

1 **Title: Are subalpine species' seedling emergence and establishment in the alpine limited**
2 **by climate or biotic interactions?**

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28 **Abstract:**

29 Plants are responding to climate change by shifting their ranges to higher elevations. These
30 range shifts are not happening at the same rate for all species, for example, subalpine species
31 are generally moving faster upslope than alpine species, but with large variation within groups.
32 This asymmetry in migration rates will result in novel communities and interactions between
33 plant species that have not previously co-occurred. While seed dispersal is obviously critical
34 for species' range shifts, seedling emergence and survival are also major bottlenecks for
35 successful colonization in new areas. As seedlings generally constitute the most vulnerable
36 stages in the life-history of plants, variation in seedling establishment success can potentially
37 be important determinants of species' range shift rates. Previous studies have found that
38 warming *per se* tends to increase seedling establishment in alpine climates, but it also increases
39 plant productivity and thus competition for nutrients and light from the resident vegetation,
40 which acts limiting on seedling establishment. This study will attempt to disentangle the
41 relative importance of these abiotic and biotic factors on sub-alpine species' seedling
42 emergence and survival in alpine habitats, to help further understanding and prediction of future
43 lowland plant colonization in alpine habitats. We will also explore if species' life strategies
44 impact their ability to colonize new locations, predicting that species with resource acquisitive
45 traits will emerge earlier and faster than resource conservative species. To address these
46 questions, we will perform a seed transplant experiment where we assess seedling emergence
47 and establishment in the alpine. Seeds will be sown in plots with and without experimental
48 warming, crossed with manipulation of biotic interactions, and using seeds from both resource
49 conservative and resource acquisitive subalpine species. In addition, we will explore if the
50 observed responses are general or context-dependent by replicating this experiment along a
51 regional bioclimatic precipitation gradient.

52 INTRODUCTION

53 Climate warming is generally happening faster at higher elevations than in adjacent lower-
54 elevation areas (Pepin *et al.*, 2015), triggering range shifts of species along elevational
55 gradients (Rumpf *et al.*, 2019). We observe faster upslope colonization by subalpine species
56 compared to high elevation species (Mamantov *et al.*, 2021), resulting in altered plant
57 community composition and novel interactions between species that have not previously co-
58 occurred (Alexander, Diez and Levine, 2015). The nature of these novel interactions will
59 depend on the life strategy of the range expanding species, and in particular on adaptations
60 affecting their competitive effects and responses (Goldberg and Landa, 1991; Kraft *et al.*, 2014;
61 Funk and Wolf, 2016). At higher elevations, adverse climatic conditions limit plant life
62 processes, and alpine plant communities are therefore generally characterised by low
63 productivity, facilitative or neutral plant-plant interactions, and species with resource
64 conservative life strategies (Körner, 1989; Read *et al.*, 2014; Olsen *et al.*, 2016). At lower
65 elevations, where climate is less limiting, plant communities are generally more productive,
66 and characterized by more intense competition for light, and more functionally diverse
67 communities harbouring both species with resource acquisitive and resource conservative life
68 strategies (Callaway *et al.*, 2002). Warming is predicted to cause increased productivity, taller
69 vegetation and more standing biomass, and increased competition for light in the alpine (Olsen
70 *et al.*, 2016; Steinbauer *et al.*, 2018). This suggests that resource-acquisitive species from the
71 lowlands might have a competitive advantage over the extant species in alpine habitats under
72 climate change. However, for subalpine species to colonize alpine locations they need to be
73 able to disperse to and establish in the alpine locations.

74 For a majority of plant species, seeds are the only means of long-distance dispersal, and are
75 therefore a critical part of their ability to shift their ranges (Nathan and Muller-Landau, 2000;
76 Mondoni *et al.*, 2015). Germinating seeds and young seedlings are vulnerable to numerous
77 abiotic and biotic factors (Fenner and Thompson, 2005; Baskin and Baskin, 2014), and the
78 seedling stage represents, arguably, the most vulnerable part of the life cycle of a plant.
79 Dispersal to and arrival at a new site is no guarantee for establishment, and a species' ability
80 to shift its range is therefore dependent not only on dispersal *per se*, but also on successful seed
81 recruitment in the new sites as the seed must emerge and the seedling must survive (Eriksson,
82 2000). Both seed dispersal and seedling establishment are therefore considered major
83 bottlenecks in the life history of plants in many ecosystems as they can limit species from

84 shifting their ranges to higher elevations (Shevtsova *et al.*, 2009; Guittar *et al.*, 2020). Despite
85 the critical importance of seeds and seedlings for species migration and persistence, most
86 studies on climate change in alpine areas focus on the response of adult plants to warming
87 (Briceño, Hoyle and Nicotra, 2015; Larson and Funk, 2016). As climate change is expected to
88 greatly impact a host of biotic and abiotic factors that are known to affect regeneration success
89 in the alpine, there is a need for insight into what factors might limit seed establishment in
90 alpine environments today and under future climates (Mondoni *et al.*, 2015).

91 In alpine ecosystems, plant development and performance are co-limited by abiotic factors like
92 low temperatures, short growing seasons, and variable moisture availability during the growing
93 season (Shevtsova *et al.*, 2009). Interactions between these limiting factors complicate
94 predictions of climate change impacts. On one hand, climate warming can lead to decreased
95 abiotic stress and extend the period of favourable temperatures for seedling emergence and
96 establishment (Shevtsova *et al.*, 2009; Wipf and Rixen, 2010). On the other hand, this increase
97 in temperature can also result in earlier snowmelt and generally higher evaporation losses,
98 which may both increase drought risks later in the growing season (Horton *et al.*, 2006). In
99 general, lower availability of moisture is related to lower rates of seedling establishment in
100 alpine environments (Forbis, 2003; Meineri *et al.* 2013). Differences in moisture availability,
101 for instance due to different precipitation regimes, may enhance, moderate, or even shift the
102 direction of the effects of temperature (Töpfer *et al.*, 2018), which raises the question of how
103 the net-effect of warming and reduced moisture availability on seedling establishment depends
104 on the local climatic context.

105 Climate change will affect plants through direct physiological responses to temperature and
106 precipitation, but also indirectly through biotic interactions (Adler, Dalglish and Ellner, 2012).
107 In environments with less abiotic stress we generally expect more competitive interactions for
108 light (Choler, Michalet and Callaway, 2001), while toward environments with increased abiotic
109 stress we expect these biotic interactions to shift towards less intense competitive interactions,
110 or even to facilitative interactions (He, Bertness and Altieri, 2013). Under warming we
111 therefore expect that both the nature and intensity of biotic interactions will change, as
112 demonstrated in studies that report increased intensity of plant-plant competition for light with
113 warming (Olsen and Klanderud, 2014; Meineri *et al.*, 2020). Especially for early life-history
114 stages such indirect, biotic effects of climate warming may be of high importance in addition
115 to direct, abiotic effects (Louthan *et al.*, 2018; Klanderud *et al.*, 2021). Increased competition

116 for light within a denser and taller resident vegetation as the climate warms may decrease
117 community invasibility and increase competitive effects (Olsen and Klanderud, 2014;
118 Klanderud *et al.*, 2017; Meineri *et al.*, 2020). This might give an advantage to colonizing
119 species with ‘lowland traits’ such as a resource-acquisitive life strategy that may better enable
120 them to compete for light and also exploit low and variable light conditions (Adler *et al.*, 2013).

121 To explore the abiotic and biotic factors limiting establishment of subalpine plant species in
122 alpine locations, we perform a seed transplant experiment. Seeds of subalpine species are sown
123 in alpine locations inside and outside Open Top Chambers (OTCs), that elevate air
124 temperatures by approximately 2°C. This allows us to assess whether seedling recruitment
125 success of subalpine species in the alpine are temperature limited under current climates and
126 will increase under future warmer climates. To test for effects of biotic interactions, the seeds
127 were sown in plots where the above-ground vegetation had been removed (bare-ground gaps)
128 and in plots with intact vegetation both inside and outside the OTCs. To test for differences in
129 responses between resource-acquisitive and resource-conservative species, we selected three
130 species with a resource acquisitive strategy (*Succisa pratensis*, *Hypericum maculatum* and
131 *Carex pallescens*) and three with a resource conservative strategy for the experiment (*Veronica*
132 *officinalis*, *Viola canina* and *Carex pilulifera*) (see Figure 1). To test for climate context-
133 dependencies in the seedling emergence response to warming and biotic interactions, the
134 experiments were replicated at four sites along a precipitation gradient in western Norway,
135 where annual precipitation ranges from 600-3000 mm/year. For each of the four alpine study
136 sites, seeds were collected at four nearby subalpine locations differing by approximately 2°C
137 in mean summer temperature (i.e., approximately 400 m elevation difference, www.met.no).
138 This design resulted in a total of 160 plots and 480 species’ contrasts (4 sites x 2 warming
139 treatments x 2 biotic treatments x 5 replicate blocks x 2 functional groups x 3 replicate species).

140 From the argumentation outlined above we expect earlier and faster emergence in the
141 experimentally warmed plots relative to the control plots outside the OTCs. As we predict
142 biotic interactions will shift from competitive to neutral or facilitative with decreasing
143 temperature, we expect the effect of vegetation removal (i.e., isolating the abiotic effect, as the
144 biotic interactions from the above-ground vegetation is removed) to increase seedling
145 emergence and establishment in the warmed plots, but have a neutral to negative effect in the
146 control plots. We expect the resource acquisitive subalpine species to emerge earlier and
147 establish faster than the resource conservative ones, an effect that we expect will be amplified

148 in the warmer microclimate inside the OTCs as emergence rate increases in general. Due to
 149 interactions between temperature and moisture effects on seedlings, we expect context-
 150 dependencies in these patterns along the precipitation gradient, and specifically that the abiotic
 151 and biotic effects of warming on recruitment described above should be more pronounced in
 152 the wetter sites, where warming mainly increases productivity relative to drier sites, where
 153 warming also increases drought risk.



Figure 1: Study species as adults and seedlings. (a) *Hypericum maculatum*, (b) *Succisa pratensis*, (c) *Carex pallescens*, (d) *Veronica officinalis*, (e) *Viola canina*, (f) *Carex pilulifera*. (Photos: adult individuals a-b, seedlings a-f Ingrid Dahle; adult individuals c-f Ragnhild Gya)

154 ### Figure 1 ###

155 METHODS

156 Study sites

157 The study was conducted at four alpine locations along a precipitation gradient from
 158 continental east to oceanic west in southwest of Norway (Figure 2). The annual precipitation
 159 ranges from 600-3000 mm/year, whereas all alpine sites had mean temperature during the
 160 growing season at around 6°C (four warmest months per year) (met.no). Seeds were collected
 161 from four subalpine locations that were paired with the alpine study localities, selected to

162 represent the same precipitation gradient,
 163 but with a mean temperature during the
 164 growing season at around 8°C (sub-alpine
 165 sites in Klanderud, Vandvik and Goldberg,
 166 2015). The seeds were transplanted to the
 167 alpine locations from the paired subalpine
 168 locations with corresponding amount of
 169 precipitation, or from subalpine sites with
 170 as similar in precipitation as possible when
 171 seeds were not available from the paired
 172 locations (See Table 2 in Appendix I for
 173 full overview). For one species (*Succisa*
 174 *pratensis*) we collected seeds at a different
 175 location due to low amounts of flowering
 176 individuals in the subalpine sites (see green
 177 square in Figure 2, and Bolstadøyri in Table

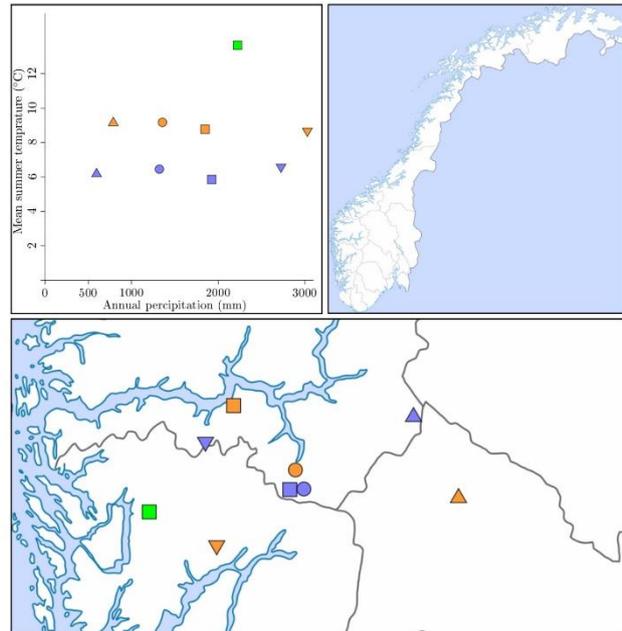


Figure 2: Map of locations in Western Norway with two levels of temperatures measured with mean of four warmest months and four levels of precipitation measured in mean annual precipitation. The experiment was conducted in the alpine locations (marked blue), while seeds were collected from the subalpine locations (marked in orange) and Bolstadøyri (green).

178 1). To facilitate comparison along the precipitation gradient, the sites were chosen to keep
 179 factors other than climate as similar as possible, for example grazing regime and history,
 180 bedrock, vegetation type and structure, slope, and exposure (Table 1). The sites are all
 181 grasslands associated with calcareous bedrock (Klanderud, Vandvik and Goldberg, 2015).

182 ### Figure 2 ###

183 **Table 1: Overview of locations with mean summer temperature, annual precipitation, bedrock, and**
 184 **coordinates.** *Bolstadøyri is boreal, not subalpine. Bedrock data collected from: <http://geo.ngu.no/kart/berggrunn/>;
 185 Climate data collected from: met.no. Table modified from Klanderud, 2015 and Gya, 2017.

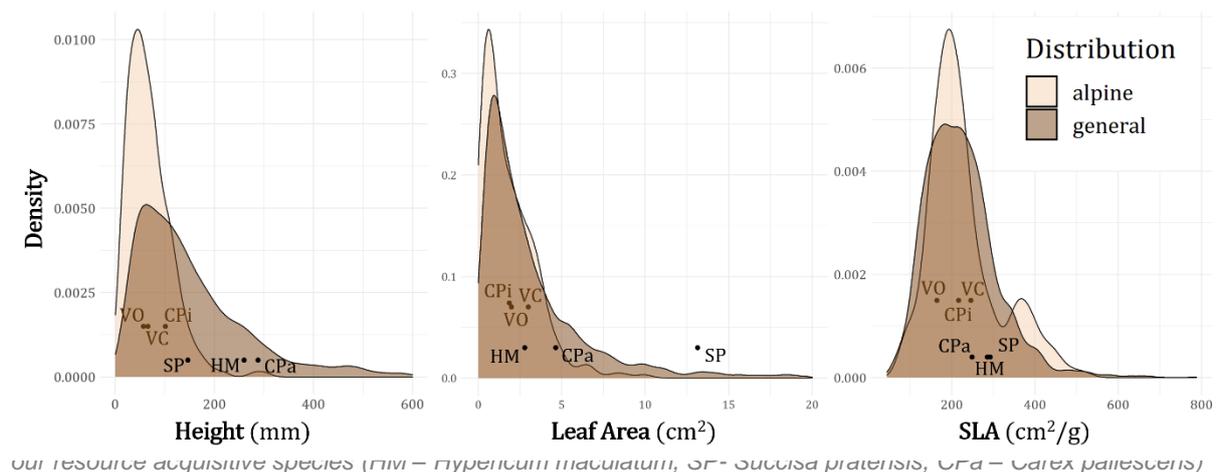
Vegetation zone	Site	Longitude	Latitude	Altitude (m.a.s.l.)	Temperature (°C)	Precipitation (mm year ⁻¹)	Bedrock
Alpine	Skjellingahaugen	60.9335	6.41504	1088	6.58	2725	Marble
	Gudmedalen	60.8328	7.17561	1213	5.85	1925	Rhyolite, Rhyodacite, Dacite
	Låvisdalen	60.8231	7.27596	1097	6.45	1321	Rhyolite, Rhyodacite, Dacite
	Ulvehaugen	61.0243	8.12343	1208	6.17	596	Rhyolite, Rhyodacite, Dacite
Subalpine	Veskre	60.5445	6.51468	797	8.67	3029	(Meta) sandstone, Shale
	Rambera	61.0866	6.63028	769	8.77	1848	Phyllite, Mica schist
	Høgsete	60.8760	7.17666	700	9.17	1356	Phyllite, Mica schist

Álrust	60.8203	8.70466	815	9.14	789	(Meta) sandstone, Shale
Bolstadøyri*	60.6479	9.00120	42	13.65	2223	Phyllite

186 Selection of species and seed collection

187 Six target species for the transplant experiment were selected to represent two contrasting
188 resource strategies, resource conservative and resource acquisitive species (Díaz *et al.*, 2004).
189 The resource conservative species were chosen so that their adult functional trait values
190 resemble those found in the alpine plant communities, whereas the resource acquisitive species
191 were chosen to be more resource acquisitive in terms of at least two of three functional traits
192 (i) higher vegetative height, (ii) lower specific leaf area (SLA), and/or (iii) larger leaf area
193 (Figure 3). These traits were used as they indicate performance with respect to either light
194 interception or growth rate, which has been found to be important for competitive ability for
195 light/space of adult colonizing species (Van Kleunen, Weber and Fischer, 2010). Generally,
196 the functional traits of adult plants can give an indication of the resource strategy consistent
197 across life-history stages (Adler *et al.*, 2013; Zhu *et al.*, 2018). This may however not always
198 be the case, as ontogenetic shifts in resource strategies between juveniles and adult individuals
199 have been documented in the literature (Šmilauerová and Šmilauer, 2007; Mediavilla *et al.*,
200 2014; Dayrell *et al.*, 2018). Our study species were primarily chosen due to the expected impact
201 of their adult traits on alpine ecosystems, whether they will introduce functional novelty to the
202 system (acquisitive resource strategy) or not (conservative resource strategy), and we will test
203 whether their ability to emerge differs between these strategies.

204 Based on this rationale and using functional trait data collected from species in the study sites
205 (Gya, 2017), we selected *Veronica officinalis*, *Viola canina* and *Carex pilulifera* as the
206 resource-conservative species and *Succisa pratensis*, *Hypericum maculatum* and *Carex*
207 *pallescens* as the resource-acquisitive species (see Figure 3).

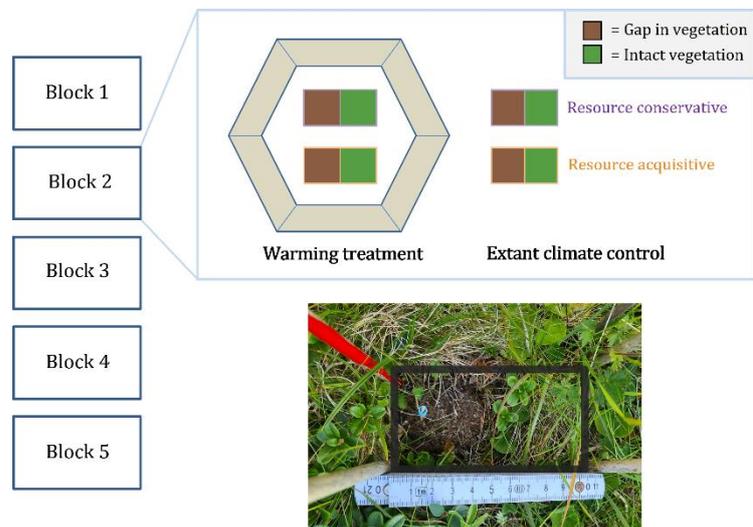


208 For each of these species, as many seeds as possible were collected during the 2020 season, in
 209 August and September, from between 10 to 50 individuals per site depending on species and
 210 how many seeds each individual plant produced. Seeds were stored in room temperature under
 211 dry conditions until seeds could be sown in the field.

212 #### Figure 3 ####

213 Experimental design

214 In each of the sites, we selected
 215 five blocks randomly to fit the
 216 target vegetation and for practical
 217 reasons. These blocks are all
 218 located in alpine grassland
 219 vegetation and consist of a paired
 220 design of plots under an OTC and
 221 a warming control. In each OTC
 222 and control, we created two paired
 223 adjacent 5x5 cm² vegetated and
 224 bare ground treatment plots.
 225 Within the pairs, the right-hand
 226 plot, when facing the plots up-



227 **Figure 4:** The **Experimental design** comprises a full-factorial
 228 combination of both resource strategies and the experimental
 229 treatments (warming and gaps), replicated in five random blocks at
 230 each site. Picture of adjacent bare ground plot and intact vegetation
 231 plot (Photo: Ingrid Dahle)

227 slope, was allocated to the intact vegetation treatment and the left-hand plot was allocated to
 228 the bare-ground treatment. Bare ground gaps were created by cutting around the edges and
 229 turning upside down the grassland turf in each 5x5 cm² plot. One of the pairs of plots within
 230 each OTC or control climate was allocated to the resource conservative species, the other to
 231 the resource acquisitive species. This design resulted in in a total 40 5x5 cm² plots per site (5
 232 blocks x 2 OTC treatments x 2 vegetation treatments x 2 life-history strategies) (Figure 4).

233 #### Figure 4 ####

234 The collected seeds were allocated to the plots at all four locations as follows: 30 seeds per plot
 235 were sown of each of *Hypericum maculatum*, *Veronica officinalis* and *Carex pallescens*, 20
 236 seeds each of *Viola canina* and *Succisa pratensis*, whereas 25 seeds of *Carex pilulifera* were
 237 sown in all plots at only one location due to low seed availability (Skjellingahaugen – the
 238 wettest location). This resulted in a total of 10 900 seeds being sown out. During collection we

239 aimed to collect 20 to 30 seeds of each species based on previous studies that had carried out
240 similar experiments (Meineri, Spindelböck and Vandvik, 2013), and the number of seeds varied
241 between the different species based on the amount of seeds we were able to collect in the field.
242 Seeds were sown out in October of 2020 to allow the seeds to experience cold stratification *in*
243 *situ* during the winter to break any potential dormancy, which is common in boreal species
244 (Baskin and Baskin, 2014).

245 During sowing, the seeds were scattered evenly on the bare soil in the gaps and onto the intact
246 vegetation. To prevent the seeds from being blown or washed away from the gap plots, seeds
247 were pressed down slightly/few millimetres into the soil surface, but not covered, following
248 the method of Tingstad *et al.* (2015).

249 During the 2021 growing season the seedling emergence and survival will be measured in 2-
250 week intervals from early to late growing season (around beginning of June to end of August,
251 depending on snowmelt). Seedlings will be marked with numbered toothpicks to distinguish
252 survived and freshly emerged seedlings between scoring rounds.

253 In the plots with intact vegetation, vegetation height, moss depth, and percentage cover of
254 vascular plants and of moss will be measured during peak growing season as indicators of
255 biomass / productivity.

256 **Climate data**

257 We use Tomst loggers (TMS-4) to collect microclimate data; air temperature (15 cm above the
258 ground), temperature in the vegetation (2 cm above the ground), and soil temperature (6 cm
259 below the ground). Soil moisture is measured at 6 cm below the soil surface. We have one
260 logger per warmed and unwarmed replicate within 1.5 meters of the experimental plot. We will
261 use this climate data to document the temperature increase inside the OTC and report on the
262 climatic difference between the warmed and unwarmed treatments.

263 **Proposed data analysis**

264 We will use generalized linear mixed effects models (GLMM) to investigate the effects of
265 warming, precipitation context, gaps, and resource strategy on seedling emergence and
266 establishment. All statistical analyses will be performed in R (R Core Team, 2020), using the
267 lme4 package (Bates *et al.*, 2015). Our predictor variables will be warming treatment (2 levels),
268 gaps (2 levels), life strategy (2 levels), and precipitation context (4 levels). For emergence, we

269 will run models on (i) the total proportion seedlings emerged using a binomial error distribution
270 and logit-link, and on (ii) days to 50% emergence from start of emergence using a Poisson error
271 distribution with log-link. For seedling establishment, we will run a model on total proportion
272 of survived seedlings using a binomial error distribution and logit-link. We will include site,
273 and if model convergence allows, block, as well as species in all models as random effects to
274 account for the nested structure of the study design.

275 As our hypotheses concern interactions between several of our factors we will run full models
276 including, if possible, a four-factor interaction to test our hypotheses that warming,
277 precipitation, intact vegetation or gaps and the life strategy of the subalpine species will affect
278 the emergence success. Note that the four-way interaction is not strictly speaking needed to test
279 our hypotheses, as our specific questions below all deal with three-way interactions within the
280 proposed fixed-effects parameterization. Starting from a full factorial approach, we will
281 perform a backward elimination to identify the best, but most parsimonious model, and use the
282 significance and effect sizes from the final model to test hypotheses and discuss the biological
283 importance of the different predictor variables. This backward selection approach is preferred
284 over a full model approach due to ease of interpretation and avoidance of overfitting. Model
285 suitability with respect to statistical assumptions will be assessed by running model diagnostics
286 including tests for homoscedasticity and normality of errors. Using this modelling approach,
287 we will address the following questions and test a number of specific predictions:

288 *1) Do species with differing life strategies vary in their seedling emergence and*
289 *establishment under warming, and do these relationships change along a precipitation*
290 *gradient?*

291 For *question one* we will test the following predictions: **P1)** We expect higher emergence rate
292 and earlier emergence in the experimentally warmed plots compared to the control plots outside
293 the OTCs, **P2)** We expect that the emergence of the subalpine species will start earlier and
294 emerge at a faster rate towards the wetter locations, and **P3)** We expect the resource acquisitive
295 subalpine species to emerge earlier and faster than the resource conservative species, which
296 will be amplified in the warmer microclimate inside the OTCs, and toward the wetter locations.
297 Note that this question, if confirmed, will emerge in the full factorial model as a significant
298 interaction between the independent variables' life strategy, experimental warming, and
299 precipitation.

300 2) *Does the nature and intensity of biotic interactions increase with warming, and do these*
301 *relationships change along a precipitation gradient?*

302 For *question two* we will test the following predictions: **P4)** We expect that gaps in vegetation
303 will enhance the total proportion of seedlings emerged and decrease time to 50% emergence in
304 the warmed plots, and **P5)** This effect will be enhanced toward the wetter locations. Note that
305 this question, if confirmed, will emerge in the full factorial model as a significant interaction
306 between the independent variables' biotic interactions, experimental warming, and
307 precipitation.

308 3) *Do seedling emergence and establishment for species with differing life strategies vary*
309 *in their response to biotic interactions under warming?*

310 For *question three* we will test the following predictions: **P6)** We expect that resource
311 acquisitive species will tolerate competition from the resident vegetation better than resource
312 conservative species, and this difference will be amplified in the warmer plots. Note that this
313 question, if confirmed, will emerge in the full factorial model as a significant interaction
314 between the independent variables' life strategy, biotic interactions, and experimental
315 warming.

316 **Data availability**

317 BioArchive

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453

454 **Appendix I**

455 **Table 2: Overview over the sites that the seeds originated from.** Seeds were moved from subalpine locations
 456 to alpine locations along the same precipitation gradient. Green indicates seeds were moved from source site at
 457 same precipitation level as our alpine location. Yellow indicates source site was one level drier or wetter, orange
 458 indicates source site was two levels drier or wetter, and red indicates source site was three levels drier or wetter.
 459 At two locations one species had seeds that were a mix from two source sites (approximately 50% of seeds from
 460 each location).

Species\locations	Skjellingahaugen	Gudmedalen	Låvisdalen	Ulvehaugen
<i>Veronica officinalis</i>	Høgsete	Rambera/Høgsete	Høgsete	Ålrust
<i>Viola canina</i>	Veskre/Ålrust	Ålrust	Høgsete	Ålrust
<i>Carex pilulifera</i>	Rambera	-	-	-
<i>Succisa pratensis</i>	Bolstadøyri	Bolstadøyri	Bolstadøyri	Bolstadøyri
<i>Hypericum maculatum</i>	Veskre	Høgsete	Høgsete	Ålrust
<i>Carex pallescens</i>	Veskre	Rambera	Høgsete	Ålrust

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