# Microclimate regulates seed germination phenology in Temperate and Mediterranean alpine communities.

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## Abstract (max 250 words)

Understanding the plasticity of seed germination phenology is important to predict the resilience of plant communities to climate change; yet we know very little about the influence of alpine microclimates on germination phenology. We conducted a continuous seasonal temperature experiment with fresh seeds to investigate germination phenology in incubator chambers. We defined two contrasting microclimatic scenarios mirroring yearly temperature data series recorded in alpine soils: (1) fellfield scenario (warmer temperatures and snow-free) and (2) snowbed scenario (cooler temperatures and lengthy snow period). We replicated the experiment for species sampled in Mediterranean (N = 21) and temperate (N = 38) alpine communities from the same biogeographical region in the Cantabrian Mountains (northern Spain). By defining seven traits related to germination phenology, we found consistent effects of fellfield and snowbed scenarios in the two communities. In autumn and spring, communities germinated more in the fellfield scenario, while the opposite trend was observed during winter and summer, with higher germination in snowbed conditions. The germination responses were consistent with the expected germination syndromes of both communities. Lower dormancy and higher autumn germination were observed in the Mediterranean rather than in the temperate community, which experienced higher germination after cold stratification and warm temperatures. Our results suggest that a warming scenario with reduced snow cover and higher temperatures will lead to advanced and accelerated germination and will likely have disrupting effects on communities with strict cold germination requirements, especially in temperate alpine communities.

## 1. Introduction

The alpine biome is characterized by extreme climatic conditions, short growing seasons, and high topographic roughness (Körner 2021). At fine scales, topographic roughness translates into a mosaic of microclimatic conditions (Scherrer & Körner 2011) especially incident in the snow-melting gradient and the temperature regimes (Körner 2021). These microclimatic conditions show a sharp temperature gradient over a few centimeters (Graham et al. 2012); likely modifying plant community assembly processes and favoring the development of specific adaptations (Körner 2021). The micro-topographic gradient also determines local richness (Schöb et al. 2009), compositional (Jiménez-Alfaro et al. 2014), and functional diversity (García-Gutiérrez et al. 2018). Thus, seems logical to think that the regeneration niche (Grubb 1977) may also differ according to this micro-topographic gradient. Recent studies highlight the importance of integrating regeneration traits in plant community ecology (Jiménez-Alfaro et al. 2016) that can explain an independent axis of variation (Hoyle et al. 2015). Germination, which can be considered the first stage of regeneration, is a sensitive (Hoyle et al. 2015) and irreversible process (Baskin & Baskin 2014). Therefore, germination strategies and phenology have strong fitness implications for plant development and survival (Donohue 2005; Poschlod et al. 2013). Recent studies defined a global “alpine germination syndrome”, characterized by the requirement of a period of cold stratification followed by warm temperatures to initiate germination (Baskin & Baskin 2014; Fernández-Pascual et al. 2021). This strategy avoids adverse periods and ensure germination at the beginning of growing season when water is available, and seedlings have time to develop a deep root system before summer drought periods and the following winter (Billings & Mooney 1968).

Even though this alpine syndrome has been detected, the data available behind it mostly originated in temperate regions (Fernández-Pascual et al. 2021), thus is geographically limited. Considering that germination strategies are highly variable in alpine ecosystems (Wagner & Simons 2009) it is reasonable to think that they might differ across latitudinal ranges. A different germination syndrome was proposed for high altitude areas with Mediterranean climate where species germinate immediately after dispersal if water is available and show improved germination after cold stratification, referred to as “Mediterranean germination syndrome” (Giménez-Benavides et al. 2005). Nevertheless, the underlying causes of the variation observed deviating from the main germination syndromes are still unknown. In case-specific studies, germination variability was partly explained by species altitudinal range (Fernández-Pascual et al., 2017), bedrock (Tudela-Isanta, Fernández-Pascual, et al. 2018; Tudela-Isanta, Ladouceur, et al. 2018), species order of appearance in glacier foreland succession (Schwienbacher et al. 2012) or species realized niche within the snowmelt gradient (Rosbakh et al. 2022). Thus, potentially microclimatic conditions can be another source of variation in germination responses. However, the few studies that consider microclimatic variability found contrasting results. (Shimono & Kudo 2005) found no differences between fellfield and snowbeds specialist while Rosbakh et al. 2022 did found that species germination was affected by the position laong the snowmelt gradient. Nonetheless, these studies are based on standard laboratory procedures with seeds subjected to specific treatments constant throughout the experiment and for a short period of time. These experimental designs barely mimic real field climatic conditions and fluctuations, especially in the alpine environment (see “paper Picos”). To draw more robust conclusions about real-life germination strategies happening in alpine areas we need habitat specific detailed climatic data (Shimono & Kudo 2005) and accurate experimental settings that can provide that level of detail. Filling these knowledge gaps will help us understand and predict community responses to future climate scenarios.

The approach we present here is to study germination phenology across a whole year in two contrasting microclimatic scenarios through a variety of germination traits. For the study purpose, we defined two microclimatic scenarios: one mimicking exposed micro-edges (referred to as “fellfield scenario”) i.e., more open and exposed areas subjected to wind, freeze and thaw cycles without snow protections in winter, and dry periods in summer; and the other mimicking micro-valleys (referred to as “snowbed scenario”) i.e., areas with dense plant cover, long snow cover and high moisture. The specific questions we want to investigate are: (1) will microclimatic scenarios modify the germination phenology of alpine communities? And (2) do alpine communities from different macroclimates show different patterns of germination phenology?

Regarding our first question, we hypothesize that microclimatic scenarios will result in differences in the germination phenology of alpine communities. Exposed micro-edges have higher annual temperatures, longer growing seasons, shorter winters, and more frequent freezing events than micro-valleys. Thus, we expect the fellfield scenario to result in faster germination, higher germination in early season, higher total germination and lower or no germination in winter. In the snowbed scenario, we expect the opposite germination pattern. Considering our second question, we hypothesize that a temperate alpine community will show a higher concordance with the global alpine germination syndrome (Fernández-Pascual et al. 2021) than a Mediterranean alpine community. In the temperate alpine community, we expect more germination after cold stratification and under warmer temperatures, while in the Mediterranean community we expect faster germination and germination at colder temperatures (Giménez-Benavides et al. 2005).

## 2. Methods

### 2.1 Study system

Our study focuses on alpine grasslands between 1900 and 2500 m a.s.l in the Cantabrian Mountains, a mountain range running E-W in northern Spain. The Cantabrian mountains are considered a transitional biogeographical hub between Eurosiberian and Mediterranean regions (Jiménez-Alfaro et al. 2021), influenced by mediterranean/continental climate in southern slopes and temperate/oceanic climate in northern slopes (Fig 1). The particularity of its geographic location facilitates the coexistence of a complex array of communities with species adapted to both climates. We established two study communities in two contrasting ecosystems of the Cantabrian high mountains (Fig 1): (1) Mediterranean high mountain grasslands in the Valles de Omaña and Luna Biosphere Reserve; and (2) temperate alpine grasslands in the Picos de Europa National Park. Plant communities are dominated mostly by *Poaceae* and *Cyperaceae*, but they are also rich in Hemicryptophytes and Chamaephytes. The local alpine diversity is regulated by meso-topographic gradients that modify the relative abundance of species with Eurosiberian, Mediterranean or endemic origin (Jiménez-Alfaro et al. 2014). The temperate community presents higher richness with some relict alpine species. This community is located above calcareous bedrock (pH 6.5 - 6.8, own non-published data) and has an average annual precipitation around 3000 mm (usually less than 1-month dry periods in summer). Growing season starts in May until early October with a mean annual soil temperature of 5ºC. Grazing impact is restricted to wild populations of Cantabrian chamois (*Rupricapra pyrenaica parva*). The Mediterranean community is located above an acidic bedrock (pH 3.8 – 4.8, own non-published data), has a lower plant richness and experience 2-month dry period in summer (average annual precipitation of 1050 mm, mostly accumulated in spring and autumn). Growing season stretches from March to October with a mean annual soil temperature of 8ºC. Grazing impact is also restricted to wild populations of Cantabrian chamois.

### 2.1 Seed sampling

Within each community we established four seed sampling sites, separated at least 500 m from each other, assuming they form the same meta-population. In each collection site, we recorded all vascular plant species co-occurring in a central representative plot of 3 m radius. We considered the species recorded in the eight collection sites as the target community in our experiment (49 species in the temperate and 22 species in the Mediterranean communities).

During August-September 2021 we visited the collection sites every two weeks during the reproductive season and sampled ripe seeds or fruits (hereafter ‘seeds’ for simplicity) directly from the mother plants according to target species maturity peak. In general, we followed standard protocols for sampling seeds of wild populations to maximize intraspecific genetic diversity (ENSCONET 2009). Sampling took place within a 50 m radius from the central plot of each collection site, and we collected seeds from at least 20 - 50 individuals chosen at random. The goal was to collect at least 200 seeds from each target species in two sampling sites, maximizing spatial sampling within the community. In the temperate community we obtained seeds from 38 target species, of which 19 were represented by 2 sites. In the Mediterranean community we obtained enough seeds from 21 target species, covering two collection sites for each species except in 2 cases. Only three species (*Jurinea humilis*, *Thymus praecox* and *Silene ciliata*) were present in both communities (with two collection sites sampled in each community).

### 2.2 Microclimatic scenarios

We performed a continuous seasonal germination experiment to mimic one year of temperature regimes previously recorded by us in the study communities. We used the temperate sites to establish our microclimatic scenarios because we had the longest temperature records (10 years vs. 1 year for the Mediterranean sites) and because the temperate system shows the highest microclimatic variation between micro-valleys (snowbeds) and micro-edges (fellfields). To create our microclimatic scenarios, we took 10 years of hourly temperature data (2008 - 2019 field data collected in alpine soils of our four sites at the Picos de Europa National Park, M-Log5W, GeoPrecision, Ettlingen, Germany; accuracy: +/- 0.1 ºC at 0 ºC, resolution: 0.01 ºC) and transformed it into weekly resolution for maximum (T max) and minimum daily temperatures (T min). We also used the registered temperatures to calculate the number of days with snow cover, estimated as days with less than one degree Celsius temperature variation around zero degrees between night and day (Zhang et al. 2005). Then, we chose the two most contrasting sites as climatic scenarios in snow cover period and temperatures to recreate those same conditions in incubation chambers (see fig 2A). The final experimental scenarios consisted of a weekly-resolution temperature program (fig 2B) with daily temperature ramps between daily Tmax and daily Tmin, and monthly-resolution photoperiod regimes. Each experimental scenario was configured using Fitolog 9000 software (version 9308, Aralab Pharmaceutical Stability software) in Aralab incubators (Aralab climatic chamber Fitoclima S600 PL, equipped with 4 led modules 11W 350mA). This software allowed us to use ramp settings for gradual temperature changes along each day and to monitor the incubators remotely. Both incubators run continuously from July 2021 to September 2022. We will refer to the incubator with warmer temperatures and snow-free mimicking micro-edge topography as “fellfield scenario” and the incubator with cooler temperatures and long snow period program mimicking micro-valleys will as “snowbed scenario”.

The major differences between incubators were the temperature regimes and the length and climatic conditions during the winter. In the fellfield scenario we programmed winter period with below 0 ºC temperatures, and daily temperature and photoperiod fluctuation for 144 days. While in the snowbed scenario we programmed constant 0 ºC and darkness for 196 days (see in Fig 2C). Consequently, the growing season length also differed, with 176 days in the fellfield scenario and 115 days in the snowbed scenario. Mean temperature differences between our two scenarios during the growing season were around three degrees Celsius each week (more detailed information about weekly programs in Supplementary table Xx) reaching a maximum mean temperature of 18.5 ºC in the fellfield scenario and 15.5 ºC in the snowbed scenario, both during last week of August.

### 2.3 Germination trials

Fresh seeds were manually cleaned and sown within 20 days of collection. Seed lots remained in room conditions between collection and sowing. We did a sequential sowing of each species according to their maturity peaks in the field, meaning seeds entered the incubators at their optimum dispersal time. Each seed lot (species x collection site, N = 95) was placed in both incubators simultaneously, sowing four replicates of 25 seeds in nine cm diameter Petri dishes (numbers were adapted for seed lots with fewer seeds available) with germination filter paper (Filtros Anoia S.A. paper for germination assays, Ref.518G085). Filter papers were kept soaked by adding two or three ml of distilled water every two weeks. Dishes were sealed with parafilm to maintain the moisture content, avoiding water stress throughout the growing season. During the winter, incubators remained closed to avoid increases of temperature that could trigger seed germination and therefore no water was added during that period.

We checked germination every two weeks before winter, and weekly after winter until the end of the experiment. As incubators remained closed during winter, we did not perform germination scores in that period. We removed seeds from the petri dishes once germination occurred (radicle > 1.5 mm long). We cut open under the binocular loupe non-germinated seeds at the end of the experiment to visually assess if they were empty, infected, or looked normal. We considered seeds with white and firm embryos viable, i.e. potentially germinable (Baskin & Baskin 2014). We did not consider empty or infected seeds for further analysis. The experiment was terminated after 14 months (July 2021 - September 2022), for a total of 28 germination scorings. We removed from further analysis populations with zero germination and those that had less than 25 % of viable seeds (N = 14), assuming we were not able to break dormancy or the seed quality during collection was not optimal. The final dataset (Supplementary X) consisted of the raw scoring data for 95 seed lots of 54 species representing 21 plant families. A total of 10,816 viable seeds were used in the experiment.

### 2.4 Data analysis

We defined a set of traits to describe germination phenology (see Table 1). These traits were chosen to synthesize the diverse patterns observed during the continuous germination experiment, by considering their functional ecological significance in the alpine ecosystem. Autumn and summer germination consider specific periods of time measured in calendar dates (i.e., equal length between incubators). Winter germination is defined by a specific thermal threshold, from last germination score before winter (11th of November, T mean < 3.5 ºC) until T mean > 2 ºC (i.e., different length between incubators). Spring germination consider germination from T mean > 2 ºC until summer solstice (germination score the 24th of June), having also different lengths between incubators (see Fig 2C). Total germination considers the accumulated germination at the end of the experiment. Finally, time to reach 50% germination (T50) and Environmental heat sum (EHS) focused on how much days and accumulated degrees the seeds experienced before reaching 50% germination (N=68).

We analyzed the data by fitting Markov Chain Monte Carlo generalized linear mixed models (MCMCglmm) with Bayesian estimation using the R package MCMCGLMM (Hadfield 2010). To model germination traits, we used binomial MCMCglmms (family = multinomial2) while for the t50 and EHS traits we scaled the values and used gaussian MCMCglmms (family = gaussian). To calculate t50 trait in days, we fitted a linear model between the two dates before and after reaching 50% germination to model the exact date and then count the number days from sowing. EHS was calculated summing the degrees experienced (considering daily mean temperature) from sowing date to T50 date for each Petri dish.

To answer the first question, we analyzed each community separately and modeled every germination trait as response variable and incubator as explanatory variable (fixed factor), while phylogeny and collection site (nested within species) were specified as random factors (germination metric ~ incubator). To answer the second question, we tested each germination trait as response variable and both incubator and community as explanatory variables (fixed factors) paying special attention to their interaction. Random factors remained the same as the first model (germination metric ~ incubator \* community). Phylogeny was included using a reconstructed tree for the 54 species, created with V.PHYLOMAKER R package (Jin & Qian 2019). In all models we used weakly informative priors, with parameter-expanded priors for the random effects. Each model was run for 1 000 000 iterations, with an initial burn of 100 000 and a thinning interval of 100. From the resulting posterior distributions, we calculated mean parameter estimates and 95% credible intervals (CI). To estimate phylogenetic signal of seed germination over all variables we used Pagels’s lambda (λ) (Pagel, 1999).

## 3. Results

### 3.1. Microclimatic scenarios responses

Visualization of the cumulative germination data showed consistent differences between microclimatic scenarios in both communities (Fig 3).

In the fellfield scenario we observed significantly higher autumn and spring germination while the opposite results were obtained in summer and winter germination with higher values in snowbed scenario (see fig 4A for size effects and fig 4B for mean values). Total germination was slightly higher in fellfield scenario in both communities, but differences were only significant in the temperate community. T50 values were consistently higher in snowbed scenario and EHS did not statistically differ between scenarios (see fig 4). The effect size was notably larger in the temperate community meaning that the differences observed between scenarios were bigger.

### 3.2 Community responses

When analyzing community patterns, we found converging patterns but significantly different strategies between communities (see fig 3).

The cumulative germination curve of the temperate community showed a significant germination delay between microclimatic scenarios from the very beginning of the experiment (see fig 3). This community showed low germination in autumn, mainly happening in the fellfield scenario, (fig4B, left panel first row) and low germination in winter, almost all happening in the snowbed scenario (fig 4b, left panel second row). In spring germination, we observed the highest germination in fellfield scenario (0.38 germination proportion) while the highest germination in snowbed scenario was reach during summer (0.31 germination proportion). At the end of the experiment, total germination averaged 0.67 of germination proportion. T50 values averaged 203 days (163 and 242 days in fellfield and snowbed respectively), and the average EHS was 470 ºC, very similar values independently of the microclimatic scenario.

The cumulative germination curve of the Mediterranean community showed a germination delay between microclimatic scenarios after the winter period. This community showed the highest germination proportion in autumn (0.58), followed by spring germination (0.15). Low germination happened during winter, mainly in the snowbed scenario (0.12) and the lowest germination was recorded in summer with a mean value of 0.05. At the end of the experiment the Mediterranean community averaged 0.84 of germination proportion between both scenarios. T50 values averaged 84 days (64 and 102 days in fellfield and snowbed scenarios respectively) and the average EHS was 289 ºC, very similar in both scenarios.

When comparing strategies between communities we found significant differences. As expected, autumn germination was significantly higher in the Mediterranean rather than in temperate community (See fig 4B 1st row and supplementary table xx). Germination in winter and summer periods only showed differences between microclimatic scenarios, with higher values in snowbed scenario (fig 4B 2nd and 4th rows). Spring germination did show significant differences with higher values in the temperate community (see fig 4B 3rd row) while total germination was significantly lower in the temperate community. To conclude, the average T50 time was significantly higher in the temperate community and EHS was only significantly lower for temperate community in the snowbed scenario (see detailed results from community model in appendix table xx). We found a significant interaction term in all germination traits except total germination, being the temperate community in snowbed scenario showing the most distinct responses, with either higher or lower germination values.

4. Discussion.

As we predicted, the microclimatic scenarios drove significant differences in the germination phenology of our two alpine communities. Fellfield scenario (mirroring micro-edges) did prompt faster germination, higher germination in early growing season, slightly higher total germination, and lower germination during winter. Conversely, in snowbed scenario (mirroring micro-valleys) we observed slower germination, higher germination in late growing season, slightly lower total germination, and higher germination in winter. The differences observed confirm that microclimatic conditions are an important source of variation in alpine germination phenology at community level. As we also expected, the temperate community diverged significantly from the Mediterranean community pattern. The temperate community followed the “alpine germination syndrome” (Baskin & Baskin 2014; Fernández-Pascual et al. 2021) with low germination before cold stratification and higher germination once the incubators reach warm temperatures. Whereas the Mediterranean community showed the highest germination in autumn and earlier in the growing season, following the previously described “Mediterranean germination syndrome” (Giménez-Benavides et al. 2005).

### 4.1 Microclimatic scenarios differences

Small microclimatic differences of two or three degrees Celsius resulted in high accumulated germination differences throughout the year. The differences are shown as a phenology delay that can potentially have a detrimental effect on plant demography since fecundity fitness and seedling survival are tightly related to the start and length of the growing season (Poschlod et al. 2013).

In communities living in micro-edges (fellfield scenario), we observed two germination peaks. The first peak in autumn, can be seen as an opportunistic strategy (Hoyle et al. 2015). This strategy would provide selective advantage because seedlings can initiate development before the next growing season. A study done by (Mondoni et al. 2015), showed low seedling mortality during the winter in several species in glacier forelands. However, ultimately the success surviving winter seems to be species-specific and more studies are needed. Below zero temperatures showed consistent detrimental effects on germination although cold stratification is provided, a possibly reason could be the physiological drought they are subjected to (Billings & Mooney 1968). Consequently, seeds that disperse into micro-edges must endure below 0 ºC temperatures and postpone germination until frozen soil thaw. This postponed germination could potentially shorten their effective growing season; nevertheless, this delay is compensated by the shorter winter period experienced. The second germination peak is triggered when temperatures rise again in early growing season and almost no germination happens in late growing season.

In communities living in micro-valleys germination peaks occurs either under snow or later in the season. Micro-valleys conditions reduced autumn germination, partly because the low temperatures experienced and seeds dormancy constraints. Contrastingly, the winter germination peak demonstrate that alpine communities are adapted to germinate under snow-like conditions (darkness and constant 0ºC). These conditions alleviate and break seed dormancy while providing water during snowmelt. Thus, species able to germinate in that very restricted conditions are using the full extent of their growing season. Additionally, species with warm temperature requirements are not fulfilled until late growing season when we observed the second germination peak.

### 4.2 Communities differences

The temperate community followed the previously described alpine germination syndrome (Baskin & Baskin 2014; Fernández-Pascual et al. 2021) corroborating the findings by many authors (Cavieres & Arroyo 2000; Mondoni et al. 2009; Schwienbacher et al. 2011; Hoyle et al. 2015). Accordingly, we observed low autumn germination likely due to a strong prevalence of physiological dormancy (Schwienbacher et al. 2011; Tudela-Isanta, Ladouceur, et al. 2018). Then, having a postponed germination after winter guarantee a drought-free period during snowmelt; but the highest germination was observed once the temperatures rose above 10-12 ºC. In micro-ridges (fellfield scenario) the thermal threshold was surpassed earlier in the growing season while in micro-valleys (snowbed scenario) it was exceeded later in the growing season. The total germination registered in this community suggests that some species might have a bet-hedging strategy, probably with fluctuating levels of dormancy and more prone to form persistent soil seed bank (Schwienbacher et al. 2010).

The Mediterranean community followed the previously described Mediterranean germination syndrome (Giménez-Benavides et al. 2005). Accordingly, we found a higher proportion of non-dormant species (82%), able to germinate immediately after dispersal when water was available confirming Giménez-Benavides results. The second germination peak was observed in early growing season suggesting that species from the community are well adapted to germinate at cooler temperatures. The higher values of total germination reached in the Mediterranean community suggest that might be more successful in generating viable seeds germinating within the first year, but also meaning that soil seed bank might not be persistent. The significantly distinct patterns observed in our two communities potentially indicate the existence of other germination syndromes still unknown in distinct biomes like tropical or artic areas.

In addition, the differential responses observed from the temperate community in snowbed scenario suggests that there are species with stricter germination requirements that might be the most vulnerable to climate warming.

### 4.3 Novelty, limitations, and further research

Our study focused on germination phenology presents a novel assessment of seed germination traits across a whole year. Our approach mimicked real in-situ soil temperatures from contrasting microclimatic conditions in two alpine communities from the same biogeographical area. Nevertheless, our two communities differed also in bedrock potentially having a cofounding factor in our study, as germination trait might differ between siliceous and calcareous bedrock in the Alps (Tudela-Isanta, Ladouceur, et al. 2018).

Nevertheless, although the microclimatic scenarios were based in the temperate community field data; the Mediterranean community showed high germination responses suggesting that these scenarios did not limit the germination capacity of the community and are therefore valid for our study purposes.

Another point worth considering is that in our experimental design seeds had water available throughout the growing season. Although literature agrees that temperature is the main factor influencing germination (Baskin & Baskin 2014; Körner 2021); the results of the Mediterranean community in our experiment, with species able to germinate at 5ºC, suggests that water availability may potentially have a stronger influence in germination than temperature in specific areas (Rosbakh & Poschlod 2015). Some studies that have approached the relationship between temperature and water availability in the soil showed that drier soils also become warmer, however to our knowledge none has been done at a microscale level (Graham 2012). Another study (Dürr et al. 2015) found that species inhabiting warmer soils tends to have a higher base temperature for germination, as they have adapted to need more heat as a cue to initiate germination. This adaptation could possibly be to prevent germination at dispersal time (Tudela-Isanta, Fernández-Pascual, et al. 2018). Nevertheless, there is still many gaps as how water availability directly affects germination, especially in water-limited ecosystems.

Looking at the generally high levels of germination reached in our study another important point would be to focus on seedling establishment and survival. Especially in alpine communities, seedlings phases have been identified as one of the more vulnerable and limiting stages of plant regeneration (REF). Seedling emergence must be perfectly timed to be successful. Germination before winter or in early spring can lead to mortality due to frost events (Rosbakh & Poschlod 2015; Fernández-Pascual et al. 2017); but with postponed germination the seedlings are at risk to an underdeveloped root system in summer period, when drought events can lead to death due to topsoil desiccation (Billings & Mooney 1968).

### 4.4 Final conclusions

In future climate scenarios, with warming happening faster above the tree line (Kullman 2004 and Körner 2023), our results suggest that germination phenology could potentially advance to earlier in the season if individual species thermal requirements are met, confirming results found by (Bernareggi et al. 2016). Nevertheless, a greater threat might come from the expanding micro-edge climatic conditions, consequently reducing the suitable area of the specialized communities adapted to micro-valleys, specially from temperate alpine areas. The seemingly stricter germination requirements in temperate communities will no longer be met and germination phenology alterations could have major implications (Mondoni et al. 2012). Like reducing the amount of successful germination and leaving seedlings vulnerable to frozen damage without snow protection (Venn et al. 2013). Nevertheless, more research is needed to study species specific adaptations to microclimatic conditions, as well as their responses to limited water availability.

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# Tables and figures

Table 1: Description of the seed traits describing germination phenology calculated in our study along with their ecological significance. Traits were calculated for petri dish and used as replicates per each seed lot.

|  |  |  |
| --- | --- | --- |
|  | Description | Ecological significance |
| Autumn germination | Germination at mid-November, last check before winter (T mean < 3.5 ºC). | Germination without cold stratification requirement. Seeds germinate fast and seedlings can develop before winter. |
| Winter germination | From last germination score before winter, T mean < 3.5 ºC, until T mean > 2 ºC. Different length in each incubator. | Germination of species able to germinate under snow-like conditions (zero degrees and darkness). Maximizes ability of taking advantage of water available during. |
| Spring germination | Germination at the summer solstice relative to end of winter period (from Tmin > 1ºC to summer solstice). Different length in each incubator. | Germination with cold stratification requirement but no need for high temperatures. Rapid onset of germination following snowmelt. |
| Summer germination | Germination at mid-September relative to spring. | Germination of species with cold stratification and warm cued germination. Germination delayed until late growing season. |
| Total germination | Total amount of seeds germinated. | Higher total germination means high potential of regeneration by seeds within the year after dispersal. Low values could potentially indicate a higher bet for long-term soil seed bank. |
| t50 | Time to reach 50% germination. Species under 50% germination were excluded from analysis (n = 68 seed lots). | Precocious vs. delayed germination along the year. Higher values indicate that germination tends to occur later in the year. |
| Environmental heat sum (EHS) | Sum of degrees (T mean) needed to reach t50. Species under 50% germination were excluded from analysis (n = 68 seed lots). | Physiological threshold to accumulate heat before germination. A species and individual trait, it should be independent of the incubator. |

Table 2

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Species** | **Autumn germination** | | **Winter germination** | | **Spring germination** | | **Summer germination** | | **Time to reach 50% germination** | | **Environmental Heat Sum** | | **Area between curves** |
| F | S | F | S | F | S | F | S | F | S | F | S |
| Androsace villosa | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.2 | NA | NA | NA | NA | -0.6 |
| Anthyllis vulneraria | 5.9 | 2.9 | 0.0 | 0.0 | 0.0 | 0.0 | 2.1 | 0.0 | NA | NA | NA | NA | 12.2 |
| Arenaria erinacea | 22.7 | 2.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | NA | NA | NA | NA | 69.1 |
| Arenaria moehringioides | 3.9 | 0.0 | 0.0 | 18.2 | 38.5 | 0.0 | 3.9 | 18.2 | 272.0 | 294.0 | 1082.5 | 792.0 | 30.8 |
| Armeria cantabrica | 0.7 | 0.0 | 0.0 | 7.7 | 65.7 | 0.6 | 30.1 | 89.1 | 238.2 | 278.0 | 654.2 | 596.8 | 30.8 |
| Carex sempervirens | 0.0 | 0.0 | 0.0 | 0.0 | 96.6 | 0.0 | 2.6 | 99.3 | 244.9 | 282.9 | 694.0 | 548.3 | 38.2 |
| Dethawia splendens | 0.0 | 0.0 | 0.0 | 91.8 | 94.9 | 6.1 | 0.0 | 2.0 | 212.9 | 230.4 | 457.6 | 251.9 | 11.9 |
| Erigeron alpinus | 0.0 | 0.0 | 0.0 | 3.0 | 100.0 | 83.8 | 0.0 | 13.1 | 219.8 | 261.6 | 463.9 | 325.1 | 43.8 |
| Euphrasia salisburgensis | 0.0 | 0.0 | 0.0 | 0.5 | 0.5 | 0.0 | 1.0 | 0.0 | NA | NA | NA | NA | 0.1 |
| Festuca hystrix | 97.1 | 71.1 | 0.0 | 7.9 | 2.9 | 0.0 | 0.0 | 7.9 | 15.1 | 122.8 | 144.8 | 178.0 | 83.2 |
| Festuca rubra | 0.0 |  | 0.0 |  | 100.0 |  | 0.0 |  | 239.5 |  | 648.0 |  | NA |
| Gentiana verna | 0.0 | 0.0 | 0.0 | 7.3 | 8.7 | 0.7 | 0.0 | 0.7 | NA | NA | NA | NA | 1.2 |
| Gentianella campestris | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | NA | NA | NA | NA | 0.0 |
| Gypsophila repens | 17.4 | 1.1 | 0.0 | 2.1 | 70.5 | 7.9 | 8.1 | 87.4 | 230.3 | 281.8 | 566.0 | 523.1 | 75.4 |
| Helianthemum canum | 19.0 | 10.2 | 0.0 | 1.8 | 5.8 | 4.5 | 4.3 | 5.2 | 279.0 | NA | 1245.0 | NA | 29.8 |
| Helianthemum urrielense | 65.6 | 75.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.1 | 0.0 | 13.3 | 14.8 | 135.3 | 91.0 | -32.5 |
| Helictotrichon sedenense | 7.1 | 0.0 | 0.0 | 85.0 | 92.9 | 0.0 | 0.0 | 15.0 | 229.6 | 231.6 | 568.3 | 277.0 | 23.0 |
| Iberis carnosa | 76.6 | 16.5 | 0.0 | 0.0 | 2.1 | 0.0 | 12.8 | 82.4 | 9.6 | 311.7 | 97.8 | 1005.9 | 183.4 |
| Jasione cavanillesii | 0.0 | 0.0 | 0.0 | 0.0 | 27.1 | 4.8 | 1.4 | 22.5 | 226.3 | 272.3 | 491.5 | 474.3 | 14.0 |
| Jurinea humilis | 42.9 | 0.0 | 0.0 | 100.0 | 57.1 | 0.0 | 0.0 | 0.0 | 119.6 | 230.5 | 376.3 | 268.5 | 94.1 |
| Kobresia myosuroides | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | NA | NA | NA | NA | 0.0 |
| Koeleria vallesiana | 100.0 | 82.4 | 0.0 | 11.2 | 0.0 | 0.0 | 0.0 | 5.4 | 12.1 | 30.0 | 132.0 | 185.9 | 54.5 |
| Minuartia CF | 25.3 | 0.0 | 0.0 | 1.0 | 14.1 | 5.0 | 5.1 | 8.0 | 227.0 | NA | 534.0 | NA | 97.2 |
| Minuartia verna | 41.5 | 8.4 | 0.0 | 0.0 | 0.0 | 1.1 | 1.1 | 3.2 | NA | NA | NA | NA | 112.4 |
| Pedicularis pyrenaica | 0.0 | 0.0 | 0.0 | 29.2 | 41.1 | 0.0 | 0.0 | 3.1 | 203.7 | 249.5 | 378.3 | 334.0 | 21.1 |
| Phyteuma orbiculare | 0.0 | 0.0 | 0.0 | 17.9 | 20.0 | 10.7 | 0.0 | 7.1 | NA | NA | NA | NA | -11.4 |
| Plantago alpina | 25.9 | 1.1 | 0.0 | 65.9 | 73.5 | 29.2 | 0.6 | 2.7 | 176.0 | 234.5 | 334.4 | 225.3 | 83.0 |
| Ranunculus carinthiacus | 0.0 | 0.0 | 0.0 | 0.0 | 26.7 | 0.0 | 0.0 | 0.0 | NA | NA | NA | NA | 24.7 |
| Salix breviserrata | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | NA | NA | NA |  | 0.0 |
| Saxifraga conifera | 66.8 | 6.4 | 0.0 | 0.0 | 0.8 | 0.0 | 24.3 | 63.5 | 62.5 | 327.6 | 338.5 | 1284.7 | 195.2 |
| Saxifraga paniculata | 0.0 | 0.0 | 0.0 | 0.0 | 96.9 | 20.2 | 0.0 | 39.3 | 222.0 | 283.5 | 499.9 | 551.5 | 84.8 |
| Scilla verna | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 10.4 | 28.6 | NA | NA | NA | NA | -1.4 |
| Sedum album cf | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | NA | NA | NA | NA | 0.0 |
| Sesleria caerula | 93.3 | 36.2 | 0.0 | 15.9 | 5.3 | 1.5 | 1.3 | 43.5 | 25.1 | 195.4 | 267.8 | 304.6 | 146.8 |
| Silene acaulis | 6.1 | 2.9 | 0.0 | 2.2 | 6.6 | 0.6 | 35.6 | 28.1 | 303.9 | 288.0 | 1601.5 | 692.5 | 17.5 |
| Silene ciliata | 10.0 | 1.8 | 0.0 | 21.3 | 82.4 | 56.0 | 0.0 | 6.6 | 210.9 | 255.8 | 404.3 | 296.9 | 56.6 |
| Thymus praecox | 52.3 | 0.7 | 0.6 | 0.0 | 40.9 | 37.8 | 5.0 | 60.1 | 121.8 | 275.0 | 344.7 | 459.2 | 151.8 |

Table 3

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Species** | **Autumn germination** | | **Winter germination** | | **Spring germination** | | **Summer germination** | | **Time to reach 50% germination** | | **Environmental Heat Sum** | | **Area between curves** |
| F | S | F | S | F | S | F | S | F | S | F | S |
| Agrostis tileni | 0.0 | 0.0 | 0.0 | 0.0 | 100.0 | 80.0 | 0.0 | 20.0 | 225.5 | 301.7 | 574.3 | 817.5 | 69.8 |
| Armeria duriaei | 99.4 | 93.6 | 0.0 | 1.2 | 0.0 | 0.0 | 0.6 | 4.0 | 7.3 | 15.2 | 94.9 | 130.9 | 25.4 |
| Cerastium ramosissimum | 52.0 | 53.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 | 48.8 | 48.0 | 800.3 | 755.6 | -8.0 |
| Conopodium majus | 0.0 | 0.0 | 0.0 | 98.3 | 98.2 | 0.9 | 0.0 | 0.0 | 207.6 | 239.0 | 534.7 | 354.3 | 29.2 |
| Dianthus langeanus | 99.5 | 97.4 | 0.0 | 2.6 | 0.5 | 0.0 | 0.0 | 0.0 | 3.7 | 5.4 | 56.0 | 70.3 | 6.1 |
| Festuca summilusitana | 100.0 | 95.0 | 0.0 | 1.9 | 0.0 | 1.0 | 0.0 | 2.1 | 18.4 | 23.1 | 219.6 | 182.3 | 17.0 |
| Helictochloa marginata | 25.0 | 20.0 | 0.0 | 20.0 | 75.0 | 0.0 | 0.0 | 60.0 | 142.8 | 165.7 | 582.3 | 432.5 | 34.6 |
| Jurinea humilis | 81.9 | 0.0 | 0.0 | 100.0 | 18.1 | 0.0 | 0.0 | 0.0 | 9.7 | 246.5 | 141.3 | 445.5 | 191.2 |
| Luzula caespitosa | 54.2 | 0.0 | 3.1 | 94.9 | 26.7 | 0.0 | 6.4 | 1.1 | 102.4 | 245.5 | 514.6 | 432.5 | 107.0 |
| Minuartia recurva | 99.5 | 79.9 | 0.0 | 2.2 | 0.5 | 17.9 | 0.0 | 0.0 | 6.0 | 14.0 | 87.5 | 159.8 | 54.2 |
| Neoschischkinia truncatula | 93.7 | 89.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.6 | 6.8 | 8.8 | 83.4 | 75.8 | 17.6 |
| Phalacrocarpum oppositifolium | 82.8 | 77.4 | 7.1 | 22.6 | 2.2 | 0.0 | 0.0 | 0.0 | 40.3 | 82.1 | 451.7 | 278.6 | 2.7 |
| Phyteuma hemisphaericum | 0.7 | 0.7 | 0.0 | 3.9 | 29.1 | 20.8 | 1.9 | 9.0 | NA | 284.5 | NA | 547.0 | 10.1 |
| Plantago holosteum | 96.5 | 93.5 | 0.0 | 0.5 | 3.0 | 3.5 | 0.0 | 1.5 | 8.1 | 8.4 | 100.1 | 71.4 | 8.9 |
| Sedum anglicum | 57.0 | 43.7 | 4.6 | 0.0 | 7.6 | 4.9 | 5.5 | 6.1 | 83.7 | 166.2 | 293.3 | 515.2 | 62.9 |
| Sedum brevifolium | 41.9 | 34.4 | 0.0 | 0.0 | 8.7 | 1.7 | 0.6 | 10.8 | 75.0 | 84.9 | 352.6 | 240.6 | 28.4 |
| Sempervivum arachnoideum | 0.0 | 0.0 | 0.0 | 0.0 | 95.5 | 11.6 | 0.6 | 69.3 | 212.8 | 259.8 | 359.3 | 351.0 | 55.3 |
| Silene ciliata | 1.1 | 0.5 | 0.0 | 9.1 | 86.9 | 79.9 | 2.1 | 5.5 | 198.9 | 240.8 | 268.4 | 184.4 | 30.5 |
| Solidago virgaurea | 84.5 | 12.4 | 0.0 | 78.6 | 15.5 | 9.0 | 0.0 | 0.0 | 14.9 | 235.3 | 174.4 | 305.6 | 164.6 |
| Spergula morisonii | 56.9 | 73.3 | 0.0 | 0.0 | 1.3 | 0.0 | 5.4 | 0.0 | 167.8 | 36.2 | 1604.9 | 559.1 | -62.1 |
| Thymus praecox | 90.2 | 66.9 | 0.0 | 2.1 | 6.9 | 10.3 | 1.5 | 20.8 | 13.8 | 83.4 | 190.6 | 265.9 | 65.8 |

Fig 1. Map of the study sites in northwest Spain with the Cantabrian Mountain´s and the location of our two communities: Mediterranean and Temperate.

Imagen que contiene Diagrama

Descripción generada automáticamente

Fig 2A. Weekly means of soil temperatures (Tmax and Tmin at 5 cm depth) measured during 10 years in two alpine sites of the Picos de Europa National Park, Cantabrian Mountains, Spain. Image of Microlog SP3 datalogger used. Fig 2B. Experimental temperature programs with weekly resolution, daily temperature ramps and monthly photoperiods to represent fellfield and snowbed scenarios in laboratory incubators. Both incubators were configured based on real field data showed in fig 2A.

Diagrama

Descripción generada automáticamente con confianza media

Fig 3. Cumulative germination curves, based on all target species sowed from each community throughout the experiment. Within each panel, orange curve represents germination proportion in fellfield scenario and blue curve snowbed scenario. Flat areas represent cold period when no germination scores were done.

Interfaz de usuario gráfica, Diagrama

Descripción generada automáticamente

Fig 4. PCA

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | TEMPERATE | | | |  | MEDITERRANEAN | | | |
| FELLFIELD |  | Dim.1 | Dim.2 | Dim.3 |  |  | Dim.1 | Dim.2 | Dim.3 |
| autumn\_germ | 46.6999379 | 0.8554687 | 0.6299419 |  | autumn\_germ | 45.2658865 | 0.3595083 | 2.957353 |
| spring\_germ | 24.8656458 | 25.377654 | 1.0918291 |  | spring\_germ | 37.1807673 | 7.7150065 | 8.610255 |
| summer\_germ | 0.9104844 | 50.9013901 | 1.1814207 |  | summer\_germ | 1.8756284 | 45.3763963 | 1.223014 |
| winter\_germ | 2.8347942 | 0.4219571 | 96.1487794 |  | winter\_germ | 0.9673123 | 27.1932881 | 58.924314 |
| EHS | 24.6891377 | 22.4435302 | 0.9480288 |  | EHS | 14.7104055 | 19.3558009 | 28.285064 |
| SNOWBED |  | Dim.1 | Dim.2 | Dim.3 |  |  | Dim.1 | Dim.2 | Dim.3 |
| autumn\_germ | 6.034304 | 59.7757719 | 3.6849742 |  | autumn\_germ | 44.023933 | 2.610151 | 0.4745412 |
| spring\_germ | 1.137863 | 25.2137025 | 58.4207556 |  | spring\_germ | 13.956593 | 17.13096 | 40.4877445 |
| summer\_germ | 37.608091 | 0.1218658 | 0.0815135 |  | summer\_germ | 8.527374 | 20.736209 | 57.3050933 |
| winter\_germ | 18.668323 | 14.2537744 | 34.6200028 |  | winter\_germ | 6.973358 | 59.323427 | 0.728783 |
| EHS | 36.551419 | 0.6348854 | 3.1927539 |  | EHS | 26.518743 | 0.199252 | 1.003838 |

Gráfico, Gráfico de barras, Gráfico de rectángulos

Descripción generada automáticamente

Fig 5. Phenology traits responses to incubator chambers representing fellfield and snowbed microclimatic scenarios from Mediterranean and Temperate alpine communities of northern Spain. 4A. Effects of incubator according to the MCMC-glmm analysis of the data. Dots indicate mean effect size and whiskers are 95 % credible intervals (CI). The vertical dashed line marks the zero effect: when the CI crosses the zero-line, the effect is not significant. Dots on the right side of the zero-line (positive) mean higher values in the snowbed scenario (blue background), while dots on the left side of the zero-line (negative) mean higher values in the fellfield scenario (orange background). 4B. Mean germination values for the seven traits at each scenario for both communities. Notice the different scales in y-axis in 4B. Error bars in germination phenology traits autumn, winter, spring, summer and total are binomial confident intervals. Error bars in T50 and EHS are gaussian confident intervals.