

Title: Are subalpine species' seedling emergence and establishment in the alpine limited 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

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

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

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

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

Figure 1

METHODS

Study sites

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

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

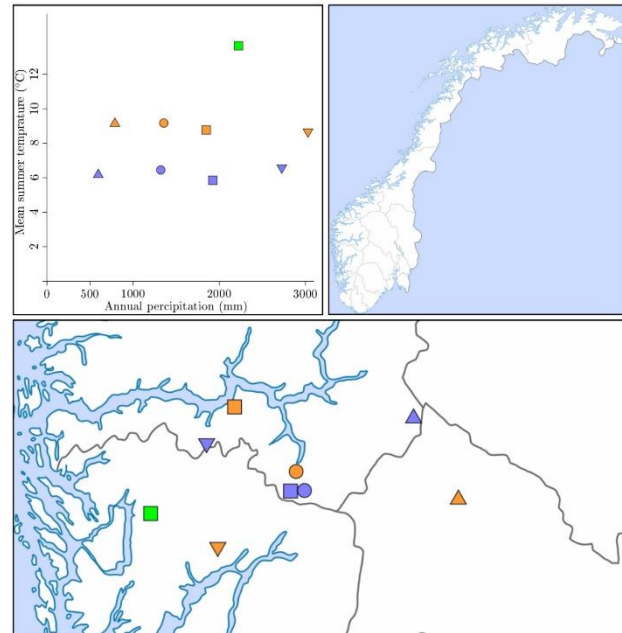


Figure 2: Map of locations in Western Norway with two levels of temperatures measured with mean of four warmest months and four levels of precipitation measured in mean annual precipitation. The experiment was conducted in the alpine locations (marked blue), while seeds were collected from the subalpine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

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

Figure 2

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

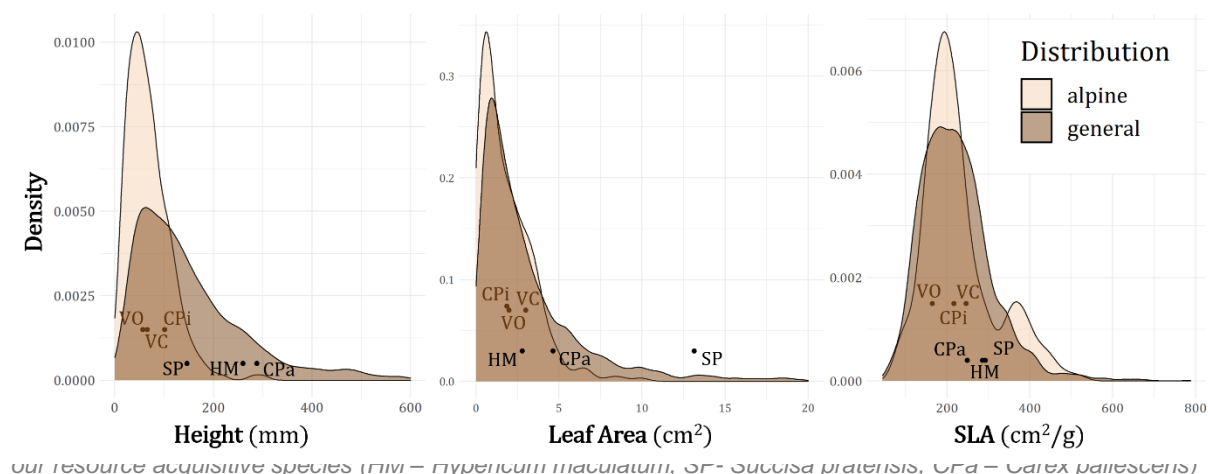
Vegetation zone	Site	Longitude	Latitude	Altitude (m.a.s.l.)	Temperature (°C)	Precipitation (mm year ⁻¹)	Bedrock
Alpine	Skjellingahaugen	60.9335	6.41504	1088	6.58	2725	Marble
	Gudmedalen	60.8328	7.17561	1213	5.85	1925	Rhyolite, Rhyodacite, Dacite
	Låvisdalen	60.8231	7.27596	1097	6.45	1321	Rhyolite, Rhyodacite, 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

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

Selection of species and seed collection

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

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



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

Figure 3

Experimental design

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

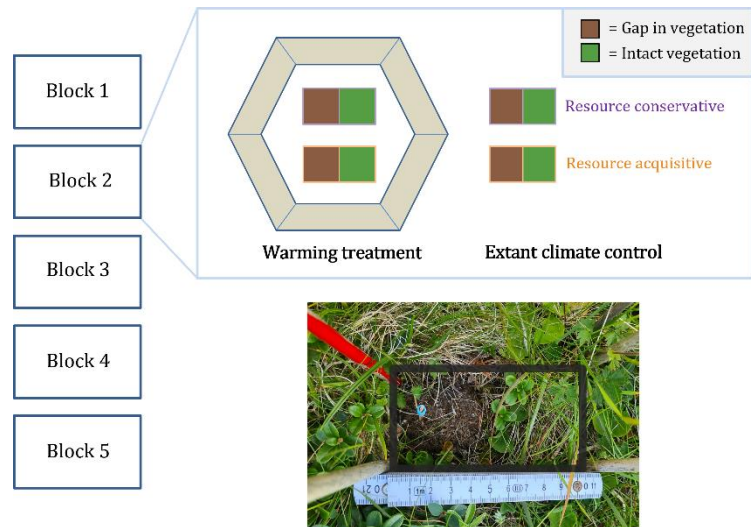


Figure 4: The **Experimental design** comprises a full-factorial combination of both resource strategies and the experimental treatments (warming and gaps), replicated in five random blocks at each site. Picture of adjacent bare ground plot and intact vegetation plot (Photo: Ingrid Dahle)

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

Figure 4

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

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

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

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

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

Climate data

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

Proposed data analysis

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

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

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

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

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

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

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

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

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

Data availability

BioArchive

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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	Ramberg/Høgsete	Høgsete	Ålrust
<i>Viola canina</i>	Veskre/Ålrust	Ålrust	Høgsete	Ålrust
<i>Carex pilulifera</i>	Ramberg	-	-	-
<i>Succisa pratensis</i>	Bolstadøyri	Bolstadøyri	Bolstadøyri	Bolstadøyri
<i>Hypericum maculatum</i>	Veskre	Høgsete	Høgsete	Ålrust
<i>Carex pallescens</i>	Veskre	Ramberg	Høgsete	Ålrust