes with respect to aspect for the entire dataset
217 ($p < 0.01$, Wilcoxon test) (Fig. 2C), with a decrease of the proportion of the overall population
218 occurring in north-exposed sites in favour of the west, south-east and south-west sectors.
219 However, among the different population sizes, only the small (S2) exhibited statistically

220 significant differences ($p=0.01$, Wilcoxon test) with respect to aspect (data not shown). Fur
221 seal damage was mainly observed below 60 m, decreased with increasing elevation, and was
222 highest from sea level up to 20 m (0-20 m = 64.6%; 21-40 m = 49.3%; 41-60 m = 22.2%;
223 above 61 m <20%).

224 The multivariate analyses (CCA) showed that the different population size classes (s1-s5,
225 smallest to largest) underwent changes between the 1960s and 2009 (Fig. 4A). The most
226 important environmental factor responsible for these changes was air warming ($p<0.01$, $F =$
227 53.8), affecting all the size classes. Topographic parameters acted as secondary factors
228 (slope: $p<0.01$, $F = 3.2$; elevation: $p<0.01$, $F = 2.9$; aspect: $p<0.01$, $F = 2.7$). The biotic
229 disturbance factors exerted a limited influence ($F<0.6$) when compared to that of air
230 warming. Among them, fur seal disturbance ($F = 0.57$) exhibited a direct relationship with the
231 dominant climate factor and was correlated to the observed population changes since the
232 1960s, but with low conditional effects (Table 2 Supplementary Materials) and, among the
233 2009 populations, a tighter association to the smallest and small populations (S1, S2).

234 With reference to the contemporary influence of biotic and anthropogenic disturbance factors
235 on *D. antarctica* (2009 data, Fig. 4B), evidence for fur seal disturbance was apparent in the
236 smallest, small and intermediate (S1, S2, S3) but not in the large and largest (S4, S5)
237 population size classes ($p<0.01$, $F = 7.47$) (Fig. 4B). Penguins ($F = 0.33$) and trails ($F = 0.94$)
238 exerted an extremely limited influence.

239

240

241 3.3 *Colobanthus quitensis*

242 In both surveys, *C. quitensis* was considerably less common than *D. antarctica*, but it again
243 showed a clear increase of 35% in the number of sites occupied across the island (Table 1).
244 New colonization again occurred adjacent to sites which were already occupied in the 1960s.

245 Total estimated percent cover increased by 208% between the two surveys (Table 1). There
246 was again no evidence of upwards migration, with a decrease of the maximum elevation of
247 sites occupied recorded from 116 to 88 m, and areas of local decrease generally at altitudes
248 below 20 m (see bars in Fig. 2D). The maximum elevation decrease was attributable to the
249 smallest (S1) and intermediate (S3) population size classes (which decreased the maximum
250 elevation of their sites to 75 m and c. 60 m, respectively) (Fig. 3B), while the small (S2),
251 large (S4) and largest (S5) classes increased their maximum elevation by between c. 20 and
252 65 m. Overall, the core distribution of the entire dataset of *C. quitensis* suffered a range
253 contraction over the last 50 y (Fig. 3B). Changes were also detected with respect to aspect
254 (Fig. 2F), with increases in the north- and north-west facing sites and decreases in the other
255 aspects, contrasting with the pattern documented for *D. antarctica*. However, the changes
256 with slope (Fig. 2E) and aspect (Fig. 2F) were not statistically significant ($p > 0.05$, Wilcoxon
257 test). Fur seal damage on *C. quitensis* was observed only below 60 m and the sites involved
258 ranged between 21.4% (0-40 m) and 37.5% (41-60 m).

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

261

262 **4. Discussion**

263 *Number of sites colonised and percent cover changes*

264 Our data show that both species exhibited large increases in the number of sites occupied and
265 percent cover, across Signy Island in the last 50 years. These results confirm the trends of
266 these two species reported at some more restricted locations in the maritime Antarctic.
267 According to Smith (1994) the large rates of increase recorded here for these two species
268 (Table 1) are greater than would be expected either in a state of climatic equilibrium (where
269 establishment of new plants should compensate loss of old plants) or during the colonization

270 of recently deglaciated sites (where the increase rate is relatively low). In the context of other
271 recent studies (Smith 1994; Fowbert and Smith 1994; Parnikoza et al 2009; Torres-Mellado
272 et al 2011; Vera 2011), it is likely that the changes observed in *D. antarctica* at Signy Island
273 have been promoted by recent climate warming (Fig. 4A). The available studies have covered
274 different time spans, smaller physical areas and overall population sizes than those described
275 here: 1960s-1990s by Fowbert and Smith (1994) and subsequently to 2007/08 by Parnikoza
276 et al (2009) in the Argentine Islands; 1980s-2009 by Torres Mellado et al (2011) for areas of
277 King George and Robert Islands. Furthermore, some of these studies have indicated that
278 trends may not be continuous (Parnikoza et al 2009), or spatially uniform, with some
279 locations showing contrasting patterns (Torres Mellado et al 2011).

280 Of the studies available, our data are most comparable with those of Parnikoza et al (2009),
281 with both studies covering a similar time period (1960s-2008/9). However, the extremely
282 small population of *C. quitensis* in the Argentine Islands means that comparisons can only be
283 made for *D. antarctica*. Over this period, in both studies this species showed similar overall
284 increases in the number of occupied sites (+136% in Parnikoza et al (2009), compared with
285 +104% in this study), even though the rate of summer warming was greater at Signy Island (β
286 = 0.0224, $p < 0.01$) than at the Argentine Islands ($\beta = 0.0128$, $p < 0.01$) (as tested by linear
287 regression).

288

289 *Environmental drivers and mechanisms of change*

290 Among the factors likely to underlie the increase in populations, environmental manipulation
291 experiments have suggested that atmospheric warming is more influential than water or
292 nutrient addition (Day et al 2008). However, air warming could also improve nutrient
293 availability due to the potential increase in the rate of soil organic matter decomposition
294 (Mack et al., 2004). The spring and autumn warming experienced at the Argentine Islands

295 may also have extended the growing season length and improved seed maturation,
296 germination and establishment (Convey 1996a), thereby enhancing the reproductive success
297 and recruitment of *D. antarctica*. As well as air warming, the strong increase in summer
298 precipitation at Signy Island (Fig. 1, Table 1 Supplementary Materials) is likely to have
299 enhanced water availability.

300 Relating to the processes of spatial colonization and development, both species adopted
301 similar strategies through recruitment primarily taking place from neighbouring pre-existing
302 populations and the formation of coalesced aggregates of individuals. This has been noted
303 elsewhere for *D. antarctica* in Antarctica (Vera et al 2013), and for other species in the
304 colonization of open and disturbed alpine and polar environments, such as at the treeline
305 (Gehrig-Fasel et al 2007) and in shrub expansion and the re-colonization of active layer
306 detachment slides (Cannone et al 2010).

307

308 Warming temperatures have led ecologists to predict that vegetation gradients will “march up
309 the hill” as climate envelopes shift with elevation (Walther et al 2002; Breshears 2008). Such
310 shifts in elevation can be understood as the result of enhanced growth and new establishment
311 at higher elevations. . However, our data are not consistent with this general prediction, with
312 both species showing a decrease of their maximum elevation below the 1960s values.
313 Further, more than 90% of the individuals of both species were located below an elevation
314 threshold of 60 m (Fig. 2A, D; Fig. 3A,B). Notably, this threshold coincides with the upper
315 boundary of fur seal occurrence confirmed by direct observations of the occurrence of seal
316 trampling/crushing of the surrounding bryophyte communities. The island’s annual fur seal
317 census also covers those parts of the island from sea level up to 60 m (Favero-Longo,
318 personal communication), with the most intense fur seal impacts occurring between sea level
319 and 20 m, then decreasing progressively with elevation.

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

330 We therefore hypothesize that the large increases in fur seals numbers recorded at Signy
331 Island since the 1970s may have induced a facilitation process at elevations between 20 and
332 60 m, which has promoted the increase of both *D. antarctica* (notably, while the % of
333 population did not change, the number of sites where *D. antarctica* occurs increased, see
334 squares in Fig. 2A) and of *C. quitensis* (with increases of the % of population and of the
335 number of occupied sites, see bars and squares in Fig. 2D), at least at locations where this
336 effect was not outweighed by the damage of physical trampling.

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

342 The presence of seabirds and marine mammals provide effective predictors for the
343 distribution of *D. antarctica* in the South Shetland Islands (Park et al 2012), due to the
344 preference of this species for fertilized soils, although soil fertility alone is not enough to

345 promote success, which depends on a combination of soil fertility, drainage and snow
346 patterns (Park et al 2012). A manipulation experiment involving fertilization carried out on
347 *D. antarctica* over a decade at Signy Island (Smith 1994) demonstrated that the success of
348 fertilization depends on soil chemical characteristics: at a high elevation site deficient in soil
349 nitrogen *D. antarctica* responded positively to nutrient addition, while there was no
350 significant change at a low elevation site with optimal soil nutrient status.

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

356 .

357

358 Above the 60 m elevation threshold, despite a small increase in the number of occupied sites
359 for both species, both species suffered a range contraction, as their maximum elevation
360 decreased from that recorded in the 1960s, although this integrated different patterns in the
361 separate population size classes (Fig. 2A,D; Fig. 3A,B).

362 Climate warming is expected to interact with the environmental envelopes of terrestrial plants
363 and animals, leading to alterations in ranges upwards or towards higher latitudes mainly in
364 response to increases in air temperature (Walther et al 2002). At sub-Antarctic Marion Island,
365 vascular plant distributions have increased their maximum elevation by around 70 ± 30 m over
366 a 40 y period (1966-2006) in response to a warming of $+1.2^\circ\text{C}$ (le Roux and McGeoch 2008).
367 Most of the species analyzed on Marion Island were habitat generalists, as are *D. antarctica*
368 and *C. quitensis* in the current study. Therefore, the heterogeneity of responses with elevation
369 observed at Signy Island may depend on the effect of other environmental drivers.

370 Disturbance can affect ecosystems and physical disturbance has been recognized to be a
371 potentially effective factor in shaping species distributions (le Roux et al 2013). At high
372 latitudes and elevations disturbance related to geomorphological processes (frost creep, frost
373 heave, cryoturbation, landslides, solifluction, gelifluction, erosion, etc.) is frequent,
374 widespread and often intense, and affects the fine-scale distribution and dynamics of many
375 biological communities (Convey 1996b; Cannone and Gerdol 2003; Walker et al 2004;
376 Engelen et al 2008; Lantz et al 2009; Cannone et al 2010; Virtanen et al 2010). The effect of
377 such physical disturbance may explain some idiosyncratic and unexpected species responses
378 to climate warming, such as instances of downslope migration or lack of upward migration,
379 that have been described worldwide in high elevation and high latitude sites (Walther et al
380 2005; Cannone et al 2007). At Signy Island the observed decreases in maximum elevation
381 since the 1960s may be related changes in the permafrost conditions on the island, and/or
382 disturbance related to the active layer thickness and dynamics, frost heave and freeze-thaw
383 cycles. At higher elevations the depth of frost action coincides with the root depth zone of
384 vascular plants (c. 10-20 cm, direct field observation) and this could limit plant colonization
385 and persistence through gelifluction, cryoturbation and/or ice segregation in the soil
386 (Guglielmin et al 2012). Manipulation experiments performed at Signy Island demonstrated
387 that at a high elevation site (Jane Col, 140 m), the survival of *D. antarctica* was reduced due
388 to the exposure to low temperatures combined with freeze-thaw cycles and the uprooting
389 effect on plants of needle ice formation (occurring in the upper 1-2 cm of the soil), while the
390 same type of manipulation did not exert negative impacts on the survival of this species at a
391 low elevation site (Factory Cove, 5 m) (Smith, 1994), where these physical disturbances did
392 not occur.

393 Snow cover thickness and persistence may also be a potential driver: snow cover is likely to
394 be thicker and spring melt occur later at higher elevations, hence reducing the growing season

395 length. An indirect confirmation of this hypothesis is provided by the distribution patterns of
396 *D. antarctica* and *C. quitensis* at Livingston Island, where at the highest altitudes both species
397 only occur at restricted sites that are frequently snow-free in the early austral summer (Vera
398 2011). Park et al (2013) reported that heavy snowfall may affect the survival of *D. antarctica*
399 and that the amount of snowfall could be an important factor limiting the species' distribution,
400 its density being higher where snow melts earlier.

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

408

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418

419

420

Figure legends

421

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

424

425 **Figure 2.** Percentage of population (columns) and number of sites (squares) occurring at
426 different ranges of elevation (0-20; 21-40; 61-80; 81-100; 101-120; 121-140 m a.s.l.), slope
427 (0-10; 11-20; 21-30; 31-40; 41-50; 51-60; 61-70; >71°) and aspect (sectors, see Materials and
428 Methods) for *Deschampsia antarctica* (A: elevation, B: slope, C: aspect) and *Colobanthus*
429 *quitensis* (D: elevation, E: slope, F: aspect). Legend: * = statistically significant differences
430 between 1960s and 2009 ($p < 0.05$); + = occurrence at one site at an elevation between 212 and
431 140 m in 1960.

432

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

438

439 **Figure 4.** Biplots of the canonical correspondence analysis (CCA) showing the position of
440 the different sized populations (s1-s5, smallest to largest, represented by quadrats of
441 increasing size) of *D. antarctica* with respect to the environmental factors (represented by
442 vectors) in: A) 1960s vs. 2009 (cumulative percentage of variance of species-environmental
443 relation: Axis 1 = 84.0%; Axis 2 = 11.2%); B) 2009 (cumulative percentage of variance of
444 species-environmental relation: Axis 1 = 72.7%; Axis 2 = 15.9%). Each biplot shows the

445 correlation between quadrats and vectors. The product of the vector length and the cosine of
446 its angle with each biplot axis (axis1, axis2) is proportional to the correlation of each vector
447 with each axis (e.g. in 1960s vs. 2009 'air warming' is the most important factor correlated
448 with axis 1 while 'aspect' and 'slope' correlate with axis 2; in 2009 'fur seals' is the most
449 important factor correlated with axis 1, while 'elevation' and 'slope' correlate with axis 2).
450 Ranking of each quadrat along a vector is inferred by projecting the quadrat onto the vector
451 (e.g. in 1960s vs. 2009 the 1960s populations show negative correlations with air warming,
452 while the 2009 populations show positive correlations with this factor; in 2009 the smallest
453 and small populations - S1, S2 - are more strongly correlated to fur seals than the large and
454 largest - S4, S5 - populations). Scores of the CCA are reported in Supplementary Materials
455 Table 2.

Figure 1

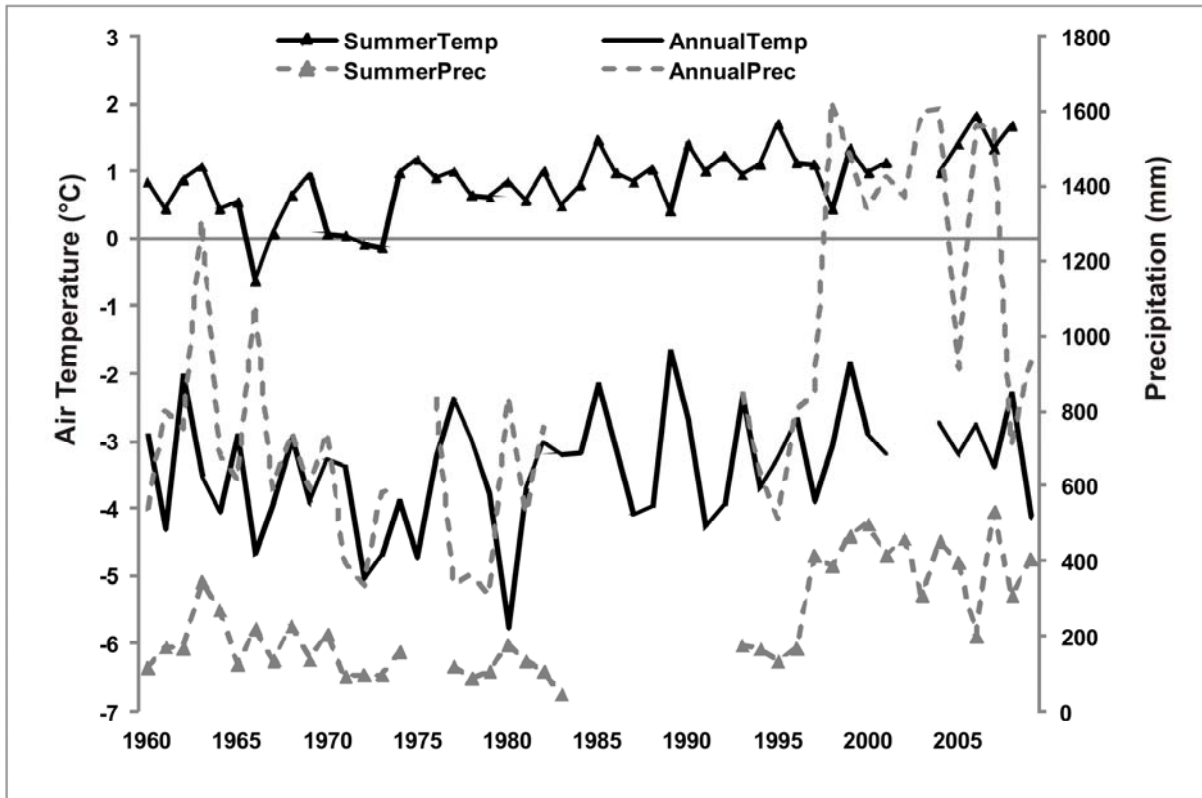


Figure 2

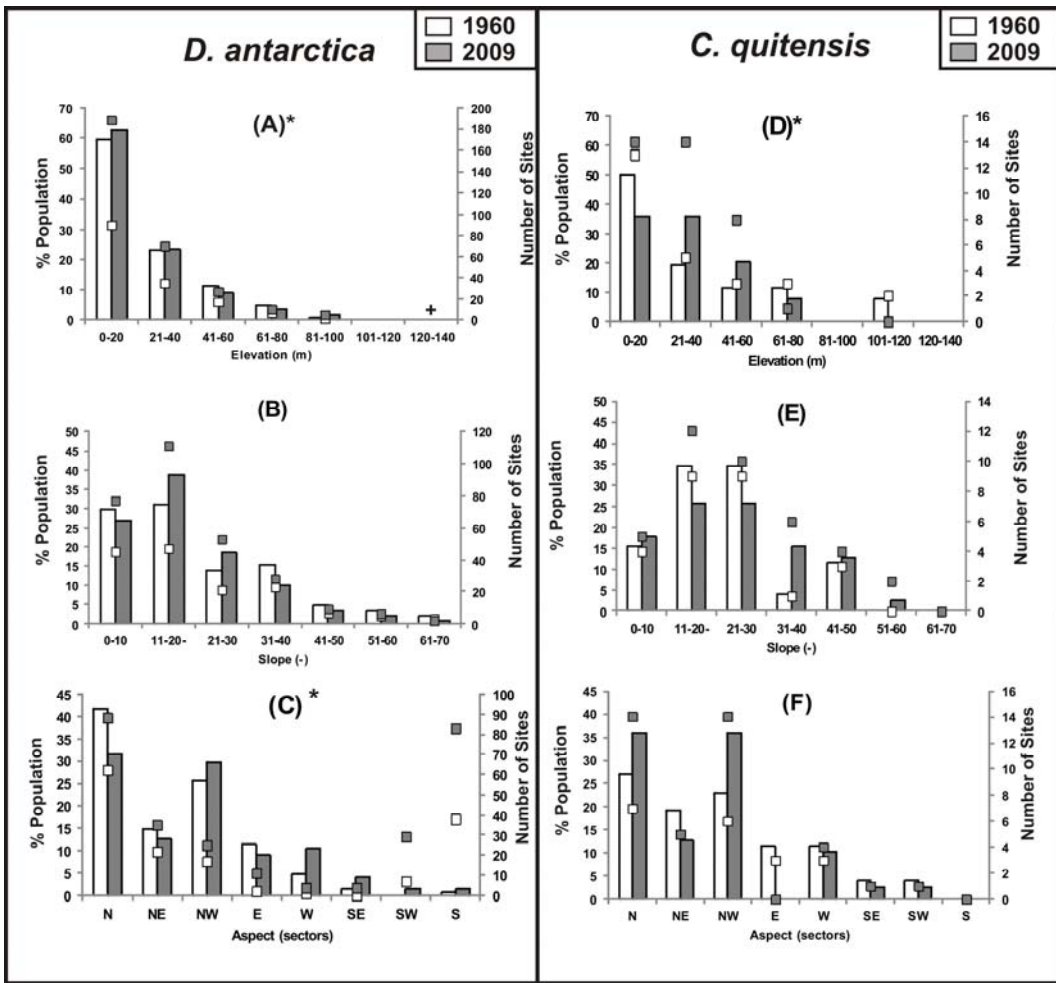


Figure 3

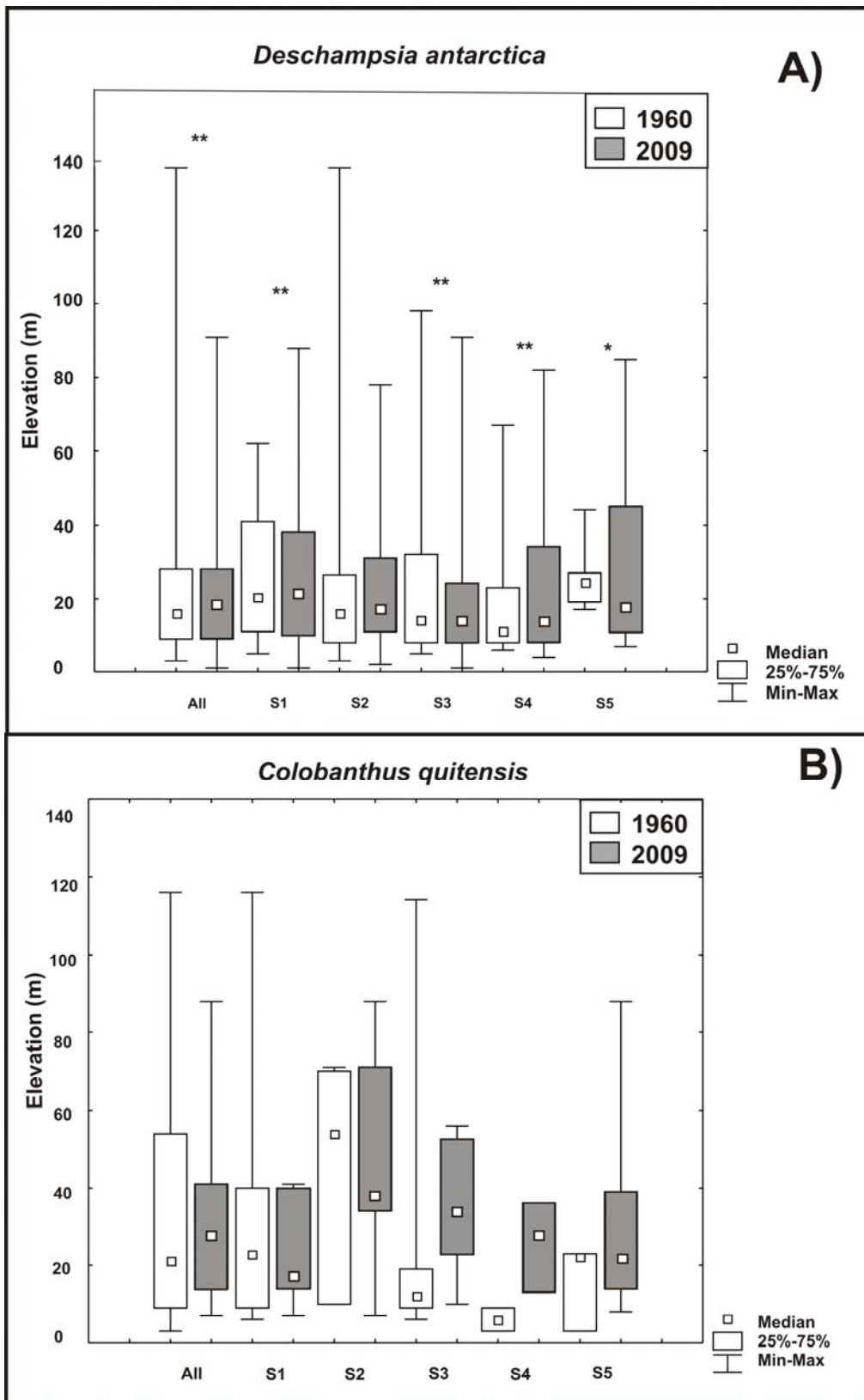
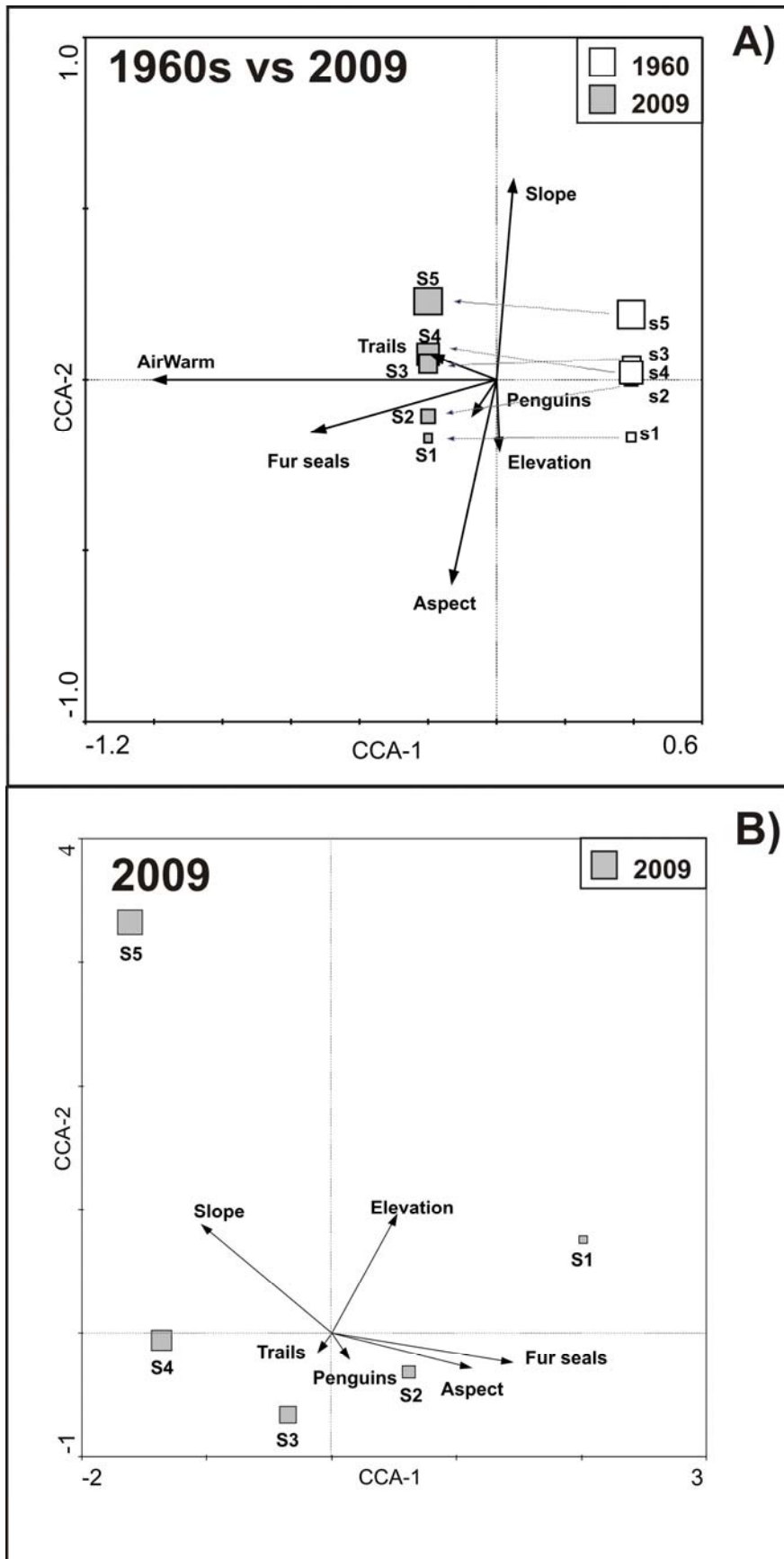


Figure 4



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

<i>Deschampsia antarctica</i>						
Site size	1960s	2009	Δ %	1960s	2009	Δ %
	Number of sites	Number of sites	Number of sites	m ²	m ²	m ²
1 plant (s1)	21	52	+148	0.21	0.52	+147
2-20 plants (s2)	56	49	-13	5.6	4.9	-12.5
>20 plants (s3)	45	139	+209	22.5	69.5	+209
< 10m² (s4)	19	41	+116	95	205	+116
> 10m² (s5)	6	19	+217	300	950	+216
Total	147	300	+104	423.31	1229.92	+191
<i>Colobanthus quitensis</i>						
Site size	1960s	2009	Δ %	1960s	2009	Δ %
	Number of sites	Number of sites	Number of sites	m ²	m ²	m ²
1 cushion (s1)	8	5	-38	0.04	0.025	-38
2-10 cushions (s2)	8	6	-25	0.16	0.12	-25
10-30 cushions (s3)	5	7	+40	0.5	0.7	+40
30-50 cushions (s4)	2	2	0	0.4	0.4	0
>50 cushions (s5)	3	15	+398	1.125	5.6	+398
Total	26	35	+35	2.225	6.845	+208

