

# Functional traits, not productivity, predict alpine plant community openness to seedling recruitment under climatic warming

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1	Functional traits, not productivity, predict alpine plant
2	community openness to seedling recruitment under climatic
3	warming
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#### 23 Abstract:

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

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

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

Seedling recruitment is an important process in the life cycle of plants, being a key 52 determinant of population dynamics, rates of community turnover, and species range 53 dynamics (Tilman 1997, Walck et al. 2011). Rates of seedling recruitment hence affect 54 55 diversity across scale, from intraspecific variability to community patterns to regional species pools. The rates of natural seedling recruitment in plant communities are controlled by both 56 57 abiotic conditions such as temperature and precipitation (Meineri et al. 2013, Klanderud et al. 2017), and by biotic characteristics of the community such as vegetation density and biomass 58 (Milbau et al. 2013, Klanderud et al. 2017, Frei et al. 2018). Biotic control of seedling 59 recruitment is typically assessed through seed sowing experiments in intact vegetation vs. 60 vegetation removal plots. While experimentally removing biomass often leads to higher 61 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 along elevation gradients in response to decreasing temperature (Bloor et al. 2010, Kardol et 64 65 al. 2010, Klanderud et al. 2015), would be sufficient to render alpine communities more open to seedling recruitment than their warmer-climate sub-alpine or boreal counterparts. 66 Understanding the role of such more subtle changes in community biomass is critical for 67 understanding how climate-related variation in biotic filtering will affect community 68 dynamics under climate change. 69

In parallel with biomass changes, the functional composition of vegetation also
varies along bioclimatic gradients. In particular, plant functional traits related to competition
for light, such as maximum plant height (Westoby 1998, Westoby et al. 2002), leaf area and

specific leaf area (SLA) (Grotkopp et al. 2002, Grotkopp and Rejmánek 2007, Gallagher et al. 73 74 2015) all decrease towards colder, alpine climates (Dubuis et al. 2013, Guittar et al. 2016). This suggests a potential alternative driver of variation in natural seedling recruitment rates 75 along elevation gradients, where the functional composition of the resident vegetation limits 76 seedling recruitment towards warmer climates (i.e. the "effect traits" of the vegetation, sensu 77 Suding et al. 2008). Note that this potential role of functional traits in affecting recruitment 78 79 through controlling the competitive effects of the extant community, and hence it's openness to recruitment, is different from the more common "response traits" framework approach 80 which explores how the traits of the colonizing species affects their ability to recruit into new 81 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 variation in seedling recruitment rates across communities (but see Blonder et al. 2018). 84

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

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 higherelevation plant communities transplanted to warmer climate and locally replanted control 105 plant communities two years after transplantation. Community openness to recruitment was 106 107 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 seedling recruitment process (Graae et al. 2011, Guittar et al. in review), we isolate variation 109 110 in and drivers of colonization success per se, and avoid confounding this event with later lifehistory stages such as differential survival due to the various processes operating on the 111 already-emerged seedlings (plant-plant interactions, predation, etc.). As such, our study tests 112 the biotic resistance of higher-elevation biodiversity to colonization by seed in the face of 113 114 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 under four precipitation levels (ca. 600 - 2700 mm of annual precipitation) allowing 116 assessment of climate context-dependencies and hence the degree of generality of responses. 117 118 Specifically, we ask: Does community openness to recruitment vary systematically along climatic 1. 119

120 gradients?

Do community biomass and functional trait composition vary along climatic 121 2. gradients? If so, do these differences in biotic characteristics remains after placing 122 colder- and warmer-climate communities under similar climatic conditions? 123 3. If such climatically driven differences in community openness to recruitment exist, are 124 they associated with differences in community biomass and/or with differences in 125 community functional trait composition between the colder-adapted and the warmer-126 adapted communities? 127 Are there climatic context-dependencies in these associations along temperature 4. 128 and/or precipitation gradients? 129 130 We hypothesize greater community openness to recruitment in colder-climate communities because of lower vascular plant biomass and/or dominance by species that have traits that 131 render them poorer competitors for light. 132

133

#### 134 Material and methods

#### 135 Study design

We used twelve calcareous grassland sites in southern Norway, situated in a climate 'grid' where three levels of summer temperature (alpine ca  $7.5^{\circ}$ C; sub-alpine ca  $9.5^{\circ}$ C; boreal ca 11.5°C) are replicated across four levels of annual precipitation (1 = continental ca 600 mm; 2 = sub-continental ca 1200 mm; 3 = sub-oceanic ca 2000 mm; 4 = oceanic ca 2700 mm). The climatic grid was designed using interpolated data from the normal period 1961-1990 at a resolution of 100 m (Norwegian Meteorological Institute, <u>www.met.no</u>).

We selected the sites to keep vegetation type, bedrock, slope, aspect, land-use regime and history as constant as possible across sites. All sites were fenced to avoid animal disturbance, but mowed at the end of each growing season to mimic a standardized grazing

regime (see Klanderud et al. 2015 for additional informations). All the plant communities 145 were within the phytosociological association *Potentillo-Festucetum ovinae* in the alpine, 146 tending towards Potentillo-Polygonum vivipari, and in some lowland sites tending towards 147 Nardo-Agrostion tenuis (Fremstad 1997, Meineri et al. 2013, Klanderud et al. 2015). 148 Within each site, we selected five replicate blocks within a patch of the target 149 grassland. Within each block, two  $25*25 \text{ cm}^2$  plots were assigned randomly to the two 150 151 treatments. The two turfs were cut and dug out to a depth of 5 to 10 cm, depending on the rooting depth. One of the cut turfs was replanted at the same site and the other was 152 transplanted into a site one level warmer at the same precipitation level in the climate grid. At 153 154 each site and block, the analyses described below contrast locally replanted turfs (hereafter warmer-climate communities or controls) vs. transplanted turfs originating from a colder 155 climate (hereafter colder-climate communities or transplants) two years after transplantation. 156 The two-year delay between transplantation and data collection removes any effects of 157 differences in current climate or other site-level factors between the control and transplanted 158 communities. The experiment thus explicitly quantifies the openness to recruitment of 159 communities that were assembled under a colder relative to a warmer climate, while 160 controlling for the current climate and other abiotic conditions during the experimental trial 161 162 (Fig. 1). A total of 80 transplanted and locally replanted turfs were used in the study, which is part of a larger experiment that also contained intact control plots (i.e., not dug out and 163 replanted) as a control of the transplantation treatment *per se*. Preliminary analyses showed 164 165 that community openness to recruitment (see below) was slightly higher in locally replanted controls than in these untouched plots (mixed effect linear models nested on block within site, 166 p.value=0.048) for the main effect of plot replanting. We therefore used the locally replanted 167 plots as controls for the remainder of this study to eliminate any effects of the transplantation 168 process itself. 169

170 The species richness of vascular plants recorded within the turfs ranged from 10 171 to 40 species, with a mean canopy height of  $9 \pm 6$  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 each turf as a measure of community openness to recruitment. We excluded graminoids 175 176 because of difficulties in distinguishing monocotyledonous seedlings from clonal offshoots. In 2011, we counted all dicotyledonous seedlings with visible cotyledons in each turf. The 177 survey was conducted at peak growing season, which is in the two first weeks of August at 178 these sites. This timing of the census enabled a fairly comprehensive index of total dicot 179 emergence, but with the trade-off that many of the seedlings were not yet identifiable to 180 species. Indeed, some species in this system require several years for fully mature leaves to 181 182 appear and allow confident identification.

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

190

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

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

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.

We assembled data on three plant functional traits, specific leaf area (SLA; 195 196  $m^{2}/kg$ ), leaf area (mm<sup>2</sup>) and potential maximum plant height (hereafter plant height; m), related to competition for light (Grime 2001, Suding et al. 2005). Data on SLA and leaf area 197 were derived from a combination of field measurements using the protocols described in 198 Cornelissen et al. (2003) and, for rare species where field measurements were not feasible, 199 from the LEDA database (Klever et al. 2008). Plant height was derived from Lid and Lid 200 201 (2005) Nordic Flora. A full description of the trait collection and database is available in Guittar et al. (2016). All trait values were log-transformed to better achieve normal 202 distribution criteria, and to prevent relatively small differences among species, which can be 203 204 biologically relevant, being overpowered by larger ones (Májeková et al. 2016). For each trait, plot, and census, community weighted means (CWMs) were calculated as the average across 205 species of the trait value of each species found in the plot x its percentage cover in that plot. 206 207 We did not detect any strong collinearity between the three CWMs.

208

#### 209 Statistical analyses

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

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

Finally, we determined whether differences in community characteristics 220 221 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 regressed differences in seedling emergence between local control warmer-climate and 223 transplanted colder-climate communities (hereafter:  $\Delta$  seedling.emergence) against 224 differences in community characteristics between the same communities (hereafter:  $\Delta$ 225 226 vascular.plants,  $\Delta$  bryophytes,  $\Delta$  SLA,  $\Delta$  leaf.area,  $\Delta$  plant.height). These analyses were based on seedling and vegetation data two years after transplantation. A separate model was fitted 227 for each individual biotic characteristic to avoid overfitting models and to ease interpretation. 228 229 In all models, interpolated values of site temperature and precipitation, as well as their interactions with the treatment (control vs. transplant) were included as covariates to 230 assess if the patterns varied systematically with the climatic context. When such interactive 231 effect were found significant, we ran additional separate mixed effect models for each 232 gradient level in order to assess where along the gradient(s) transplanted colder community 233 turfs differed significantly from the control communities. We used interpolated climate data in 234 all models. However, temperature measurements at 2m height recorded during the summer 235 236 2011 were highly correlated with the interpolated temperature data (Pearson correlation 237 coefficient = 0.98). Temperature and precipitation did not strongly correlate with our hypothesized explanatory variables (traits and biomass), excluding potential multicollinearity 238 issues. 239

For the two first models, assessing if natural seedling emergence and biotic community characteristics differed between local control warmer-climate and transplanted colder-climate communities, destination block nested within destination site was included as a random variable. This enabled us to contrast paired control - versus transplanted communities in the same blocks and sites, and to control for the experimental design (i.e., avoiding pseudo-

replication). A observation-level random term was also included in the model assessing seedling emergence to control for over-dispersion (Harrison 2014). For the last model, relating  $\Delta$  seedling.emergence to the  $\Delta$ s of community characteristics, only site was included as a random term in the analyses as the records from the paired control and transplanted community in each block were combined into one single data point.

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

261

#### 262 **Data deposition**

- 263 Data are available from the Dryad Digital Repository: < http://
- 264 dx.doi.org/10.5061/dryad.d39d356 > (Meineri et al. 2019).

265

#### 266 **Results:**

An average of 169.6 seedlings/m<sup>2</sup> emerged in the turfs transplanted from colder sites whereas
 116.8 seedlings/m<sup>2</sup> emerged in the warmer-climate control turfs. Seedling emergence was thus

on average 44% higher (based on raw means; +58% according to the model estimate) in communities originating from 2°C colder climates (p = 0.003, Table 1, Fig. 2). This means that the communities assembled under a colder climate are significantly more open to the early stages of seedling recruitment, after experimentally controlling for the effects of the current temperature. The magnitude of this effect was unaffected by climate, as we found no significant interactions between the treatment effect and the site position across the climate grid.

In 2009, before the onset of the experiment, all community characteristics 276 except vascular plant biomass were significantly lower in alpine communities compared to 277 278 subalpine communities (p<0,001 in all models). Vascular plant biomass (p=0.041), bryophyte biomass (p<0.014) and CWM plant height (p<0.001) were also lower in subalpine relative to 279 boreal communities (Table 1, Fig. 3). On average, for each colder 'step' along the temperature 280 281 gradient, vascular plant biomass decreased by 25%, bryophyte biomass decreased by 56%, SLA decreased by 2.4%, leaf area decreased by 3.5%, and plant height decreased by 36% 282 (based on raw means; note that for biomass this is based on the subalpine-boreal contrast and 283 for SLA on the alpine-subalpine contrast, as the other contrasts were not significant for these 284 variables; Table 1, Fig. 3). 285

286 Most of these differences in characteristics between transplanted communities 287 and controls remained significant two years after the plots had been transplanted to experience the same climate, albeit with smaller magnitudes (Table 1, Fig. 3). Of the original differences 288 289 in community characteristics between colder- and warmer-climate communities, 35% remained for vascular plant biomass (as for the original effect, this difference was found only 290 between sub-alpine and boreal sites), 67% for bryophyte biomass, 75% for SLA (as for the 291 original effect, only between alpine and sub-alpine sites), 74% for leaf area, and 37% for plant 292 height, (Table 1, Fig 3). 293

Among these community characteristics, only CWM leaf area (p=0.005) and 294 295 CWM plant height (p<0.001) could explain differences in seedling emergence between the local controls and transplanted colder-climate communities (Table 2, Fig.4, Appendix S1). 296 The models indicate that the consistently higher openness to seedling recruitment in colder-297 climate communities was associated with higher abundance of plants with lower stature, and 298 with smaller leaves. However, for both leaf area and plant height, these correlations were only 299 300 found for alpine communities transplanted to sub-alpine sites, as indicated by the significant interactions between the transplant treatment and temperature for both traits (p=0.009 and 301 p=0.002 for leaf area and plant height interactions with temperature, respectively, Table 2, 302 Fig. 4). For these communities, an increase of 1 cm<sup>2</sup> in CWM leaf area and 1 cm in CWM 303 plant height is associated with an average decrease of 48 and 80 seedlings/ $m^2$ , respectively. 304 305

#### 306 **Discussion:**

307 Our study demonstrates that community openness to seedling recruitment, measured as the number of naturally-emerging dicot seedlings, was consistently higher in grassland plant 308 communities originating from higher elevation (colder-climate communities) than 309 310 communities originating from lower elevation (warmer-climate communities), when these communities were experimentally grown under the same climate. The results were consistent 311 across seven out of eight replicate experimental sites, spanning broad-scale precipitation and 312 313 temperature gradients, supporting the generality of the observed pattern. Further, these differences in community openness to recruitment could not be accounted for by differences 314 315 in community biomass. Instead, they were associated with differences in plant functional 316 traits, especially between alpine and sub-alpine communities, suggesting that the functional attributes of the species within these communities, and specifically traits related to their 317 competitive effects, are important regulators of community openness to recruitment. 318

Although transplanted and local control communities had been exposed to the 319 320 same climates and seed-rains from the same surrounding area for two years, it could be argued that factors other than differences in biomass or in traits could have led to these 321 differences in openness to seedling recruitment. For example, transplantation to warmer sites 322 might enhance seed production and recruitment rates of species and seeds that were already 323 represented within the turfs. However, earlier field work in alpine and sub-alpine systems 324 325 suggests that seed production and seedling recruitment of these species are not enhanced by a warmer climate, on the contrary, they often declined (Shevtsova et al. 2009, Graae et al. 2011, 326 Milbau et al. 2013). In our specific sites, we found no changes in fecundity, assessed via 327 328 numbers of flowers and natural seedling emergence, in four forbs in the same transplanted 329 turfs across the climate grid (Töpper et al. 2018). Second, a seed transplant experiment of these same four forbs across the same sites, revealed that seeds sown into warmer climates 330 actually emerged at lower rates than seeds sown at their home sites (Meineri et al. 2013). 331 Last, we also assessed natural seedling emergence in intact vegetation in the same sites, and 332 found that emergence rate of alpine species decreases with increasing temperature (Klanderud 333 et al. 2017). A second potential explanation for the elevated numbers of seedlings in alpine 334 communities transplanted to warmer sites could simply be that colder-climate communities 335 336 have a larger seedbank or higher within-plot seedrain than warmer-climate communities, as found in other systems (Pakeman et al. 1999). However, in earlier work in the same study 337 sites, we found no patterns in seedbank density with temperature (Vandvik et al. 2016) and 338 339 seed rain density was lower, not higher, in colder sites (Guittar et al. in review). Therefore, the difference in functional traits of the communities emerges as the most likely explanation for 340 the observed systematic decrease in community openness to seedling recruitment in 341 communities originating from warmer climates. 342

Our results may underestimate the actual impact of functional differences 343 344 between the communities on openness to recruitment because the transplanted communities had already shifted somewhat in community composition and hence community traits two 345 years after transplantation (Guittar et al. 2016), and because intraspecific variation, which is 346 not accounted for, contributes significantly to realized trait trends along these gradients 347 (Albert et al. 2010, Gya 2017). Therefore, natural sub-alpine and alpine communities likely 348 349 differ even more in functional traits than the experimentally paired communities we studied, and our estimates, which imply that the considerable differences in seedling emergence 350 reported here (44% higher in communities originating from 2°C colder climates), are likely 351 352 conservative.

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

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

Higher vascular plant biomass should reduce light penetration to the soil surface, and higher
bryophyte biomass should prevent seeds from the seed rain reaching the soil and/or seeds
from the seedbank to access light (Jeschke and Kiehl 2008). High biomass of either vascular
plants or bryophytes is therefore expected to reduce community openness to seedling
recruitment (Jutila and Grace 2002, Jeschke and Kiehl 2008). If vascular plant and bryophyte
biomass is to play a role in community openness along elevation, this requires variation in

these variables along the elevation gradient. While this was generally found, it did not hold 368 369 for vascular plant biomass between alpine and subalpine sites, and it is thus not surprising that biomass did not affect community openness for this particular contrast. However, community 370 openness was also unrelated to vascular plant or bryophytes biomass across all other site and 371 elevation contrasts. Previous studies that have found strong effects of biomass on seedling 372 recruitment are typically based on seed-sowing experiments in intact vegetation vs. bare-373 374 ground plots where all vegetation has been removed (Cooper et al. 2004, Gough 2006, Jeschke and Kiehl 2008, Tingstad et al. 2015, Klanderud et al. 2017). The increase in biomass 375 caused by the ca. 2°C temperature increase between the sites at adjacent altitudinal levels is of 376 377 much smaller magnitude, which may explain why we did not find any effect of biomass on 378 community openness to recruitment. Consistent with this interpretation, Milbau et al. (2013), using small gaps of 3 cm and 6 cm in their seed-sowing experiments, concluded that in 379 380 relatively productive alpine habitats, comparable to our grasslands, larger-scale disturbance may be necessary to promote seedling recruitment. Furthermore, Milbau et al. (2013) and 381 another study in a comparable alpine habitat (Graae et al. 2011), found only weak effects of 382 productivity on seedling recruitment in intact vegetation. An alternative explanation for the 383 lack of biomass effects on seedling emergence is that we used a relatively coarse non-384 385 destructive estimate of biomass (based on cover and height), which may not have been accurate enough to detect subtle effects. 386

In contrast, we found differences in natural seedling emergence between alpine and subalpine communities to be consistently associated with the plant functional traits of the vegetation, and specifically with differences in community-weighted means of leaf area and plant height, two traits related to competition for light. Therefore, our results suggest that alpine communities are more open to recruitment than sub-alpine communities primarily because the alpine vegetation is comprised of relatively small-statured and small-leaved

species, traits that confer weak competitive effects (sensu Suding et al. 2008) relative to the 393 394 taller and larger-leaved plants dominating at lower elevations. Therefore, even if biomass increases, for example in response to warming, the dominance of alpine communities by 395 species with relatively low competitive effect traits may lead them to be inherently more open 396 397 to recruitment than their warmer-climate adapted counterparts. This relatively weaker biotic filtering in cold-adapted communities could, in turn speed up colonization and establishment 398 399 of warmer-adapted immigrant species into the alpine, eventually allowing better tracking of climate warming by lower-elevation species and shorter dispersal lags towards higher 400 altitudes, which again may cause greater loss of alpine species with nowhere to migrate to as 401 402 competitive effects from these warmer-climate adapted novel competitors set in (Alexander et 403 al. 2015).

Importantly, differences in the traits plant height and leaf area between warmer-404 and colder-communities explained differences in seedling emergence only between the alpine 405 and the subalpine communities, and not between the sub-alpine and the boreal communities. 406 This was unexpected, because these community-weighted mean trait values also differed 407 significantly between subalpine and boreal communities, suggesting there may be non-408 409 linearities in responses or shifts in the key effect traits along these gradients. In line with our 410 results, Blonder et al. (2018) suggest that the effects of several functional traits on vital rates and on seedling recruitment depend on both microenvironment and crowding by neighbors. 411 Alternatively, traits affecting light availability below the canopy may be important in both the 412 413 crowded sub-alpine and boreal environments, but with different functional traits being relevant to describe the effects of the established community on seedling recruitment in the 414 boreal zone. Using more complex trait associations via factorial analyses (Blonder et al. 2018) 415 or structural equation modelling (Shipley et al. 2016) might help to detect or to understand if 416

and to what extent climate effects on community structure indirectly affect communityopenness to recruitment.

We found no association between SLA and seedling emergence, although the 419 transplanted colder-climate alpine communities had lower community-weighted mean SLA 420 than the local control warmer-climate sub-alpine communities. High SLA species have high 421 relative growth rates, short life spans and rapid turnover of leaf material (Westoby 1998). 422 423 While these characteristics make high-SLA species good invaders i.e., they are efficient response traits (Grotkopp et al. 2002, Grotkopp and Rejmánek 2007, Gallagher et al. 2015), 424 the role of SLA as an effect trait, i.e., its effect on seedling emergence and establishment, has 425 426 not yet been systematically studied. Even if such effects exist, the differences in SLA between 427 higher- and lower-elevation communities may not be sufficient to affect seedling recruitment, since the difference in SLA between the transplanted and local control communities, although 428 significant, was only 2.5%. 429

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

437

#### 438 *Conclusion and implications under climate change*

Colder-climate alpine and subalpine plant communities were inherently more open to seedling
recruitment than warmer-climate communities, even after experimentally controlling for
differences in current climate and in local propagule pressure. This result could have

significant implications for response to climate change, because the openness of the resident 442 443 communities to recruitment in the cold climate habitats is a key factor controlling the rate and degree to which species can migrate to new locations to track climate change. If high-444 elevation communities had low openness to seedling recruitment, this would constitute a 445 strong biotic filter to colonization, limiting the degree to which the colder-climate species and 446 communities would be exposed to novel competitors from warmer climates. However, our 447 results suggest the opposite; alpine communities are more open to seedling recruitment, 448 potentially resulting in weaker biotic filtering and hence higher rates of colonization than 449 lower-elevation communities. 450

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

458

#### 459 **Declarations**

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463 Authors' contributions - VV, DG, KK and EM conceived the idea and designed the

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of the manuscript. VV designed he SeedClim grid and obtained funding. All authors
contributed critically to improve the manuscript and gave final approval for publication.

### 468 **References:**

Albert, C. H., et al. 2010. A multi-trait approach reveals the structure and the relative

470 importance of intra- vs. interspecific variability in plant traits. - Functional Ecology 24: 1192471 1201.

472 Alexander, J. M., et al. 2015. Novel competitors shape species/' responses to climate change. -

473 Nature advance online publication.

- Bates, D., et al. 2015. Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical
  Software 67: e-print.
- 476 Blonder, B., et al. 2018. Microenvironment and functional-trait context dependence predict
- 477 alpine plant community dynamics. Journal of Ecology 106: 1323-1337.
- 478 Bloor, J. M. G., et al. 2010. Effects of Warming, Summer Drought, and CO2 Enrichment on
- 479 Aboveground Biomass Production, Flowering Phenology, and Community Structure in an
- 480 Upland Grassland Ecosystem. Ecosystems 13: 888-900.
- 481 Cooper, E. J., et al. 2004. Plant recruitment in the High Arctic: Seed bank and seedling
- 482 emergence on Svalbard. Journal of Vegetation Science 15: 115-124.
- 483 Cornelissen, J., et al. 2003. A handbook of protocols for standardised and easy measurement
- 484 of plant functional traits worldwide. Australian journal of Botany 51: 335-380.
- 485 Dolezal, J., et al. 2018. Functionally distinct assembly of vascular plants colonizing alpine
- 486 cushions suggests their vulnerability to climate change. Annals of Botany 123: 569-578.
- 487 Dolezal, J., et al. 2016. Vegetation dynamics at the upper elevational limit of vascular plants
- 488 in Himalaya. Scientific reports 6: 24881.

- 489 Dubuis, A., et al. 2013. Predicting current and future spatial community patterns of plant
- 490 functional traits. Ecography 36: 1158-1168.
- 491 Frei, E. R., et al. 2018. Biotic and abiotic drivers of tree seedling recruitment across an alpine
- 492 treeline ecotone. Scientific reports 8.
- 493 Fremstad, E. 1997. Vegetasjonstyper i Norge. NINA Temahefte 12: 1-279.
- 494 Gallagher, R., et al. 2015. Trait differences between naturalized and invasive plant species
- independent of residence time and phylogeny. Conservation Biology 29: 360-369.
- 496 Gough, L. 2006. Neighbor effects on germination, survival, and growth in two arctic tundra
- 497 plant communities. Ecography 29: 44-56.
- 498 Graae, B. J., et al. 2011. Strong microsite control of seedling recruitment in tundra. -
- 499 Oecologia 166: 565-576.
- Grime, J. P. 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. Wileyand sons ltd.
- 502 Grotkopp, E. and Rejmánek, M. 2007. High seedling relative growth rate and specific leaf
- area are traits of invasive species: phylogenetically independent contrasts of woody
- angiosperms. American Journal of Botany 94: 526-532.
- 505 Grotkopp, E., et al. 2002. Toward a causal explanation of plant invasiveness: seedling growth
- and life-history strategies of 29 pine (*Pinus*) species. The American Naturalist 159: 396-419.
- 507 Guittar, J., et al. in review. The roles of dispersal limitation and seedling performance as in
- 508 constrainingts to grassland species range expansion. -.
- 509 Guittar, J., et al. 2016. Can trait patterns along gradients predict plant community responses to
- climate change? Ecology 97: 2791-2801.
- 511 Gya, R. 2017. The role of intraspecific variability in driving community trait shifts along
- temperature and precipitation gradients in alpine and boreal semi-natural grasslands. The
- 513 University of Bergen.

- Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in
  count data in ecology and evolution. PeerJ 2: e616.
- 516 Jeschke, M. and Kiehl, K. 2008. Effects of a dense moss layer on germination and
- 517 establishment of vascular plants in newly created calcareous grasslands. Flora -
- 518 Morphology, Distribution, Functional Ecology of Plants 203: 557-566.
- 519 Jutila, H. M. and Grace, J. B. 2002. Effects of disturbance on germination and seedling
- 520 establishment in a coastal prairie grassland: a test of the competitive release hypothesis. -
- 521 Journal of Ecology 90: 291-302.
- 522 Kardol, P., et al. 2010. Climate change effects on plant biomass alter dominance patterns and
- 523 community evenness in an experimental old-field ecosystem. Global Change Biology 16:
- 524 2676-2687.
- 525 Klanderud, K., et al. 2017. Biotic interaction effects on seedling recruitment along bioclimatic
- 526 gradients: testing the stress-gradient hypothesis. Journal of Vegetation Science 28: 347-356.
- 527 Klanderud, K. and Totland, O. 2007. The relative role of dispersal and local interactions for
- alpine plant community diversity under simulated climate warming. Oikos 116: 1279-1288.
- 529 Klanderud, K., et al. 2015. The importance of biotic vs. abiotic drivers of local plant
- community composition along regional bioclimatic gradients. PloS ONE 10: e0130205.
- 531 Kleyer, M., et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest
- 532 European flora. Journal of Ecology 96: 1266-1274.
- 533 Kuznetsova, A., et al. 2015. ImerTest: Tests in Linear Mixed Effects Models.
- Lid, J. and Lid, D. T. 2005. Norsk flora. Det norske samlaget.
- 535 Májeková, M., et al. 2016. Evaluating Functional Diversity: Missing Trait Data and the
- 536 Importance of Species Abundance Structure and Data Transformation. PloS ONE 11:
- 537 e0149270.

- McGill, B. J., et al. 2006. Rebuilding community ecology from functional traits. Trends in
  Ecology & Evolution 21: 178-185.
- 540 Meineri, E., et al. 2013. Seedling emergence responds to both seed source and recruitment site
- 541 climates: a climate change experiment combining transplant and gradient approaches. Plant
- 542 Ecology: 1-13.
- 543 Milbau, A., et al. 2013. Plant community type and small-scale disturbances, but not altitude,
- influence the invasibility in subarctic ecosystems. New Phytologist 197: 1002-1011.
- 545 Moles, A. T., et al. 2009. Global patterns in plant height. Journal of Ecology 97: 923-932.
- 546 Pakeman, R. J., et al. 1999. Potential climatic control of seedbank density. Seed science
- 547 research 9: 101-110.
- 548 Pedrol, N., et al. 2000. Phenotypic plasticity and acclimation to water deficits in velvet-grass:
- a long-term greenhouse experiment. Changes in leaf morphology, photosynthesis and stress-
- induced metabolites. Journal of Plant Physiology 157: 383-393.
- 551 R Development Core Team. 2018. R: A Language and Environment for Statistical
- 552 Computing. R Foundation for Statistical Computing.
- 553 Shevtsova, A., et al. 2009. Critical periods for impact of climate warming on early seedling
- establishment in subarctic tundra. Global Change Biology 15: 2662-2680.
- 555 Shipley, B., et al. 2016. Reinforcing loose foundation stones in trait-based plant ecology. -
- 556 Oecologia 180: 923-931.
- 557 Suding, K. N., et al. 2005. Functional- and abundance-based mechanisms explain diversity
- 558 loss due to N fertilization. Proceedings of the National Academy of Sciences of the United
- 559 States of America 102: 4387-4392.
- 560 Suding, K. N., et al. 2008. Scaling environmental change through the community-level: a
- trait-based response-and-effect framework for plants. Global Change Biology 14: 1125-
- 562 1140.

- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78: 81-92.
- Tingstad, L., et al. 2015. Temperature, precipitation and biotic interactions as determinants of
  tree seedling recruitment across the tree line ecotone. Oecologia 179: 599-608.
- 567 Töpper, J. P., et al. 2018. The devil is in the detail: Nonadditive and context-dependent plant
- 568 population responses to increasing temperature and precipitation. Global Change Biology
- **569** 24: 4657-4666.
- 570 Vandvik, V., et al. 2016. Seed banks are biodiversity reservoirs: species–area relationships
- above versus below ground. Oikos 125: 218-228.
- 572 Violle, C., et al. 2007. Let the concept of trait be functional! Oikos 116: 882-892.
- 573 Walck, J. L., et al. 2011. Climate change and plant regeneration from seed. Global Change
- 574 Biology 17: 2145-2161.
- 575 Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil
  576 199: 213-227.
- 577 Westoby, M., et al. 2002. Plant ecological strategies: some leading dimensions of variation
- 578 between species. Annual Review of Ecology and Systematics 33: 125-159.
- 579 Wright, I. J., et al. 2005. Modulation of leaf economic traits and trait relationships by climate.
- Global Ecology and Biogeography 14: 411-421.
- 581

## 583 Tables and figures:

Table 1: Mixed effect models assessing differences in community openness to natural seedling recruitment, biomass, and functional trait composition between colder-climate communities (transplanted turfs originating from colder sites) and warmer-climate control communities (locally replanted turfs at the experimental site). Note that the pre-treatment data were sampled when the communities of each pair were still in their origin sites, and this contrast thus reflects the pre-treatment climate gradient contrasts. Turfs were transplanted in September 2009; the communities of each pair were thereafter growing in the same site so that any remaining differences reflect the effect of community characteristics, independent of current climate. Community-weighted means are used for SLA, leaf area and plant height. A positive coefficient

590 means larger values in transplanted colder-climate relative to control warmer-climate communities. Note that natural seedling emergence was not

591 recorded in 2009. -: Factored out during stepwise selection. DF: Degrees of freedom estimated by Satterthwaite approximations. Note that DF is

592 not reported for GLMM because of ongoing discussions about their correct calculation.

593

Response variables			Pre-treatment (2009)			2 years after transplantation (2011)				
	Ν	Coeff	(200)) DF	t.value	p.value	Ν	Coeff	DF	z / t.value	p.value
Ln (Natural seedling emergence)					Friday	73				<b>F</b>
Intercept (local.control)							1.208	-	3.0	0.002
Treatment (transplant)							0.647	-	2.9	0.003
Temperature							-			-
Precipitation							-			-
Treatment : Temperature							-			-
Treatment: Precipitation							-			-
Ln (Biomass vascular plant)	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		-	-		-		-	-		-
In (Biomass bryophyte)	50					67				
Intercept (local control)	20	4.248	8.1	8.0	< 0.001	0,	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		-	-	-	-		-	-	-	-
Ln (Specific leaf area)	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
Ln (leaf area)	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		-	-	-	-		-	-	-	-
Ln (plant height)	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		-	-	-	-		-	-	-	-

Table 2: Mixed effect models assessing the effect of  $\Delta$  leaf.area and  $\Delta$  plant.height,

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

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

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608 Figure 1: Design of the turf transplant experiment. Turfs with intact plant communities were

transplanted to sites 2°C warmer (straight black arrows) or replanted at the same sites controls

610 (circular black arrows). Community openness to recruitment, measured as the number of

- 611 naturally emerging seedlings were compared between transplanted colder-climate
- 612 communities and locally replanted warmer-climate communities (double arrows) after being
- 613 exposed to the same climate and seedrain for two years. The experiment was replicated across
- two temperature levels (alpine to sub-alpine; sub-alpine to boreal) and four levels of
- precipitation (700 to 3200 mm, not shown), and in 5 blocks per site.





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



Figure 3: Averaged community characteristics in warmer-climate communities ("Ctrl":
locally replanted turfs) and colder-climate communities ("Transplant": turfs transplanted from
colder sites) before the experiment and 2 years after transplantation. Colors of symbols
reflects the climate origin of the community (see legend on b)). Straight lines: alpine vs. subalpine communities ; dotted lines: Sub-alpine vs. boreal communities. Note that the before
transplantation data were sampled when the communities of each pair were still in their

630	different origin sites, and this contrast thus reflects the pre-treatment climate contrasts
631	between adjacent sites along the temperature gradient. When significant interactions between
632	temperature and transplantation treatment were detected, indicating that the magnitude of
633	difference between plot pairs depends on the temperature regime, two p.values are reported,
634	one for each contrast. a, b: Vascular plant biomass index; c, d: Bryophyte biomass index; e, f:
635	community weighted mean (CWM) leaf area; g,h: CWM plant height; i, j: CWM specific leaf
636	area.





Figure 4: community openness to recruitment (Δseedling emergence between transplanted
plots and locally replanted controls) in response to community-weighted mean leaf area (a)
and plant height (b). Δseedling.emergence (#): differences in seedling emergence between
warmer-climate controls and colder-climate transplants in number of seedlings.; Δleaf.area,
Δplant.height: differences in community characteristics between controls and transplants.
Δseedling.emergence did not respond significantly to Δvascular plant biomass, Δbryophyte
biomass and ΔSLA (see appendix S1 for similar plots for these traits).





Appendix s1: Seedling emergence non-responses to vascular plant biomass (a), bryophyte
biomass (b) and SLA (c). Δseedling.emergence (#): differences in seedling emergence

- 650 between warmer- and colder-climate communities in number of seedlings.; Δvascular plant
- biomass,  $\Delta$  bryophyte biomass and  $\Delta$ SLA: differences in these community characteristics
- between warmer- and colder-climate communities.