

1 **Functional traits, not productivity, predict alpine plant**
2 **community openness to seedling recruitment under climatic**
3 **warming**

4

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23 **Abstract:**

24 Understanding the degree to which plant communities are open to seedling recruitment is key
25 to predicting how they will be impacted by climate change. We experimentally assessed
26 whether communities assembled under colder climates were inherently more open to
27 recruitment than warmer-climate communities, after controlling for differences in the current
28 climate under which the communities were growing. We then tested whether variation in
29 openness to recruitment could be explained by community biomass or by the plant functional
30 traits of the community.

31 The study was conducted in a climate grid of twelve grassland sites across
32 southern Norway, differing systematically in temperature and precipitation. Along a 2000 mm
33 precipitation gradient, we transplanted turfs with intact plant communities from alpine and
34 sub-alpine sites into 2°C warmer sites, and measured natural seedling emergence in these
35 transplanted turfs vs. locally replanted control turfs at the transplant destination sites. Mixed
36 effect models were used to assess the effect of origin (cold vs warm climate), biomass, and
37 functional trait composition of the communities on seedling emergence. We further assessed
38 variation in these effects across different climatic contexts (the temperature and precipitation
39 gradients).

40 Communities originating from colder climates were consistently more open to
41 recruitment, with on average 44% more seedlings emerging, than the locally replanted control
42 communities. The higher rates of seedling emergence in colder-climate communities were
43 attributable to systematic differences in plant functional traits, but not in biomass. The colder-
44 climate communities were composed of species with smaller leaves and lower maximum
45 plant heights; traits that may make these communities less effective at excluding new recruits.
46 These trait-related responses were not significant in the warmest sites and did not vary across
47 the precipitation gradient.

48 Our results suggest that alpine species lack the competitive effect traits required
49 to make their communities resistant to invasion by novel competitors under climate change.

50

51 **Introduction:**

52 Seedling recruitment is an important process in the life cycle of plants, being a key
53 determinant of population dynamics, rates of community turnover, and species range
54 dynamics (Tilman 1997, Walck et al. 2011). Rates of seedling recruitment hence affect
55 diversity across scale, from intraspecific variability to community patterns to regional species
56 pools. The rates of natural seedling recruitment in plant communities are controlled by both
57 abiotic conditions such as temperature and precipitation (Meineri et al. 2013, Klanderud et al.
58 2017), and by biotic characteristics of the community such as vegetation density and biomass
59 (Milbau et al. 2013, Klanderud et al. 2017, Frei et al. 2018). Biotic control of seedling
60 recruitment is typically assessed through seed sowing experiments in intact vegetation vs.
61 vegetation removal plots. While experimentally removing biomass often leads to higher
62 recruitment rates (Klanderud and Totland 2007, Milbau et al. 2013, Frei et al. 2018), we do
63 not know if smaller-magnitude natural variation in community biomass, such as observed
64 along elevation gradients in response to decreasing temperature (Bloor et al. 2010, Kardol et
65 al. 2010, Klanderud et al. 2015), would be sufficient to render alpine communities more open
66 to seedling recruitment than their warmer-climate sub-alpine or boreal counterparts.
67 Understanding the role of such more subtle changes in community biomass is critical for
68 understanding how climate-related variation in biotic filtering will affect community
69 dynamics under climate change.

70 In parallel with biomass changes, the functional composition of vegetation also
71 varies along bioclimatic gradients. In particular, plant functional traits related to competition
72 for light, such as maximum plant height (Westoby 1998, Westoby et al. 2002), leaf area and
73 specific leaf area (SLA) (Grotkopp et al. 2002, Grotkopp and Rejmánek 2007, Gallagher et al.
74 2015) all decrease towards colder, alpine climates (Dubuis et al. 2013, Guittar et al. 2016).
75 This suggests a potential alternative driver of variation in natural seedling recruitment rates

76 along elevation gradients, where the functional composition of the resident vegetation limits
77 seedling recruitment towards warmer climates (i.e. the “effect traits” of the vegetation, *sensu*
78 Suding et al. 2008). Note that this potential role of functional traits in affecting recruitment
79 through controlling the competitive effects of the extant community, and hence it’s openness
80 to recruitment, is different from the more common “response traits” framework approach
81 which explores how the traits of the colonizing species affects their ability to recruit into new
82 sites (e.g. Dolezal et al. 2016, Dolezal et al. 2018). Until now, very few studies have used
83 functional trait-based approaches to explore the role of community effect traits in controlling
84 variation in seedling recruitment rates across communities (but see Blonder et al. 2018).

85 In this study, we ask if colder-climate alpine or sub-alpine communities are
86 inherently more open to recruitment than warmer-climate sub-alpine or boreal communities,
87 respectively. We use an “effect traits” framework to investigate the extent to which
88 differences in community openness to recruitment are related to plant community biomass
89 and/or to the functional trait composition of the extant vegetation. These are important
90 questions in a climate change context because higher inherent community openness of colder-
91 climate communities would translate into lower biotic resistance to colonization from
92 warmer-climate species, and hence potentially higher and faster onset of negative impacts
93 from novel competitors (Alexander et al. 2015). Because community characteristics such as
94 biomass and mean trait values associate with climate (Wright et al. 2005, McGill et al. 2006,
95 Violle et al. 2007), it is non-trivial to disentangle their effects from the direct effects of
96 climate on recruitment (e.g., through variation in seed availability or germination). To solve
97 this, we performed a whole-community transplant experiment where intact grassland
98 vegetation turfs (25 x 25 cm) were moved from alpine and sub-alpine sites to sub-alpine and
99 boreal sites, respectively, resulting in a ca. 2°C experimental warming treatment (Fig 1). The
100 transplanted colder-climate ‘foreign’ communities and their paired locally replanted control

101 communities thus differ in the climate under which they assembled, and hence in vegetation
102 structure and trait characteristics (Guittar et al. 2016), but were exposed to the same climates
103 and other biotic and abiotic site conditions during the experimental trials.

104 We thus compared community openness to recruitment between paired higher-
105 elevation plant communities transplanted to warmer climate and locally replanted control
106 plant communities two years after transplantation. Community openness to recruitment was
107 approximated by quantifying natural seedling emergence in each turf, which captures the first
108 step in the seedling recruitment process. By focusing on the first and critical step in the
109 seedling recruitment process (Graae et al. 2011, Guittar et al. in review), we isolate variation
110 in and drivers of colonization success *per se*, and avoid confounding this event with later life-
111 history stages such as differential survival due to the various processes operating on the
112 already-emerged seedlings (plant-plant interactions, predation, etc.). As such, our study tests
113 the biotic resistance of higher-elevation biodiversity to colonization by seed in the face of
114 climate change. The transplant experiment was performed under two temperature regimes;
115 alpine-to-sub-alpine transplants and sub-alpine-to-boreal transplants (Fig. 1), each replicated
116 under four precipitation levels (ca. 600 – 2700 mm of annual precipitation) allowing
117 assessment of climate context-dependencies and hence the degree of generality of responses.

118 Specifically, we ask:

- 119 1. Does community openness to recruitment vary systematically along climatic
120 gradients?
- 121 2. Do community biomass and functional trait composition vary along climatic
122 gradients? If so, do these differences in biotic characteristics remains after placing
123 colder- and warmer-climate communities under similar climatic conditions?
- 124 3. If such climatically driven differences in community openness to recruitment exist, are
125 they associated with differences in community biomass and/or with differences in

126 community functional trait composition between the colder-adapted and the warmer-
127 adapted communities?

128 4. Are there climatic context-dependencies in these associations along temperature
129 and/or precipitation gradients?

130 We hypothesize greater community openness to recruitment in colder-climate communities
131 because of lower vascular plant biomass and/or dominance by species that have traits that
132 render them poorer competitors for light.

133

134 **Material and methods**

135 **Study design**

136 We used twelve calcareous grassland sites in southern Norway, situated in a climate ‘grid’
137 where three levels of summer temperature (alpine ca 7.5°C; sub-alpine ca 9.5°C; boreal ca
138 11.5°C) are replicated across four levels of annual precipitation (1 = continental ca 600 mm; 2
139 = sub-continental ca 1200 mm; 3 = sub-oceanic ca 2000 mm; 4 = oceanic ca 2700 mm). The
140 climatic grid was designed using interpolated data from the normal period 1961-1990 at a
141 resolution of 100 m (Norwegian Meteorological Institute, www.met.no).

142 We selected the sites to keep vegetation type, bedrock, slope, aspect, land-use
143 regime and history as constant as possible across sites. All sites were fenced to avoid animal
144 disturbance, but mowed at the end of each growing season to mimic a standardized grazing
145 regime (see Klanderud et al. 2015 for additional informations). All the plant communities
146 were within the phytosociological association *Potentillo-Festucetum ovinae* in the alpine,
147 tending towards *Potentillo-Polygonum vivipari*, and in some lowland sites tending towards
148 *Nardo-Agrostion tenuis* (Fremstad 1997, Meineri et al. 2013, Klanderud et al. 2015).

149 Within each site, we selected five replicate blocks within a patch of the target
150 grassland. Within each block, two 25*25 cm² plots were assigned randomly to the two
151 treatments. The two turfs were cut and dug out to a depth of 5 to 10 cm, depending on the
152 rooting depth. One of the cut turfs was replanted at the same site and the other was
153 transplanted into a site one level warmer at the same precipitation level in the climate grid. At
154 each site and block, the analyses described below contrast locally replanted turfs (hereafter
155 warmer-climate communities or controls) vs. transplanted turfs originating from a colder
156 climate (hereafter colder-climate communities or transplants) two years after transplantation.
157 The two-year delay between transplantation and data collection removes any effects of
158 differences in current climate or other site-level factors between the control and transplanted
159 communities. The experiment thus explicitly quantifies the openness to recruitment of
160 communities that were assembled under a colder relative to a warmer climate, while
161 controlling for the current climate and other abiotic conditions during the experimental trial
162 (Fig. 1). A total of 80 transplanted and locally replanted turfs were used in the study, which is
163 part of a larger experiment that also contained intact control plots (i.e., not dug out and
164 replanted) as a control of the transplantation treatment *per se*. Preliminary analyses showed
165 that community openness to recruitment (see below) was slightly higher in locally replanted
166 controls than in these untouched plots (mixed effect linear models nested on block within site,
167 p.value=0.048) for the main effect of plot replanting. We therefore used the locally replanted
168 plots as controls for the remainder of this study to eliminate any effects of the transplantation
169 process itself.

170 The species richness of vascular plants recorded within the turfs ranged from 10
171 to 40 species, with a mean canopy height of 9 ±6 cm (SD) (Guittar et al. 2016).

172

173 **Seedling counts and vegetation sampling**

174 We used the total number of naturally occurring dicotyledonous seedlings emerging within
175 each turf as a measure of community openness to recruitment. We excluded graminoids
176 because of difficulties in distinguishing monocotyledonous seedlings from clonal offshoots. In
177 2011, we counted all dicotyledonous seedlings with visible cotyledons in each turf. The
178 survey was conducted at peak growing season, which is in the two first weeks of August at
179 these sites. This timing of the census enabled a fairly comprehensive index of total dicot
180 emergence, but with the trade-off that many of the seedlings were not yet identifiable to
181 species. Indeed, some species in this system require several years for fully mature leaves to
182 appear and allow confident identification.

183 To characterise the community, vegetation analyses of all turfs were conducted
184 at peak season in 2009, before transplantation, and again in 2011. We recorded the percentage
185 cover of each vascular plant species in each turf, and the total cover of all vascular plants and
186 bryophytes. Height of vascular plants and height of the moss layer were recorded at four fixed
187 positions within each turf during each census, and averaged to obtain one value per variable,
188 turf and census. For each turf, we calculated a biomass index for vascular plants (V_{bryo}) and
189 bryophytes (B_{bryo}) as:

190
$$B_{vasc} = COV_{vasc} \times H_{vasc}$$

191
$$B_{bryo} = COV_{bryo} \times H_{bryo}$$

192 Where COV_{vasc} and COV_{bryo} are the total percentage cover of vascular plants and bryophytes,
193 respectively; and H_{vasc} and H_{bryo} are the average height of vascular plants and the bryophyte
194 layer, respectively.

195 We assembled data on three plant functional traits, specific leaf area (SLA;
196 m^2/kg), leaf area (mm^2) and potential maximum plant height (hereafter plant height; m),
197 related to competition for light (Grime 2001, Suding et al. 2005). Data on SLA and leaf area

198 were derived from a combination of field measurements using the protocols described in
199 Cornelissen et al. (2003) and, for rare species where field measurements were not feasible,
200 from the LEDA database (Kleyer et al. 2008). Plant height was derived from Lid and Lid
201 (2005) Nordic Flora. A full description of the trait collection and database is available in
202 Guittar et al. (2016). All trait values were log-transformed to better achieve normal
203 distribution criteria, and to prevent relatively small differences among species, which can be
204 biologically relevant, being overpowered by larger ones (Májeková et al. 2016). For each trait,
205 plot, and census, community weighted means (CWMs) were calculated as the average across
206 species of the trait value of each species found in the plot x its percentage cover in that plot.
207 We did not detect any strong collinearity between the three CWMs.

208

209 **Statistical analyses**

210 We used a log-linear mixed effect model to test if colder-climate communities were more
211 open to recruitment than warmer-climate communities. Specifically, the model compared the
212 natural seedling emergence recorded in each locally replanted control turf to the emergence in
213 the paired transplanted turf originating from a colder site. This approach focuses on
214 differences based on climatic origin while experimentally controlling for abiotic factors
215 between the sites (Fig. 1).

216 We then compared the measured biotic characteristics (biomass of vascular
217 plants and bryophytes, CWM of the traits SLA, leaf area, and plant height) between the
218 control warmer-climate communities and transplanted colder-climate communities both
219 before and two years after transplantation, using linear mixed effect models.

220 Finally, we determined whether differences in community characteristics
221 between control warmer-climate and transplanted colder-climate communities could explain
222 differences in seedling emergence between the turfs, using linear mixed effect models. We

223 regressed differences in seedling emergence between local control warmer-climate and
224 transplanted colder-climate communities (hereafter: Δ seedling.emergence) against
225 differences in community characteristics between the same communities (hereafter: Δ
226 vascular.plants, Δ bryophytes, Δ SLA, Δ leaf.area, Δ plant.height). These analyses were based
227 on seedling and vegetation data two years after transplantation. A separate model was fitted
228 for each individual biotic characteristic to avoid overfitting models and to ease interpretation.

229 In all models, interpolated values of site temperature and precipitation, as well
230 as their interactions with the treatment (control vs. transplant) were included as covariates to
231 assess if the patterns varied systematically with the climatic context. When such interactive
232 effect were found significant, we ran additional separate mixed effect models for each
233 gradient level in order to assess where along the gradient(s) transplanted colder community
234 turfs differed significantly from the control communities. We used interpolated climate data in
235 all models. However, temperature measurements at 2m height recorded during the summer
236 2011 were highly correlated with the interpolated temperature data (Pearson correlation
237 coefficient = 0.98). Temperature and precipitation did not strongly correlate with our
238 hypothesized explanatory variables (traits and biomass), excluding potential multicollinearity
239 issues.

240 For the two first models, assessing if natural seedling emergence and biotic
241 community characteristics differed between local control warmer-climate and transplanted
242 colder-climate communities, destination block nested within destination site was included as a
243 random variable. This enabled us to contrast paired control - versus transplanted communities
244 in the same blocks and sites, and to control for the experimental design (i.e., avoiding pseudo-
245 replication). A observation-level random term was also included in the model assessing
246 seedling emergence to control for over-dispersion (Harrison 2014). For the last model,
247 relating Δ seedling.emergence to the Δ s of community characteristics, only site was included

248 as a random term in the analyses as the records from the paired control and transplanted
249 community in each block were combined into one single data point.

250 Three turf pairs were clear outliers due to very high seedling numbers and were
251 omitted from the analyses (this was due to locally high densities of annual *Euphrasia* spp.
252 seedlings in these plots). The intercepts of all models were set at the sub-alpine sites and
253 average precipitation. Precipitation was expressed in 100 mm units to obtain coefficients of
254 similar magnitude for the two climate variables. Centering the models was chosen over full
255 standardization in order to keep the units of the variables for their respective model
256 coefficients and thus facilitate their quantitative interpretation. Stepwise backward variable
257 selections were applied based on maximum likelihood ratio tests to meet the principle of
258 parsimony and avoid overfitting models. All analysis were run in R (R Development Core
259 Team 2018; version 3.5.2) and all models were fitted with the packages lme4 (Bates et al.
260 2015; version 1.1-20) and lmerTest (Kuznetsova et al. 2015; version 3.1-0).

261

262 **Results:**

263 An average of 169.6 seedlings/m² emerged in the turfs transplanted from colder sites whereas
264 116.8 seedlings/m² emerged in the warmer-climate control turfs. Seedling emergence was thus
265 on average 44% higher (based on raw means; +58% according to the model estimate) in
266 communities originating from 2°C colder climates ($p = 0.003$, Table 1, Fig. 2). This means
267 that the communities assembled under a colder climate are significantly more open to the
268 early stages of seedling recruitment, after experimentally controlling for the effects of the
269 current temperature. The magnitude of this effect was unaffected by climate, as we found no
270 significant interactions between the treatment effect and the site position across the climate
271 grid.

272 In 2009, before the onset of the experiment, all community characteristics
273 except vascular plant biomass were significantly lower in alpine communities compared to
274 subalpine communities ($p < 0.001$ in all models). Vascular plant biomass ($p = 0.041$), bryophyte
275 biomass ($p < 0.014$) and CWM plant height ($p < 0.001$) were also lower in subalpine relative to
276 boreal communities (Table 1, Fig. 3). On average, for each colder 'step' along the temperature
277 gradient, vascular plant biomass decreased by 25%, bryophyte biomass decreased by 56%,
278 SLA decreased by 2.4% , leaf area decreased by 3.5%, and plant height decreased by 36%
279 (based on raw means; note that for biomass this is based on the subalpine-boreal contrast and
280 for SLA on the alpine-subalpine contrast, as the other contrasts were not significant for these
281 variables; Table 1, Fig. 3).

282 Most of these differences in characteristics between transplanted communities
283 and controls remained significant two years after the plots had been transplanted to experience
284 the same climate, albeit with smaller magnitudes (Table 1, Fig. 3). Of the original differences
285 in community characteristics between colder- and warmer-climate communities, 35%
286 remained for vascular plant biomass (as for the original effect, this difference was found only
287 between sub-alpine and boreal sites), 67% for bryophyte biomass, 75% for SLA (as for the
288 original effect, only between alpine and sub-alpine sites), 74% for leaf area, and 37% for plant
289 height, (Table 1, Fig 3).

290 Among these community characteristics, only CWM leaf area ($p = 0.005$) and
291 CWM plant height ($p < 0.001$) could explain differences in seedling emergence between the
292 local controls and transplanted colder-climate communities (Table 2, Fig.4, Appendix S1).
293 The models indicate that the consistently higher openness to seedling recruitment in colder-
294 climate communities was associated with higher abundance of plants with lower stature, and
295 with smaller leaves. However, for both leaf area and plant height, these correlations were only
296 found for alpine communities transplanted to sub-alpine sites, as indicated by the significant

297 interactions between the transplant treatment and temperature for both traits ($p=0.009$ and
298 $p=0.002$ for leaf area and plant height interactions with temperature, respectively, Table 2,
299 Fig. 4). For these communities, an increase of 1 cm^2 in CWM leaf area and 1 cm in CWM
300 plant height is associated with an average decrease of 48 and 80 seedlings/ m^2 , respectively.
301

302 **Discussion:**

303 Our study demonstrates that community openness to seedling recruitment, measured as the
304 number of naturally-emerging dicot seedlings, was consistently higher in grassland plant
305 communities originating from higher elevation (colder-climate communities) than
306 communities originating from lower elevation (warmer-climate communities), when these
307 communities were experimentally grown under the same climate. The results were consistent
308 across seven out of eight replicate experimental sites, spanning broad-scale precipitation and
309 temperature gradients, supporting the generality of the observed pattern. Further, these
310 differences in community openness to recruitment could not be accounted for by differences
311 in community biomass. Instead, they were associated with differences in plant functional
312 traits, especially between alpine and sub-alpine communities, suggesting that the functional
313 attributes of the species within these communities, and specifically traits related to their
314 competitive effects, are important regulators of community openness to recruitment.

315 Although transplanted and local control communities had been exposed to the
316 same climates and seed-rains from the same surrounding area for two years, it could be
317 argued that factors other than differences in biomass or in traits could have led to these
318 differences in openness to seedling recruitment. For example, transplantation to warmer sites
319 might enhance seed production and recruitment rates of species and seeds that were already
320 represented within the turfs. However, earlier field work in alpine and sub-alpine systems
321 suggests that seed production and seedling recruitment of these species are not enhanced by a

322 warmer climate, on the contrary, they often declined (Shevtsova et al. 2009, Graae et al. 2011,
323 Milbau et al. 2013). In our specific sites, we found no changes in fecundity, assessed via
324 numbers of flowers and natural seedling emergence, in four forbs in the same transplanted
325 turfs across the climate grid (Töpfer et al. 2018). Second, a seed transplant experiment of
326 these same four forbs across the same sites, revealed that seeds sown into warmer climates
327 actually emerged at lower rates than seeds sown at their home sites (Meineri et al. 2013).
328 Last, we also assessed natural seedling emergence in intact vegetation in the same sites, and
329 found that emergence rate of alpine species decreases with increasing temperature (Klanderud
330 et al. 2017). A second potential explanation for the elevated numbers of seedlings in alpine
331 communities transplanted to warmer sites could simply be that colder-climate communities
332 have a larger seedbank or higher within-plot seedrain than warmer-climate communities, as
333 found in other systems (Pakeman et al. 1999). However, in earlier work in the same study
334 sites, we found no patterns in seedbank density with temperature (Vandvik et al. 2016) and
335 seed rain density was lower, not higher, in colder sites (Guittar et al. in review). Therefore, the
336 difference in functional traits of the communities emerges as the most likely explanation for
337 the observed systematic decrease in community openness to seedling recruitment in
338 communities originating from warmer climates.

339 Our results may underestimate the actual impact of functional differences
340 between the communities on openness to recruitment because the transplanted communities
341 had already shifted somewhat in community composition and hence community traits two
342 years after transplantation (Guittar et al. 2016), and because intraspecific variation, which is
343 not accounted for, contributes significantly to realized trait trends along these gradients
344 (Albert et al. 2010, Gya 2017). Therefore, natural sub-alpine and alpine communities likely
345 differ even more in functional traits than the experimentally paired communities we studied,
346 and our estimates, which imply that the considerable differences in seedling emergence

347 reported here (44% higher in communities originating from 2°C colder climates), are likely
348 conservative.

349 In this study we focus on seedling emergence as a simple metric to compare the
350 openness of warm- vs. cold-climate communities. Longer-term survival and growth of these
351 recruits may, of course, show different patterns, potentially enhancing or dampening the
352 patterns we observe here, although the early seedling emergence phase has been shown to be
353 highly selective and important for population and community dynamics in our and similar
354 systems (Graae et al. 2011, Guittar et al. in review) suggesting it is reasonable to expect that
355 the consequences of these differences will remain into later stages of the life-cycle.

356

357 ***Biomass and trait effects on community openness to recruitment***

358 Higher vascular plant biomass should reduce light penetration to the soil surface, and higher
359 bryophyte biomass should prevent seeds from the seed rain reaching the soil and/or seeds
360 from the seedbank to access light (Jeschke and Kiehl 2008). High biomass of either vascular
361 plants or bryophytes is therefore expected to reduce community openness to seedling
362 recruitment (Juttila and Grace 2002, Jeschke and Kiehl 2008). If vascular plant and bryophyte
363 biomass is to play a role in community openness along elevation, this requires variation in
364 these variables along the elevation gradient. While this was generally found, it did not hold
365 for vascular plant biomass between alpine and subalpine sites, and it is thus not surprising that
366 biomass did not affect community openness for this particular contrast. However, community
367 openness was also unrelated to vascular plant or bryophytes biomass across all other site and
368 elevation contrasts. Previous studies that have found strong effects of biomass on seedling
369 recruitment are typically based on seed-sowing experiments in intact vegetation vs. bare-
370 ground plots where all vegetation has been removed (Cooper et al. 2004, Gough 2006,
371 Jeschke and Kiehl 2008, Tingstad et al. 2015, Klanderud et al. 2017). The increase in biomass

372 caused by the ca. 2°C temperature increase between the sites at adjacent altitudinal levels is of
373 much smaller magnitude, which may explain why we did not find any effect of biomass on
374 community openness to recruitment. Consistent with this interpretation, Milbau et al. (2013),
375 using small gaps of 3 cm and 6 cm in their seed-sowing experiments, concluded that in
376 relatively productive alpine habitats, comparable to our grasslands, larger-scale disturbance
377 may be necessary to promote seedling recruitment. Furthermore, Milbau et al. (2013) and
378 another study in a comparable alpine habitat (Graae et al. 2011), found only weak effects of
379 productivity on seedling recruitment in intact vegetation. An alternative explanation for the
380 lack of biomass effects on seedling emergence is that we used a relatively coarse non-
381 destructive estimate of biomass (based on cover and height), which may not have been
382 accurate enough to detect subtle effects.

383 In contrast, we found differences in natural seedling emergence between alpine
384 and subalpine communities to be consistently associated with the plant functional traits of the
385 vegetation, and specifically with differences in community-weighted means of leaf area and
386 plant height, two traits related to competition for light. Therefore, our results suggest that
387 alpine communities are more open to recruitment than sub-alpine communities primarily
388 because the alpine vegetation is comprised of relatively small-statured and small-leaved
389 species, traits that confer weak competitive effects (*sensu* Suding et al. 2008) relative to the
390 taller and larger-leaved plants dominating at lower elevations. Therefore, even if biomass
391 increases, for example in response to warming, the dominance of alpine communities by
392 species with relatively low competitive effect traits may lead them to be inherently more open
393 to recruitment than their warmer-climate adapted counterparts. This relatively weaker biotic
394 filtering in cold-adapted communities could, in turn speed up colonization and establishment
395 of warmer-adapted immigrant species into the alpine, eventually allowing better tracking of
396 climate warming by lower-elevation species and shorter dispersal lags towards higher

397 altitudes, which again may cause greater loss of alpine species with nowhere to migrate to as
398 competitive effects from these warmer-climate adapted novel competitors set in (Alexander et
399 al. 2015).

400 Importantly, differences in the traits plant height and leaf area between warmer-
401 and colder-communities explained differences in seedling emergence only between the alpine
402 and the subalpine communities, and not between the sub-alpine and the boreal communities.
403 This was unexpected, because these community-weighted mean trait values also differed
404 significantly between subalpine and boreal communities, suggesting there may be non-
405 linearities in responses or shifts in the key effect traits along these gradients. In line with our
406 results, Blonder et al. (2018) suggest that the effects of several functional traits on vital rates
407 and on seedling recruitment depend on both microenvironment and crowding by neighbors.
408 Alternatively, traits affecting light availability below the canopy may be important in both the
409 crowded sub-alpine and boreal environments, but with different functional traits being
410 relevant to describe the effects of the established community on seedling recruitment in the
411 boreal zone. Using more complex trait associations via factorial analyses (Blonder et al. 2018)
412 or structural equation modelling (Shipley et al. 2016) might help to detect or to understand if
413 and to what extent climate effects on community structure indirectly affect community
414 openness to recruitment.

415 We found no association between SLA and seedling emergence, although the
416 transplanted colder-climate alpine communities had lower community-weighted mean SLA
417 than the local control warmer-climate sub-alpine communities. High SLA species have high
418 relative growth rates, short life spans and rapid turnover of leaf material (Westoby 1998).
419 While these characteristics make high-SLA species good invaders i.e., they are efficient
420 response traits (Grotkopp et al. 2002, Grotkopp and Rejmánek 2007, Gallagher et al. 2015),
421 the role of SLA as an effect trait, i.e., its effect on seedling emergence and establishment, has

422 not yet been systematically studied. Even if such effects exist, the differences in SLA between
423 higher- and lower-elevation communities may not be sufficient to affect seedling recruitment,
424 since the difference in SLA between the transplanted and local control communities, although
425 significant, was only 2.5%.

426 We found no relationship between community openness to recruitment and
427 precipitation regime. This is unsurprising, given the lack of precipitation-based trends in
428 biomass and community trait values in our system (Guittar et al. 2016). Annual precipitation
429 at our sites ranges from ca. 600 mm to 2700 mm; hence, water is likely not a limiting resource
430 in any of our sites. Seedling recruitment may thus trend with precipitation in other systems,
431 where water is more limiting and/or where biomass or traits change with precipitation (Pedrol
432 et al. 2000, Moles et al. 2009, Kardol et al. 2010).

433

434 *Conclusion and implications under climate change*

435 Colder-climate alpine and subalpine plant communities were inherently more open to seedling
436 recruitment than warmer-climate communities, even after experimentally controlling for
437 differences in current climate and in local propagule pressure. This result could have
438 significant implications for response to climate change, because the openness of the resident
439 communities to recruitment in the cold climate habitats is a key factor controlling the rate and
440 degree to which species can migrate to new locations to track climate change. If high-
441 elevation communities had low openness to seedling recruitment, this would constitute a
442 strong biotic filter to colonization, limiting the degree to which the colder-climate species and
443 communities would be exposed to novel competitors from warmer climates. However, our
444 results suggest the opposite; alpine communities are more open to seedling recruitment,
445 potentially resulting in weaker biotic filtering and hence higher rates of colonization than
446 lower-elevation communities.

447 In contrast to earlier studies, which have mostly focused on biomass constraints
448 and ignored potential effects of plant functional composition, our results suggest that the
449 effect traits of the vegetation, specifically lower community-weighted mean plant height and
450 leaf area, may explain the higher openness of alpine communities relative to sub-alpine
451 communities. Our results therefore suggest that alpine species may lack the competitive effect
452 traits needed to make their communities resistant to the expected colonization of novel species
453 from lower elevation under a warming climate.

454

455 **Declarations**

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459 **Authors' contributions** - VV, DG, KK and EM conceived the idea and designed the
460 methodology; VV, KK, JG collected the data; EM analyzed the data; EM wrote the first draft
461 of the manuscript. VV designed he SeedClim grid and obtained funding. All authors
462 contributed critically to improve the manuscript and gave final approval for publication.

463

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577

578

579 **Tables and figures:**

580 Table 1: Mixed effect models assessing differences in community openness to natural seedling recruitment, biomass, and functional trait
 581 composition between colder-climate communities (transplanted turfs originating from colder sites) and warmer-climate control communities
 582 (locally replanted turfs at the experimental site). Note that the pre-treatment data were sampled when the communities of each pair were still in
 583 their origin sites, and this contrast thus reflects the pre-treatment climate gradient contrasts. Turfs were transplanted in September 2009; the
 584 communities of each pair were thereafter growing in the same site so that any remaining differences reflect the effect of community
 585 characteristics, independent of current climate. Community-weighted means are used for SLA, leaf area and plant height. A positive coefficient
 586 means larger values in transplanted colder-climate relative to control warmer-climate communities. Note that natural seedling emergence was not
 587 recorded in 2009. -: Factored out during stepwise selection. DF: Degrees of freedom estimated by Satterthwaite approximations. Note that DF is
 588 not reported for GLMM because of ongoing discussions about their correct calculation.
 589
 590

Response variables	Pre-treatment (2009)					2 years after transplantation (2011)				
	N	Coeff	DF	t.value	p.value	N	Coeff	DF	z / t.value	p.value
<i>Ln (Natural seedling emergence)</i>						73				
Intercept (local.control)							1.208	-	3.0	0.002
Treatment (transplant)							0.647	-	2.9	0.003
Temperature							-			-
Precipitation							-			-
Treatment : Temperature							-			-
Treatment: Precipitation							-			-
<i>Ln (Biomass vascular plant)</i>	70					71				
Intercept (local.control)		5.826	17.7	34.8	<0.001		6.457	9.1	40.2	<0.001
Treatment (transplant)		-0.316	60.9	-1.5	0.141		0.247	30.3	1.8	0.077
Temperature		0.576	15.5	4.2	<0.001		0.572	8.6	4.2	0.002
Precipitation		-	-	-	-		-	-	-	-
Treatment : Temperature		-0.402	60.7	-2.4	0.022		-0.287	31.1	-2.6	0.015
Treatment: Precipitation		-	-	-	-		-	-	-	-

Response variables	Pre-treatment (2009)					2 years after transplantation (2011)				
	N	Coeff	DF	t.value	p.value	N	Coeff	DF	z / t.value	p.value
<i>Ln (Biomass bryophyte)</i>	50					67				
Intercept (local.control)		4.248	8.1	8.0	<0.001		3.817	8.5	8.9	<0.001
Treatment (transplant)		-1.350	45.1	-3.8	<0.001		-0.655	32.2	-2.6	0.014
Temperature		-	-	-	-		-	-	-	-
Precipitation		-	-	-	-		-	-	-	-
Treatment : Temperature		-	-	-	-		-	-	-	-
Treatment : Precipitation		-	-	-	-		-	-	-	-
<i>Ln (Specific leaf area)</i>	73					73				
Intercept (local.control)		1.334	17.7	136.4	<0.001		1.325	6.2	88.5	<0.001
Treatment (transplant)		-0.053	62.5	-4.1	<0.001		-0.046	33.4	-4.4	<0.001
Temperature		0.005	15.3	0.6	0.546		0.012	6.5	0.9	0.378
Precipitation		0.001	15.1	1.5	0.162		0.000	6.5	0.1	0.914
Treatment : Temperature		0.021	63.3	2.0	0.047		0.020	34.1	2.4	0.021
Treatment : Precipitation		-0.002	62.2	-2.8	0.008		-0.003	32.8	-3.1	0.004
<i>Ln (leaf area)</i>	73					73				
Intercept (local.control)		2.446	7.7	48.9	<0.001		2.461	8.4	77.1	<0.001
Treatment (transplant)		-0.154	35.8	-4.6	<0.001		-0.049	37.8	-2.4	0.023
Temperature		0.020	7.4	0.5	0.546		-	-	-	-
Precipitation		-	-	-	-		-	-	-	-
Treatment : Temperature		0.077	36.4	2.8	0.008		-	-	-	-
Treatment : Precipitation		-	-	-	-		-	-	-	-
<i>Ln (plant height)</i>	73					73				
Intercept (local.control)		-0.435	11.0	-16.2	<0.001		-0.442	7.5	-22.0	<0.001
Treatment (transplant)		-0.131	64.6	-5.7	<0.001		-0.037	38.7	-2.6	0.013
Temperature		0.068	6.9	3.3	0.013		0.047	5.4	3.0	0.029
Precipitation		-	-	-	-		-0.004	5.3	-2.6	0.043
Treatment : Temperature		-	-	-	-		-	-	-	-
Treatment : Precipitation		-	-	-	-		-	-	-	-

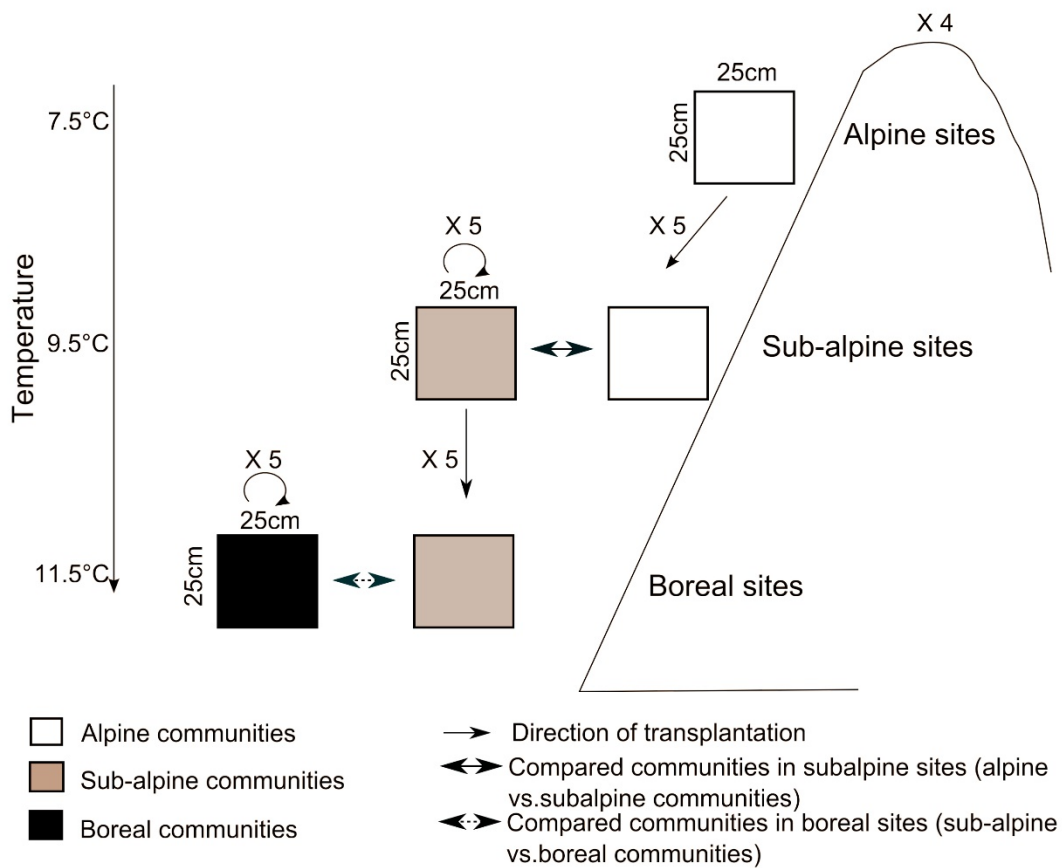
592 Table 2: Mixed effect models assessing the effect of Δ leaf.area and Δ plant.height,
 593 respectively, on Δ seedling.emergence along climatic gradients. The Δ s are calculated for each
 594 block within each site as the difference between the colder-climate community (transplanted
 595 turf originating from a colder site) and the warmer-climate community (control turfs replanted
 596 locally). Community-weighted means were used for leaf area and plant height. -: Factored out
 597 during stepwise selection. DF: Degrees of freedom estimated by Satterthwaite approximations
 598 Similar analyses using Δ biomass vascular plant, Δ bryophyte biomass, and Δ SLA showed no
 599 significant effects on Δ seedling.emergence (Fig. S1).

<i>Δseedling.emergence explained by:</i>	N	Coeff	DF	t.value	p.value
<i>Ln (leaf area)</i>	36				
Intercept		-1.83	6.9	-0.6	0.544
Δ leaf.area		-38.12	28.1	28.1	0.005
Temperature		-1.37	5.6	-0.6	0.576
Precipitation		-		-	-
Δ leaf.area : Temperature		30.48	31.8	2.8	0.009
Δ plant.height : Precipitation		-	-	-	-
<i>Ln (plant height)</i>	36				
Intercept		-1.89	6.6	-0.7	0.537
Δ plant.height		-68.60	29.5	-3.6	0.001
Temperature		-1.23	6.1	-0.5	0.630
Precipitation		-		-	-
Δ plant.height : Temperature		38.58	28.9	2.4	0.022
Δ plant.height : Precipitation		-	-	-	-

600

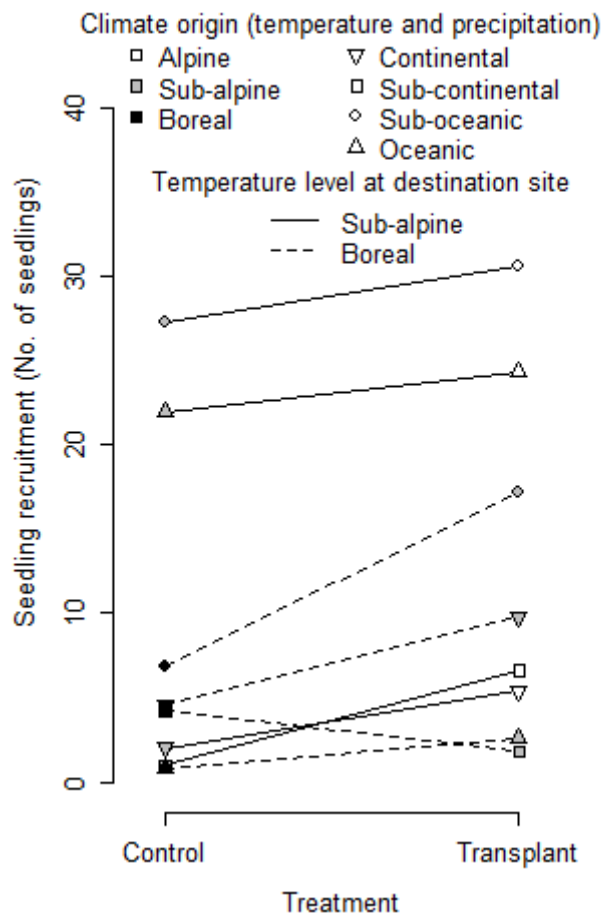
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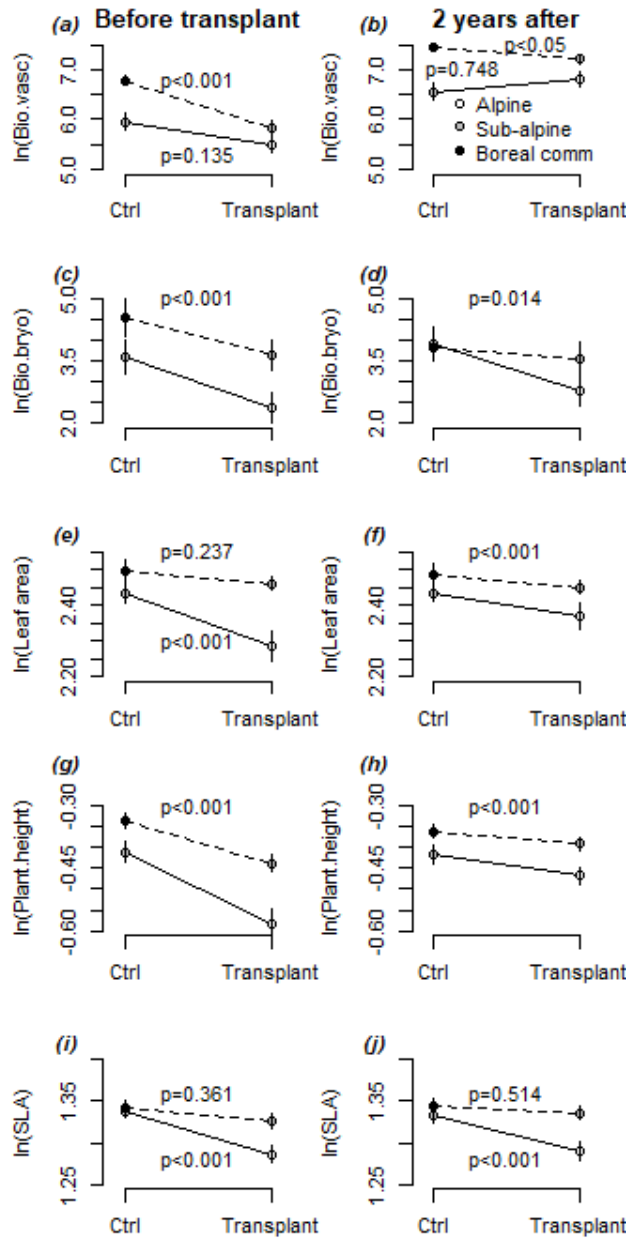
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604 Figure 1: Design of the turf transplant experiment. Turfs with intact plant communities were
 605 transplanted to sites 2°C warmer (straight black arrows) or replanted at the same sites controls
 606 (circular black arrows). Community openness to recruitment, measured as the number of
 607 naturally emerging seedlings were compared between transplanted colder-climate
 608 communities and locally replanted warmer-climate communities (double arrows) after being
 609 exposed to the same climate and seedrain for two years. The experiment was replicated across
 610 two temperature levels (alpine to sub-alpine; sub-alpine to boreal) and four levels of
 611 precipitation (700 to 3200 mm, not shown), and in 5 blocks per site.



612

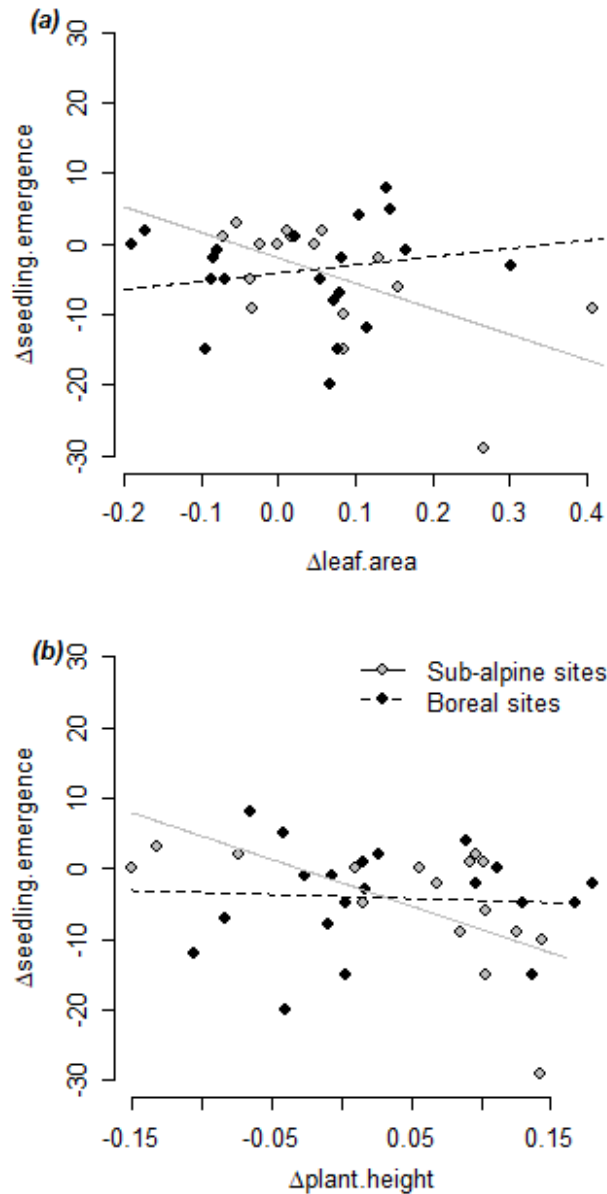
613 Figure 2: Effect of climate of origin on community openness to recruitment. The figure
 614 compares mean seedling emergence within locally replanted turfs (Control) versus
 615 transplanted turfs originating from 2°C colder sites (Transplant) across eight experimental
 616 contrasts differing in temperature and precipitation (see legend). Each symbol represents the
 617 mean of five replicate blocks.
 618



619

620 Figure 3: Averaged community characteristics in warmer-climate communities (“Ctrl”:
 621 locally replanted turfs) and colder-climate communities (“Transplant”: turfs transplanted from
 622 colder sites) before the experiment and 2 years after transplantation. Colors of symbols
 623 reflects the climate origin of the community (see legend on b)). Straight lines: alpine vs. sub-
 624 alpine communities ; dotted lines: Sub-alpine vs. boreal communities. Note that the before
 625 transplantation data were sampled when the communities of each pair were still in their
 626 different origin sites, and this contrast thus reflects the pre-treatment climate contrasts
 627 between adjacent sites along the temperature gradient. When significant interactions between
 628 temperature and transplantation treatment were detected, indicating that the magnitude of
 629 difference between plot pairs depends on the temperature regime, two p.values are reported,
 630 one for each contrast. a, b: Vascular plant biomass index; c, d: Bryophyte biomass index; e, f:
 631 community weighted mean (CWM) leaf area; g,h: CWM plant height; i, j: CWM specific leaf
 632 area.

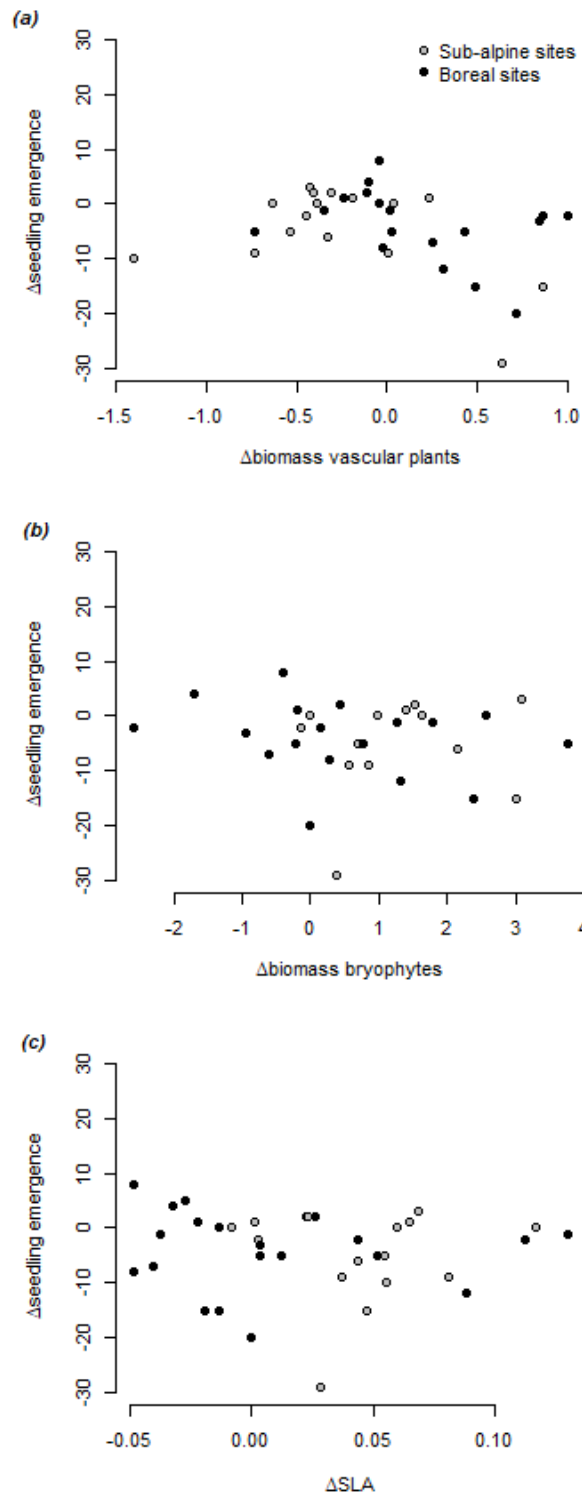
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634

635 Figure 4: community openness to recruitment (Δ seedling emergence between transplanted
 636 plots and locally replanted controls) in response to community-weighted mean leaf area (a)
 637 and plant height (b). Δ seedling.emergence (#): differences in seedling emergence between
 638 warmer-climate controls and colder-climate transplants in number of seedlings.; Δ leaf.area,
 639 Δ plant.height: differences in community characteristics between controls and transplants.
 640 Δ seedling.emergence did not respond significantly to Δ vascular plant biomass, Δ bryophyte
 641 biomass and Δ SLA (see appendix S1 for similar plots for these traits).
 642

643 **Supplementary material:**



644

645 Appendix s1: Seedling emergence non-responses to vascular plant biomass (a), bryophyte
646 biomass (b) and SLA (c). Δ seedling.emergence (#): differences in seedling emergence
647 between warmer- and colder-climate communities in number of seedlings.; Δ vascular plant
648 biomass, Δ bryophyte biomass and Δ SLA: differences in these community characteristics
649 between warmer- and colder-climate communities.