

Geographic location, local environment, and individual size mediate the effects of climate warming and neighbors on a benefactor plant

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Declaration of authorship:

WFM conceived the study and JV and MBG set up the experiment. JV monitored the plants and performed data analysis. JV wrote the manuscript with help from WFM and MBG.

1 **Abstract**

2 Predictions of plant responses to global warming frequently ignore biotic interactions and
3 intraspecific variation across geographical ranges. Benefactor species play an important role in
4 plant communities by protecting other taxa from harsh environments, but the combined effects
5 of warming and beneficiary species on their performance have been largely unexamined. We
6 analyzed the joint effects of elevated temperature and neighbor removal on the benefactor plant
7 *Silene acaulis*, in factorial experiments near its low- and high-latitude range limits in Europe.
8 We recorded growth, probability of reproduction and fruit set during three years. The effects of
9 enhanced temperature were positive near the northern limit and negative in the south for some
10 performance measures. This pattern was stronger in the presence of neighbors, possibly due to
11 differential thermal tolerances between *S. acaulis* and beneficiary species in each location.
12 Neighbors generally had a negative or null impact on *S. acaulis*, in agreement with previous
13 reviews of overall effects of plant-plant interactions on benefactors. However, small *S. acaulis*
14 individuals in the north showed higher growth when surrounded by neighbors. Finally, the local
15 habitat within each location influenced some effects of experimental treatments. Overall, we
16 show that plant responses to rising temperatures may strongly depend on their position within
17 the geographic range, and on species interactions. Our results also highlight the need to consider
18 features of the interacting taxa, such as whether they are benefactor species, as well as local-
19 scale environmental variation, to predict the joint effects of global warming and biotic
20 interactions on species and communities.

21

22

23 **Keywords**

24 Arctic-alpine communities; distribution range limits; global warming; plant-plant interactions;
25 stress gradient hypothesis

26 **Introduction**

27

28 Ongoing anthropogenic climate change is significantly affecting plant performance, for example
29 by modifying growth and reproduction (Myneni et al. 1997; Sala et al. 2000; Walther et al.
30 2002) and shifting the geographical ranges of some species (Parmesan and Yohe 2003). Its
31 consequences on populations may differ across a species' range (O'Neill et al. 2008; Doak and
32 Morris 2010), but such intraspecific variation is frequently overlooked in assessments of climate
33 change effects. Another important shortcoming when predicting responses to global warming is
34 the neglect of biotic interactions (Adler et al 2012; Cavieres et al. 2014; Ehrlén and Morris
35 2015; Valladares et al. 2015). Interactions between species can have a profound direct effect on
36 their performance, and also mediate the effects of environmental changes (Davis et al. 1998;
37 Brooker 2006). Moreover, the impact of biotic interactions on the performance of a focal
38 species may also differ across its geographical range (Doxford et al. 2013, Louthan et al. 2018).
39 For example, the stress gradient hypothesis posits that neighboring plants will be competitors at
40 the more benign end of a stress gradient, but benefactors at the more stressful end of the
41 gradient (Bertness and Callaway 1994). This hypothesis was first tested on altitudinal gradients
42 (e.g. Choler et al. 2001; Callaway et al. 2002), but an equivalent gradient across latitude may
43 also influence the joint effect of global warming and biotic interactions on plant performance
44 (Bertness and Ewanchuk 2002; Anthelme et al. 2014). For example, warming could exacerbate
45 competition at more benign low latitudes but reduce abiotic stress and thus facilitation at high
46 latitudes (Klanderud 2005; Klanderud and Totland 2005; Anthelme et al. 2014; but see Cavieres
47 and Sierra-Almeida 2012).

48

49 However, predicting the combined effects of climate warming and neighbors on a focal species
50 at its low- and high-latitude range limits may require us to account for some complicating
51 factors. First, whether interactions with neighbors decrease or increase the performance of a
52 focal species may depend on the ecological role played by that species (Butterfield 2009). While
53 many studies have analyzed the effects of biotic interactions on beneficiary plants (i.e., those

54 that are facilitated by benefactor species; see references in Callaway 2007; Soliveres et al.
55 2015), there is much less information on the consequences of these interactions for benefactors
56 (Bronstein 2009; Schöb et al. 2014), despite their pivotal role in supporting diversity in their
57 communities. The evidence that does exist suggests that the net effects of beneficiary plants on
58 the benefactors are predominantly negative (McIntire 2014; Schöb et al. 2014; Michalet et al.
59 2016; but see García et al. 2016), probably because benefactors are already adapted to stressful
60 conditions and cannot be facilitated by less-adapted neighbors (Butterfield 2009). Another
61 complicating factor is that co-occurring species may respond differently to warming (Gilman et
62 al. 2010), for example if their thermal niches differ. The effects of beneficiary species on the
63 benefactor will thus depend on their relative responses to warming. In Fig. 1, we illustrate some
64 plausible ways these factors could result in complex responses to climate warming across the
65 latitudinal range of a benefactor plant. We assume that plant performance is a unimodal function
66 of temperature, falling off at temperatures both above and below an optimum range, as is often
67 observed (Doak and Morris 2010; Angert et al. 2011; Peterson et al. 2018). The direct effect of
68 global warming (i.e., in the absence of neighbors) would thus be negative at low latitudes (Fig.
69 1 a-c) but positive at high latitudes (Fig. 1 d-f). The presence of neighbors may have an
70 independent effect on performance (Fig. 1 a,d), or it may exacerbate (Fig. 1 b,f) or reverse (Fig.
71 1 c,e) the effects of elevated temperatures. These interactive effects will thus determine whether
72 the net effect of warming in the presence of neighbors is beneficial or detrimental.

73

74 Despite the complexity already apparent in Fig. 1, yet more factors can influence how global
75 warming and species interactions affect plant performance. Species responses may differ
76 depending on the size and ontogenetic phase of the individuals, or the vital rate being
77 considered (Soliveres et al. 2015). For example, younger or smaller plants may be more
78 vulnerable to climate change, but they may also be more likely to benefit from facilitation
79 (Miriti 2006), and García et al (2016) found contrasting effects of species interactions on
80 flowering and fruiting rates of a benefactor plant. Furthermore, in addition to large-scale
81 environmental gradients, variation in local conditions can also alter the effects of global climatic

82 trends (Kennedy 1997; Williams et al. 2008). Several studies have shown contrasting plant
83 responses to temperature or rainfall manipulations, depending on local factors such as soil
84 characteristics, level of grazing, or water stress (Liancourt et al. 2013; Spence et al. 2014;
85 Eskelinen and Harrison 2015; Sharkhuu et al. 2016). Overall, if we want to address plant
86 responses to global warming, we will need to consider the influences of interactive effects of
87 neighbors, species' ecological roles and life cycles, non-linear responses to temperature, and the
88 effects of the local environment across the geographical distribution.

89

90 Factorial experiments are a standard method to assess interactive effects of neighbors and either
91 abiotic (Klanderud 2005; Klanderud and Totland 2005; Rixen and Mulder 2009) or biotic
92 (Louthan et al. 2015) stressors on performance of a focal species. However, to our knowledge,
93 such studies have never been performed simultaneously at both ends of the latitudinal range of a
94 species to better evaluate potential range shifts. Here we report the results of a factorial
95 experiment conducted over three years, in which we combined warming with neighbor removal
96 near both the low- and high-latitude range limits of the benefactor cushion plant *Silene acaulis*
97 (moss campion) in continental Europe. We analyzed the interactive effects of temperature and
98 neighbor presence on plant performance, as well as intraspecific variation in response to these
99 effects due to local environmental heterogeneity and individual size. Moreover, to have a more
100 integrative view of the species' response, we considered effects of warming on both growth and
101 reproduction. We expected overall negative effects of warming on plant performance in the
102 south (where the species may already be near its upper thermal limit), but positive effects in the
103 north (where it may be closer to its lower thermal limit). Given that *S. acaulis* is a benefactor
104 (e.g., Molenda et al. 2012; Aubert et al. 2014), we expected a generally negative effect of
105 neighbor presence in both regions, but recognized that different responses of neighbors to
106 warming relative to that of *S. acaulis* could lead to different outcomes at the two extremes of the
107 latitudinal range.

108

109 **Methods**

110

111 *Study species*

112 *Silene acaulis* (L.) Jacq. (Caryophyllaceae; “moss campion”) is a long-lived perennial plant that
113 forms a low-growing cushion with a single taproot. The species is gynodioecious, with both
114 female and hermaphrodite individuals. Flowers are pollinated by insects. *S. acaulis* is found in
115 arctic and alpine tundra habitats throughout the northern hemisphere (Jones and Richards 1962).
116 In Europe, it is present from the high Arctic to the Pyrenees and the Apennine Mountains. The
117 study species has been found to facilitate the establishment of other species in different
118 boreoalpine habitats in N Europe and N America, although this facilitation effect may vary with
119 individual gender and abiotic stress (Antonsson et al 2009, Molenda et al. 2012, Cranston et al.
120 2012).

121

122 *Location and establishment of the experiment*

123 We conducted factorial experiments at the latitudinal extremes of the distribution of *S. acaulis*
124 in continental Europe to measure the separate and combined effects of elevated temperature and
125 neighbors on individual performance. The northern site, in the Latnjajaure valley in Swedish
126 Lapland (GPS coordinates: 68°21'N, 18°29'E; 1000 m.a.s.l.), has a mean annual temperature of
127 -2.0 °C and mean annual precipitation of 839 mm (Antonsson et al. 2009). The plant community
128 in the Swedish site is mainly composed of circumboreal and boreo-alpine vascular plants (e.g.,
129 *Carex vaginata*, *Festuca ovina*, *Cassiope tetragona*, *Thalictrum alpinum*, *Betula nana*,
130 *Calamagrostis lapponica*), mosses (e.g., *Hylocomium splendens*, *Dicranum groenlandicum*,
131 *Kiaeria starkei*, *Polytrichum juniperinum*) and lichens (e.g., *Cetraria* and *Cladina* species;
132 Molau and Alatalo 1998). The southern site is located in the Aisa valley in the Spanish Pyrenees
133 (GPS coordinates 42°43'N, 0°33'W; 2040-2105 m.a.s.l.). Its closest weather station (Aisa
134 village, ca. 8 km from the study site at 1100 m.a.s.l.) shows a mean annual temperature of 10°C
135 and mean annual precipitation of 1100 mm (García-Ruiz et al 1996). The plant community in
136 the Spanish site is composed of vascular species with different distributions (M.B. García, *pers.*
137 *obs.*; D. Gómez, *pers. comm.*): Mediterranean (e.g., *Koeleria vallesiana*, *Bupleurum*

138 *ranunculoides*, *Galium pyrenaicum*, *Sideritis hyssopifolia*), alpine from southern or central
139 European mountains (e.g., *Festuca gautieri*, *Astragalus sempervirens*, *Anthyllis montana*,
140 *Carduus carlinifolius*), boreoalpine (e.g., *Gentiana verna*) or wider (e.g., *Androsace villosa*).
141 These species have lower altitudinal limits than the boreoalpine *S. acaulis*, most reaching
142 altitudes below 1300 m.a.s.l. (whereas *S. acaulis* rarely occurs below 1800 m.a.s.l.; Atlas of
143 Aragon Flora, <http://floragon.ipe.csic.es/index.php>).

144
145 Local-scale variation in environmental conditions can modify the demography of *S. acaulis* at
146 both high and low latitudes (Morris and Doak 2005; Vilellas et al. 2016). Thus, we located at
147 each site of our study a more mesic area with higher vegetation cover (HC) and a drier area with
148 lower vegetation cover (LC). These two areas were separated from each other by ca. 1 km in
149 both sites. To characterize HC and LC locations, we used a visual estimate of vegetation cover
150 (0-25, 25-50, 50-75 or 75-100% of total vegetation cover). All plots from HC habitats showed a
151 vegetation cover of 75-100%, whereas plots from LC habitats showed a vegetation cover of 25-
152 50%. In each site and habitat, we established permanent plots when the snow melted in 2013
153 (12 plots per habitat in the northern site, and in the southern site, 10 plots LC habitat and 14 in
154 the HC habitat). In half of the plots per site and habitat, we installed hexagonal open-top
155 chambers (OTCs) to increase temperature, leaving the other half at ambient temperature
156 (control). OTCs were constructed following one of the standard designs of the International
157 Tundra Experiment (ITEX; <http://www.geog.ubc.ca/itex/>). Specifically, they had fiberglass
158 walls that admitted sunlight and open tops that admitted precipitation and pollinators, and were
159 2.08 m in diameter at the base and 0.58 m high, with sides inclined at 30 degrees. Control plots
160 had a similar size as OTC plots.

161
162 In each plot, we identified all *S. acaulis* individuals with 20 or more branch tips that were
163 separated by at least 10 cm from conspecifics (we did not consider individuals in the periphery
164 of the chambers to minimize edge effects). Plots contained an average of 9 plants, for a total of
165 422 monitored individuals (218 in Sweden and 204 in Spain) in 48 plots. One half of the plants

166 within each plot were randomly assigned to have all neighboring plants within 10 cm from the
167 edge of the focal plant clipped at the ground level, avoiding damage to *S. acaulis* roots or
168 leaves. Neighboring plants growing within the cushion were also clipped where they emerged
169 from the cushion. Clipping was repeated at the beginning and end of each growing season.
170 Overall, the experiment included on average 53 plants in each of the four treatment
171 combinations (OTC/control crossed with neighbor removal/presence) per site.

172

173 To measure the effect of the OTCs on surface soil temperature, we buried a small temperature
174 logger (iButton; [https://www.maximintegrated.com/en/products/digital/data-](https://www.maximintegrated.com/en/products/digital/data-loggers/DS1921G.html)
175 [loggers/DS1921G.html](https://www.maximintegrated.com/en/products/digital/data-loggers/DS1921G.html)) enclosed in a waterproof plastic vial just below the ground surface in 5
176 OTC and 5 control plots in each habitat in each site. iButtons registered temperature every 4 hr
177 during three growing seasons (from late June to September in the Spain site, and from early July
178 to late August in the Sweden site). At the end of the experiment, mean daily temperature during
179 the growing season was found to be significantly higher in OTC than in control plots, according
180 to a linear model including warming treatment, site, habitat, and year as fixed main effects (*lm*
181 function, *stats* package, R Core Team 2017; $t = 4.31$, $p < 0.001$). OTCs increased temperature
182 by 1.0 ± 0.08 °C (mean \pm standard error) in Spain and 0.5 ± 0.21 °C in Sweden. We verified
183 with likelihood ratio tests (*anova* function, *stats* package, R) that the addition of interactions
184 between the warming treatment and either site ($p = 0.154$) or habitat ($p = 0.496$) did not
185 significantly improve the fit of the model. The increase in air temperature just above ground is
186 probably higher than the 0.5-1 °C we observed just below the ground surface, and lies at the low
187 end of the range of air temperature increases obtained in previous OTC studies (Marion et al.
188 1997). OTCs were taken down during winter in Spain due to a high exposure to wind but were
189 left in place in Sweden. Three (out of 12) OTCs in Spain were damaged after the first growing
190 season and were not replaced for the following years (plants from those plots were thus only
191 sampled in the first growing period).

192

193 *Plant measurements*

194 When we established the plots at the beginning of the first growing season, we marked each
195 plant with a colored plastic toothpick. We also determined the area of their cushions (by
196 measuring the major and minor axes, using the formula for an ellipse, and subtracting the area
197 of that ellipse that was not living plant tissue; cf. Doak and Morris 2010). At the end of the
198 growing season (late August – September) in 2013, 2014, and 2015, we recorded which plants
199 were still alive, and, for live plants, the cushion area and the number of fruits produced that
200 season.

201

202 We measured the effects of the OTC and neighbor removal treatments on three response
203 variables: growth in size from the start to the end of the experiment, whether a plant produced
204 fruits or not in a given year, and the number of fruits per cm² of cushion area per year
205 (conditional on producing fruits). To reduce the impact of measurement error on our assessment
206 of growth, we treated growth as a binary variable and considered any plant that increased in area
207 by 5% or more to have grown. We assessed growth over the entire three year period because
208 these tundra plants grow slowly. We only analyzed probability of reproduction and fruit
209 production on female individuals, because hermaphrodites produced on average only one fifth
210 as many fruits per unit area as did females (cf. Morris and Doak 1998), and showed no clear
211 response to the warming or neighbor removal treatments in preliminary analyses. Across the
212 two sites, an average of 90% of the plants survived to the end of the experiment, so we had little
213 power to detect treatment effects on survival, and did not assess them.

214

215 *Analyses of plant performance*

216 We tested for effects of warming and neighbor removal treatments on plant performance in each
217 site using generalized linear mixed models (GLMMs). The error distribution was set as
218 binomial for the probability of growth and the probability of reproduction, and normal for
219 number of fruits per unit area (hereafter “fecundity”). We constructed for each performance
220 measure a full model with the fixed effects of: 1) warming treatment (control vs elevated
221 temperature); 2) neighbor removal treatment (neighbors / no neighbors); 3) habitat (lower vs

222 higher vegetation cover); 4) focal plant size (log-transformed); and 5) two-way interactions
223 between warming and neighbor treatments, and between each of them and both habitat and plant
224 size (Table 1). Plant size was included in the analyses to avoid possible confounding effects,
225 since cushions were larger in Spain (mean area = 226.67 cm²; SE = 22.46 cm²) than in Sweden
226 (mean area = 189.64 cm²; SE = 17.35 cm²). There were no differences in mean plant size
227 between habitats within each site. More complex models with three-way interactions did not
228 show additional significant effects in a preliminary analysis, and are not shown. In the analyses
229 of growth and reproduction, the full model also included a random effect of plot, but there were
230 not enough reproductive individuals per plot to include a random effect of plot on fecundity.
231 Additionally, in the analyses of reproduction and fecundity, the full model included a fixed
232 effect of year and a random effect of individual.

233

234 To test the effects of warming and neighbor treatments, either alone or through interactions, we
235 compared for each site and performance measure the full models with all possible models
236 including subsets of the predictors (*MuMIn* package, R). Specifically, we searched for the model
237 that provided the best fit to the data using the Akaike Information Criteria corrected for finite
238 sample sizes (AICc; Burnham and Anderson 2003; Johnson and Omland 2004). When warming
239 or neighbor removal treatments showed significant interactions with habitat in the optimum
240 model, we repeated the analyses for each habitat separately. To evaluate the consistency of the
241 best models, we selected the set of competing models with ΔAICc values < 2 . We then
242 calculated the weight for each effect in the full model, by summing the Akaike weights of the
243 competing models in which they appear (Burnham and Anderson 2003). The weight for each
244 effect can go from 1 (present in the best model and all the competing models) to 0 (not present
245 in any model), and was used to compare the importance of the effects appearing in the best
246 model to those not included. Finally, we calculated least-squares means of performance traits
247 for warming and neighbor removal treatments (*lsmeans* function, *lsmeans* package, R).

248

249 **Results**

250

251 *Plant responses in Spain*

252 At the low-latitude site, the warming treatment had different effects on *S. acaulis* depending on
253 the measure of plant performance, whereas the effect of neighbor presence was always negative
254 or null (Fig. 2a-d, 3a-b). The effect of warming on growth differed between habitats (as
255 indicated by the Warming \times Habitat interaction in the best model; Table 1): warming decreased
256 growth in the habitat with low vegetation cover, but had no effect in the habitat with high
257 vegetation cover (Fig. 2a-b). The impact of warming on the probability of reproduction
258 depended on the neighbor removal treatment (Warming \times Neighbor interaction; Table 1),
259 turning from a positive effect in the absence of immediate neighbors to a negative effect in the
260 presence of immediate neighbors (Fig. 2c). The impact of warming on the probability of
261 reproduction also depended on plant size (Warming \times Plant size interaction), and was negative
262 on small plants and weakly positive on large plants (Fig. 3a). Finally, the warming treatment did
263 not have any significant effect on fecundity (Fig. 2d). There was a negative effect of neighbor
264 presence on fecundity, which was more pronounced in the largest plants (Neighbor removal \times
265 Plant size interaction; Fig. 3c).

266

267 *Plant responses in Sweden*

268 At the high-latitude site, the effect of warming on *S. acaulis* also differed depending on the
269 performance measure and other factors (Fig. 2e-h). Warming had a positive effect on growth,
270 although the effect was weaker in the absence than in the presence of neighbors (Fig. 2e;
271 Warming \times Neighbor interaction, Table 1). Reproduction was unaffected by the warming
272 treatment (Fig. 2f). The effect of warming on fruit production was different depending on the
273 habitat (Warming \times Habitat interaction; Table 1): warming had a positive effect in the habitat
274 with high vegetation cover (Fig. 2h), but exerted no significant effect where vegetation cover
275 was low (Fig. 2g). The effect of neighbor presence was generally null or negative (Figs. 2e-h,
276 3b,d). Reproduction was affected by an interaction between neighbors and plant size, in which
277 neighbor presence was negative for smaller plants but had no effect on larger plants (Fig. 3d).

278 However, neighbors did have a positive effect on growth of small individuals (Fig. 3b; see
279 Neighbor \times Plant size interactions in the best model in Table 1).

280

281 *Consistency of best models*

282 Results were in general very consistent across the set of competing models. In fact, the factors
283 found in the best models had an average weight of 0.92 of a possible 1.0 (Table 1), and showed
284 no important qualitative changes in their effects across competing models (Online Resource 1).

285 In contrast, the effects that were missing from the best model but which were present in any of
286 the other competing models showed on average a weight of 0.30, and always showed

287 confidence intervals overlapping zero. The estimates of the effects and *p*-values from the best
288 model in each set of analyses are also provided for further information (Online Resource 2).

289

290 **Discussion**

291

292 In our study, we addressed a critical gap in global warming studies by assessing experimentally
293 how increased temperature and species interactions will jointly affect plant performance across
294 a species' geographical range. We also aimed to shed light on the less studied effects of plant-
295 plant interactions on benefactors. The effects of experimental warming on the benefactor
296 cushion plant *S. acaulis* were positive at the northern limit and negative at the southern limit for
297 some performance measures, although this pattern was stronger in the presence than in the
298 absence of neighbors (Fig. 2c,e). In contrast, the effects of neighbors were in general negative or
299 null both in the northern and southern locations. Finally, the effects of warming and neighbors
300 also varied with the local habitat and the size of the cushion. Our study thus shows some general
301 patterns regarding the overall response of a benefactor plant to warming and biotic interactions,
302 but also highlights the influence of additional individual-level and environmental factors on the
303 consequences of these drivers.

304

305 The finding that warming had in general more negative effects in the southern location of this
306 boreoalpine plant supports our hypothesis that southern populations are already experiencing
307 ambient temperatures close to the species' upper thermal tolerance. In contrast, northern
308 populations are exposed to colder temperatures, and experimental warming seems to improve
309 some of their performance measures by ameliorating the thermal conditions they experience.
310 Similarly, previous studies have predicted population declines at the southern limit for this
311 (Doak and Morris 2010) and other (Lesica and McCune 2004) boreoalpine species if warming
312 persists, whereas positive effects of enhanced temperature on *S. acaulis* have been found near
313 the northern range edge (Alatalo and Totland 1997; but see Alatalo and Little 2014). However,
314 the expected effects of warming in our experiment changed in some cases depending on the
315 local conditions. In the southern location, the negative effect of enhanced temperature on
316 growth disappeared in the local habitat with higher vegetation cover. The higher abundance of
317 vegetation in the local community could have created or reflected more mesic and sheltered
318 conditions that would allow *S. acaulis* to better cope with thermal stress. This suggests that the
319 species thermal tolerance may be higher for some performance measures, such as growth, as
320 long as water is abundant. Conversely, in the northern population, fruit production was not
321 positively affected by warming when vegetation cover was low (Fig. 2g). Possibly, reduced
322 water availability with higher temperatures hampers reproduction in such exposed conditions.
323 OTCs could also partially alter water availability through rain exclusion or dew increase
324 (Marion et al. 1997), although the large top of chambers used and belowground water diffusion
325 probably minimize these effects. Soil water content - and how warming affects it - may be key
326 for predicting species responses to global change (e.g., Giménez-Benavides et al. 2017), but
327 such local effects should be confirmed by monitoring replicated habitats with controlled high
328 and low water availability. Contrasting effects of experimental warming across local conditions
329 have also been found in other plants in cold biomes (Liancourt et al. 2013; Spence et al. 2014;
330 Sharkhuu et al. 2016), highlighting the relevance of fine-scale environmental information for
331 evaluating species performance in these ecosystems.

332

333 The general pattern of positive effects of warming in the north and negative effects in the south
334 was stronger when *S. acaulis* was surrounded by neighbors, indicating that the consequences of
335 global warming and species interactions should not be evaluated alone (see also Davis et al.
336 1998; Brooker 2006; Cavieres et al. 2014). In our southern location, even though warming had a
337 positive direct effect on reproduction, its net effect was negative when neighbors were present
338 (Fig. 2c). This might be explained by a differential response to warming between the
339 boreoalpine *S. acaulis* and some surrounding taxa with more Mediterranean or southern alpine
340 distributions. For example, lower-altitude Poaceae and Fabaceae species may have benefitted
341 more than the focal species from higher temperatures and become more competitive, a process
342 known as thermophilization (Gottfried et al. 2012). The second interaction between warming
343 and neighbor effects was found in the northern location, where the negative effect of neighbor
344 competition on *S. acaulis* growth found under ambient temperature disappeared with warming.
345 Mosses, which are abundant in this area (Molau and Alatalo 1998; J. Vilellas, *pers. obs*), have
346 been reported to suffer negative consequences of increased temperatures in previous
347 experiments (Alatalo 1998, Hobbie et al 1999). If this phenomenon also took place in our
348 warmed plots, a diminished competitive ability in mosses (or in other species with similar
349 thermal tolerances) could explain the observed positive consequences for *S. acaulis*. This
350 decrease in competition with an amelioration of the environment seems to contrast with
351 expectations from the stress-gradient hypothesis and results from most previous studies
352 (Shevtsova et al 1997; Klanderud 2005; Klanderud and Totland 2005; Rixen and Mulder 2009;
353 but see Hobbie et al 1999; Cavieres and Sierra-Alemida 2012). However, this contrast is only
354 apparent, since warming would not constitute an amelioration of the environment for mosses,
355 only for *S. acaulis*. Our results in both southern and northern locations suggest that the joint
356 effects of warming and biotic interactions may depend on the relative thermal tolerances of the
357 interacting taxa (Hobbie et al 1999, Gilman et al. 2010). This could be particularly relevant
358 when co-occurring species are located in different parts of their respective geographical
359 distributions (e.g., central vs. peripheral; Brooker 2006). However, factorial experiments

360 analyzing the abundance and performance of both beneficiary and benefactor plants across
361 ranges will be needed to confirm this hypothesis.

362

363 Irrespective of warming treatment, the effect of neighbor presence was in general negative or
364 null both in the northern and southern localities, as we had expected for a benefactor cushion
365 plant. Moreover, for some performance measures, the effect of neighbors was more negative in
366 the local habitats with higher vegetation cover (Fig. 2a-b, g-h), probably because those
367 neighbors were also more abundant in HC than in LC habitats. Although both negative and
368 positive effects of beneficiary species on benefactors may be found (Cranston et al. 2012;
369 McIntire 2014), the net effects have been predominantly negative in previous studies (McIntire
370 2014; Schöb et al. 2014; Michalet et al. 2016). Our results thus support the view that community
371 role (being a benefactor) may be more important for the outcome of species interactions than
372 environmental conditions (Soliveres et al. 2015). In our study, we focused on the overall effects
373 of the beneficiary community on *S. acaulis*, and we assumed that this community included both
374 plants within *S. acaulis* cushions and those growing within a radius of 10 cm around. In the
375 future, additional experiments differentiating both types of neighbors would help to define in
376 more detail the components of the beneficiary community.

377

378 Individual plant size modified the effect of neighbors on *S. acaulis*, in agreement with previous
379 studies in both benefactor and beneficiary plants (Escudero et al. 2005; le Roux et al. 2013;
380 Nuche and Alados 2017). In fact, the only positive effect of neighbor presence found on *S.*
381 *acaulis* was on growth of small individuals in the northern location. When an interaction
382 between neighbors and plant size was detected in our study, the effect of neighbors was in
383 general more negative for larger plants (Fig. 3 b,c), possibly because they host a larger and more
384 diverse set of species within their cushions and thus receive more competition. However, in the
385 case of probability of reproduction in Sweden, the effect of neighbor presence was less harmful
386 in the largest plants (Fig. 3d). Competition may be counterbalanced by a higher attraction of
387 pollinators due to a higher flower abundance in the immediate vicinity, increasing the

388 probability of reproduction in a region where insect presence is probably lower than in the
389 south. Facilitation through pollinator attraction has been reported in other plant communities
390 (Hunter and Aarssen 1988; Ghazoul 2006).

391

392 That warming and neighbors do not always have consistent effects on growth and reproduction
393 highlights the importance of considering multiple demographic rates to evaluate plant responses
394 to global warming and biotic interactions (Arft et al. 1999; Goldberg et al. 1999). Maestre et al.
395 (2005) found that both the outcome of plant interactions and the effect of abiotic stress on that
396 outcome depended on the measure of performance. Contrasting responses of a benefactor plant
397 to species interactions have even been found for closely related reproductive measures, such as
398 flowering and fruiting rates (García et al 2016). In our experiment, the responses of growth and
399 reproduction differed not only across treatments, but also across habitats and plant sizes. As a
400 next step, population models that integrate the effects of the different vital rates (growth,
401 survival, reproduction and recruitment) will be needed to assess responses of the population
402 growth rate to biotic and abiotic drivers. For example, population models could help to evaluate
403 if the generally more negative effects of warming found in the southern location of *S. acaulis*,
404 especially in the presence of neighbors, will lead to a contraction at the species' southern range
405 margin in Europe, as has been suggested may occur in North America (Doak and Morris 2010).

406

407 In conclusion, the different patterns found in *S. acaulis* near the southern and northern limits
408 show that plant responses to rising temperatures may strongly depend on the location of
409 populations within species' ranges, but also on the influence of biotic interactions. We thus
410 advocate for refining predictions of global warming effects on plant performance by including
411 information both on species interrelations and geographic variation among populations, as
412 suggested previously (O'Neill et al. 2008; Ehrlén and Morris 2015; Valladares et al. 2015). Our
413 results also highlight the importance of the ecological roles of species for plant-plant
414 interactions. To our knowledge, this is the first study evaluating feedback effects of beneficiary
415 species in the southern and northern range limits of a benefactor, and the predominantly

416 negative impact detected agrees with previous reviews (Schöb et al. 2014). Finally, we found
417 that additional factors, such as local-scale variation in environmental conditions, the size of
418 individuals or the chosen measure of performance, influenced the results of our experiment.
419 Overall, understanding the joint effects of global warming and species interactions on plant
420 performance seems to be more complicated than choosing one of the possible scenarios
421 proposed in the initial conceptual figure (Fig. 1), and will require integrative approaches that
422 consider geographic, environmental and species-specific factors.

423

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431

432 **Conflict of interest**

433 The authors declare that they have no conflict of interest.

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627 **Figure legends**

628

629 **Fig. 1** Predicted combined effects of warming and neighbors on performance in a benefactor
630 cushion plant (other outcomes are possible). Neighbors are assumed to be competitors at
631 ambient temperature. In panels a-c), ambient temperature is at or above the optimum
632 temperature for the focal species (as might be typical near the low-latitude range limit). a)
633 Warming and neighbors decrease performance independently. b) Warming has direct negative
634 effects, which are exacerbated by the presence of neighbors (if they benefit from warming). c)
635 Warming has direct negative effects, but neighbor presence is only negative at ambient
636 temperature (if neighbors are more negatively affected by warming than the benefactor). In
637 panels d-f), ambient temperature is below the optimum temperature for the focal species (as
638 might be typical near the high-latitude range limit). d) Independent effects from warming
639 (positive) and neighbor presence (negative). e) Warming is beneficial in isolation, but the effect
640 is reversed in the presence of neighbors (competition is exacerbated due to more positive effects
641 of warming on neighbors than on the benefactor). f) Benefit from warming is enhanced by the
642 presence of neighbors (competition disappears if warming is less beneficial for neighbors than
643 for the benefactor). Color version of this figure is available online

644

645 **Fig. 2** Combined effects of warming and neighbor treatments on *Silene acaulis* performance in
646 Spain (left panels) and Sweden (right panels), according to best models. The three measures of
647 performance are a, b, e) probability of growing (% growth), c, f) probability of fruiting (%
648 reproduction;), and d, g, h) fruit production per unit area conditional on reproducing (Fruits cm⁻²).
649 Plant performance at ambient (grey) and elevated (red) temperature is compared both in the
650 absence and presence of neighbors. Bars represent least-squares means \pm standard errors,
651 maintaining the other factors present in the best models constant. Significant effects of warming
652 treatment (WT), neighbor treatment (NT), plant size (SZ), or the interactions among them
653 (WT \times NT, WT \times SZ, NT \times SZ; see also Fig. 3), are indicated at the top-right corners of the panels.
654 When there is a significant interaction between habitat and either warming or neighbor

655 treatments (Table 1), plant performance is displayed separately for habitats with low (LC) and
656 high (HC) vegetation cover (a-b, g-h). Color version of this figure is available online
657

658 **Fig. 3** Combined effects of plant size and either warming or neighbor treatments on the
659 performance measures of *Silene acaulis*, according to best models. Plant performance is shown
660 for ambient (grey) and elevated (red) temperatures, or in the absence (grey) or presence (green)
661 of neighbors. Bars represent least-squares means (\pm standard errors) for individuals of the 0.05
662 (small), 0.5 (medium) and 0.95 (large) quantiles of the size distribution in each analysis,
663 maintaining the other factors present in the best models constant. Results are shown for Spain
664 (left panels) and Sweden (right panels). Color version of this figure is available online

Tables

Table 1. Full model for testing the effects of warming (WT) and neighbor (NT) treatments on three performance measures, and best model for each measure at each site according to the Akaike Information Criteria for limited sample sizes (AICc). The additional effects of habitat (HB), cushion size (SZ) and year (YR; only for reproduction and fecundity), and the two-way interactions of either WT or NT with HB or SZ, are also considered. The Akaike weight for each effect across competing models is shown in parentheses (see Methods for details). Additional analyses for LC and HC habitats separately are shown when WT or NT present significant interactions with habitat in main model

Performance		
measure	Site	Predictors
-	-	Full model: Performance ~ WT + NT + HB + SZ + YR + WT×NT + WT×HB + NT×HB + WT×SZ + NT×SZ
Growth	Spain	WT(0.84) + NT(1) + HB(1) + WT×HB(0.84) + NT×HB(1)
	Spain (LC)	WT(0.71)
	Spain (HC)	NT(1) + SZ(1)
	Sweden	WT(1) + NT(0.82) + HB(1) + SZ(1) + WT×NT(0.82) + NT×SZ(0.64)
Reproduction	Spain	WT(1) + NT(1) + SZ(1) + YR(1) + WT×NT(1) + WT×SZ(1)
	Sweden	NT(1) + SZ(1) + YR(1) + NT×SZ(0.72)
Fecundity	Spain	NT(1) + SZ(1) + YR(1) + NT×SZ(0.75)
	Sweden	WT(0.73) + NT(0.83) + HB(1) + SZ(1) + YR(1) + WT×HB(0.73) + NT×HB(0.83)
	Sweden (LC)	YR(1)
	Sweden (HC)	WT(0.81) + NT(1) + SZ(0.81) + YR(1)

Figures

Figure 1

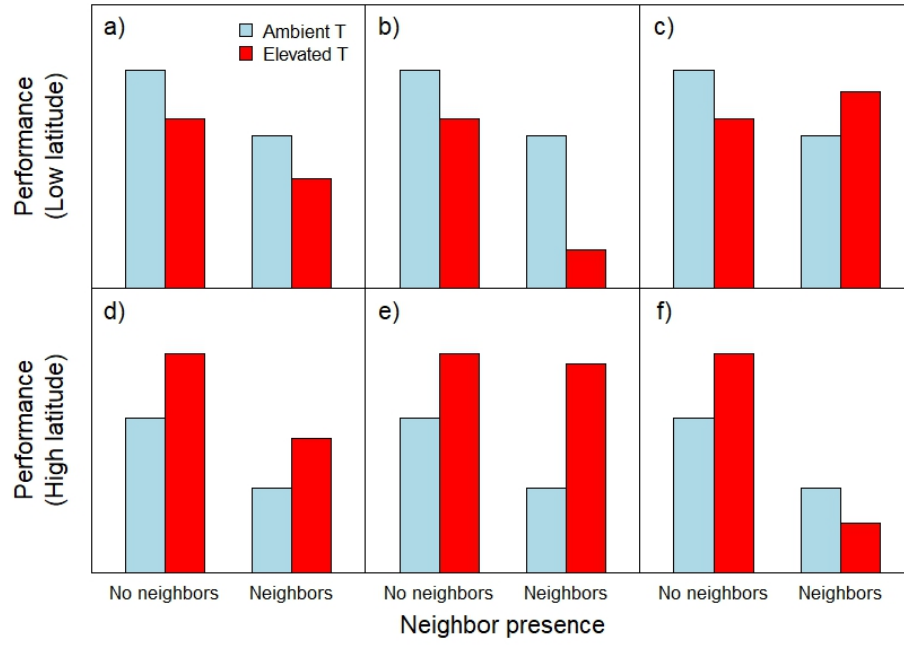


Figure 2

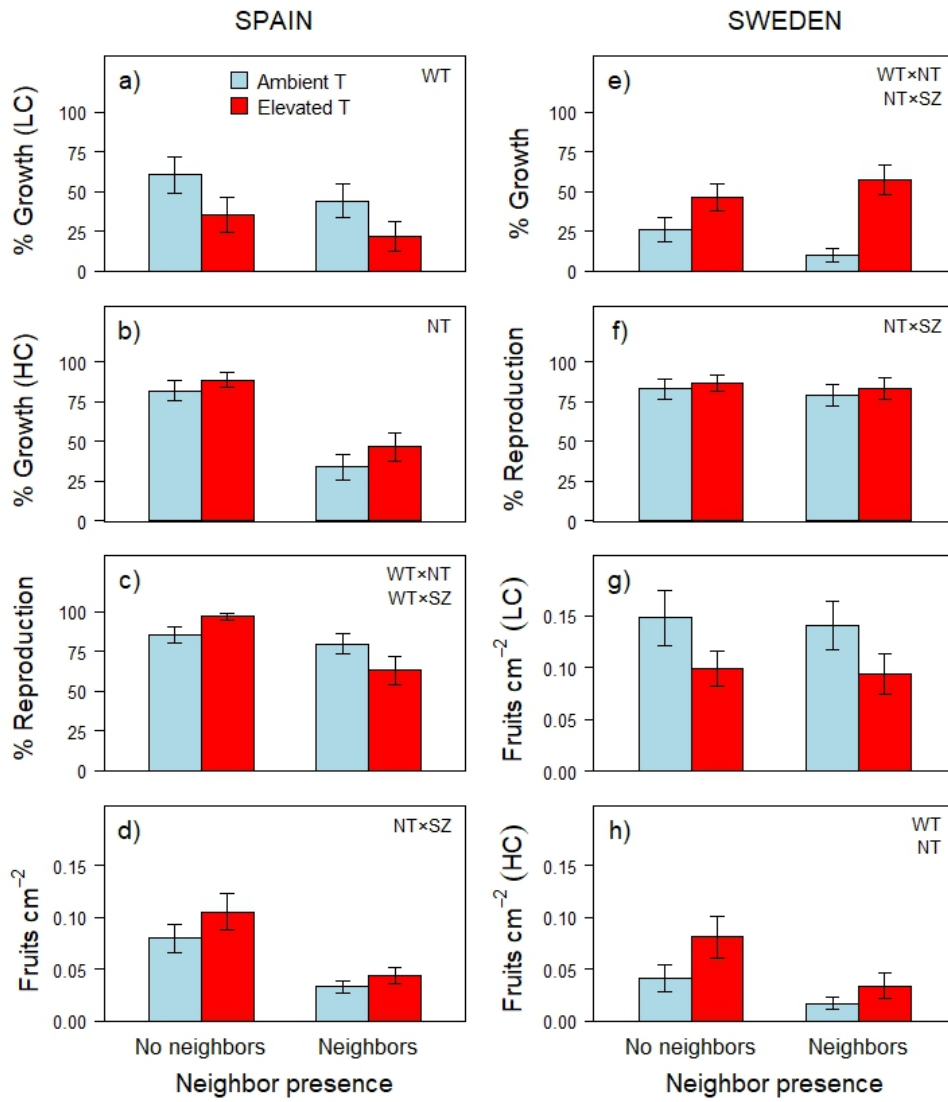


Figure 3

