# Germination phenology of alpine plants is similarly driven by microclimate in temperate and mediterranean communities

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## Summary (max 200 words) (now: 203 words)

Understanding seed germination phenology is important to predict the survival and resilience of plant communities; yet little is known about the influence of microclimatic conditions on seed responses from seasonal ecosystems.

We conducted a continuous seasonal experiment with fresh seeds to investigate the germination phenology of 54 species in two alpine systems influenced by temperate and mediterranean climates. Using field microclimatic data series, we mimicked two contrasting scenarios: (1) exposed edges with snow-free conditions and warmer temperatures (fellfield), and (2) micro-valley conditions with lengthy snow cover and cooler temperatures (snowbed).

The laboratory experiments were validated by germination phenology recorded in field sowing experiments. We found a germination delay in snowbed compared to fellfield conditions in the two study systems. Despite macroecological effects, resulting in lower dormancy and higher autumn germination in the mediterranean than in the temperate system, all traits related to germination phenology showed similar responses under both microclimatic scenarios.

Our results suggest a generalizable and quantifiable phenological shift in the germination of alpine plants along microclimatic gradients. In a warming scenario with reduced snow cover and higher temperatures, alpine species are expected to anticipate germination between 10 and 50 days in both temperate and mediterranean alpine ecosystems.

Keywords: alpine microhabitats, climate change, germination phenology, germination shift, microclimatic conditions, reproductive phenology.

## 1. Introduction

Plant phenology informs about cyclical patterns of growth and developmental stages (Hopp, 1974) which are especially responsive to climate change (Scranton & Amarasekare 2017). In seasonal climates, plant reproductive strategies and their phenology have strong fitness implications for communities' evolvement and survival (Donohue, 2005; Poschlod *et al.*, 2013). Studies focusing on reproductive phenology have centred on flowering time, seed maturation and dispersal onset, describing a fast-slow continuum of reproductive phenology (Segrestin *et al.*, 2018; Segrestin, Navas and Garnier, 2020). Comparatively, very few studies have focused on seed germination phenology, despite this is a sensitive and irreversible process fundamental for plant regeneration (Baskin and Baskin, 2014). Early season germination can benefit individuals with longer growing seasons (Donohue *et al.*, 2010) and give a competitive edge to limiting resources against individuals germinating later during the season (Verdú and Traveset, 2005). However, early germination also involves higher mortality risks (Thomson, King and Schultz, 2017) due to warm spells or frost events compared to a more conservative strategy of seeds germinating later (ten Brink, Gremer and Kokko, 2020). Germination timing is therefore a key trait for regeneration and seedling survival, influencing population and community dynamics in response to climatic changes (Kimball *et al.*, 2011; Levine, Mceachern and Cowan, 2011; Huang *et al.*, 2016). Common adaptations of plants to regulate germination phenology include the bet-hedging strategy that spreads the mortality risk with several germination pulses (Simons, 2011); the response to environmental cues that trigger germination process under certain amount of temperature, moisture or light (Donohue *et al.*, 2010; Baskin and Baskin, 2014); or a combination of both (Graham, Smith and Simons, 2014).

The environmental regulation of germination phenology in largely unexplored in natural ecosystems, and most studies have focused on annual species from unpredictable water-dependent communities (XX XXX XXX; XXXX XXXX XX). However, changes in germination phenology are also expected in other systems influenced by seasonality and climate change (Walck et al. 2011). One important example is found in alpine and arctic ecosystems, where seed production and germination are strongly influenced by climate warming (Mondoni et al. 2022). Alpine areas are characterized by short growing seasons and display changing climatic conditions at different spatial scales (Körner, 2021). Under these circumstances, germination phenology is of vital importance to match favourable conditions and to prevent unsuitable winter climate during seed regeneration (Gremer *et al.*, 2020). The germination of alpine species has been generally described by two general syndromes. The global alpine germination syndrome occurs mainly in temperate climate and it is characterized by a period of cold stratification followed by warm temperatures (Baskin and Baskin, 2014; Fernández-Pascual *et al.*, 2021). In addition, a Mediterranean germination syndrome has been proposed for areas with Mediterranean-like climates, in which species germinate immediately after dispersal if water is available, even at relatively low temperatures (Giménez-Benavides, Escudero and Pérez-García, 2005). However, germination strategies of alpine species may change dramatically within the same region, as a response to local elevation gradients (Fernández-Pascual et al., 2017), light exposures (Wagner and Simons, 2009), bedrock typology (Tudela-Isanta, Fernández-Pascual, *et al.*, 2018; Tudela-Isanta, Ladouceur, *et al.*, 2018) or successional stages in e.g. glacier forelands (Schwienbacher *et al.*, 2012).

At the local scale, the high topographic roughness of alpine landscapes translates into a mosaic of microclimatic conditions (Scherrer and Körner, 2011) with sharp temperature and snow-melting gradients (Körner, 2021) even at distances of few centimetres (Graham *et al.*, 2012). The impact of these microclimatic variation on germination phenology is largely unknown, and the few studies that consider its effect on seed germination patterns show contrasting results. Comparing germination patterns between specialists of snowbeds and fellfields, Shimono & Kudo (2005) found no differences in the response of 27 alpine species to microhabitats, temperature and light in Japan. In contrast, Rosbakh *et al* (2022) found different germination responses to temperature among 17 species occurring in contrasting alpine habitats from the Caucasus. This suggests that germination patterns in alpine landscapes may differ in systems representing different ecological gradients or regional features (e.g., ecological or evolutionary history). In addition, germination experiments are limited by the use of fixed temperature conditions in incubation chambers (e.g., 12-h cycles of 20/10 and 15/5 ºC), which are decoupled from the continuous temperature cycles occurring in nature. To draw more robust conclusions about real-life germination strategies in alpine areas we need habitat specific detailed climatic data (Shimono and Kudo, 2005) and accurate experimental settings mirroring real field conditions in the best way possible (Hoyle et al. 2015). This is especially relevant if we want to understand the phenological responses of seed germination under contrasting microclimatic conditions. In alpine habitats, the spatial and temporal variation of microclimate is strongly dependent on the length of snow cover (Jiménez-Alfaro et al. 2024), making it necessary to consider the seasonal variation of snow and related temperature cycles in phenologically-driven studies.

In this study, we investigate seed germination phenology in 54 species from two alpine systems influenced by Temperate and Mediterranean climatic conditions in the same ecoregion. Our main aim is to understand how microclimatic variation affect germination phenology and the potential implications of such responses to plant regeneration in alpine communities. We conducted a continuous seasonal experiment in the laboratory based on the recreation of hourly data series of temperature and snow measured in alpine soils from the same region. Our experimental approach focused on two contrasting microclimatic regimes: fellfield conditions occurring in open and exposed areas subjected to wind, freeze and thaw cycles without snow protection in winter, with warmer and longer growing seasons; and snowbed conditions occurring in areas with dense plant cover, long snow cover and cooler and shorter growing seasons. We complemented the laboratory data with reciprocal sowing experiments in the field conducted in snowbed and fellfield conditions for subset of species. Firstly, we asked at what extent microclimatic contrasting conditions occurring in alpine systems modify germination phenology. We hypothesized that fellfield conditions will result in higher total germination, earlier germination, and lower or no germination during winter, while the snowbed conditions will show opposite patterns and some germination under winter (snow-covered) conditions. Secondly, we ask whether alpine species from different macroclimates show similar phenological responses to microclimatic conditions. We hypothesize that species from the temperate system will germinate better after cold stratification and under warmer temperatures, in concordance with the global alpine germination syndrome, while the species from the mediterranean system will germinate mainly in autumn and at colder temperatures, following the Mediterranean germination syndrome. However, it is unclear whether the individual responses of alpine species will follow these syndromes homogenously, and whether germination phenology tested in the field will align with the results obtained in the laboratory.

## 2. Material and Methods

## 2.1 Study systems

We studied alpine communities between 1900 and 2500 m a.s.l. in the Cantabrian Mountains, a mountain range running E-W in northern Spain, forming a transitional biogeographical hub between Eurosiberian and Mediterranean regions in Europe (Jiménez-Alfaro *et al.*, 2021). The biogeographic location of the region facilitates the coexistence of climatically temperate alpine communities and mediterranean alpine communities in northern and southern slopes of the mountain range, respectively. We selected one study system for each macroclimate: (1) temperate alpine calcareous grasslands in the Picos de Europa National Park (NE of the Cantabrian mountains, Fig.1A in green); and (2) Mediterranean alpine acidic grasslands in the Valles de Omaña and Luna Biosphere Reserve (SW of the Cantabrian mountains, Fig.1A in yellow). The temperate system shows higher plant diversity, soil pH is 6.5 - 6.8 (own data), mean annual air temperature is 2.5 ºC and mean summer precipitation is 260 kg·m2 (based on 47 locations, values extracted from Chelsa 2.1, bio 1 and bio 17, Fig.1B). Growing season starts in May until early October with a mean annual soil temperature of 5ºC (based on eight locations, soil values recorded from 2008 to 2019, data not shown). The Mediterranean system supports lower plant richness and is located on acidic bedrock with pH 3.8 – 4.8. The system experiences a 2-month dry period in summer (average precipitation of 160 kg·m2) and mean annual air temperature is 4.5 ºC (Fig.1B). Growing season stretches from March to early November with a mean annual soil temperature of 8ºC (based on four locations, soil values recorded from 2021 to 2023). The two study systems are dominated mostly by *Poaceae* and *Cyperaceae*, and the main lifeforms are Hemicryptophytes and Chamaephytes. Grazing impact is restricted to wild populations of Cantabrian chamois (*Rupricapra pyrenaica parva*).

## 2.2 Seed sampling

Within each study system, we established four seed sampling sites separated a minimum of 500 m from each other, maximizing the topographic diversity and the expected microclimatic variation among sites. In each sampling site, we recorded all vascular plant species co-occurring in a central representative plot of 3 m radius and considered them our target communities (49 species in the temperate and 22 species in the Mediterranean system). During August-September 2021, we visited the sampling sites every two weeks during the reproductive season and sampled ripe seeds or fruits (hereafter ‘seeds’ for simplicity) from the target species. Sampling took place within a 50 m radius of the central plot of each site from at least 20 – 50 randomly chosen individuals. Following standard protocols for sampling seeds of wild populations, the goal was to collect 200 seeds from each target species in two sampling sites, maximizing spatial sampling and intraspecific genetic diversity (ENSCONET 2009). In the temperate system, we obtained seeds from 38 target species, of which 19 were collected in two sites. In the Mediterranean system, we obtained enough seeds from 21 target species, covering two sampling sites for each species except in 2 cases. Only three species (*Jurinea humilis*, *Thymus praecox* and *Silene ciliata*) were present in both systems. Seed lots (species x sampling site, N = 95) remained in room conditions while we manually clean and sown each seed lot within 25 days of collection.

## 2.3 Experimental setting

We used a temperature data series collected in the sites of the Temperate system (Picos de Europa National Park) from 2008 to 2019 as a reference for regional alpine microclimate. The data were collected with M-Log5W loggers, GeoPrecision, Ettlingen, Germany, accuracy +/- 0.1 ºC at 0 ºC and 0.01 ºC resolution. We selected the most contrasting sites, representing snowbed and fellfield conditions (Fig. 1c), which were further validated with temperature data available from the Mediterranean sites, based on a field data series from 2020 to 2022 collected with SP3 loggers, EMS, Czech Republic, accuracy +/- 0.1 ºC at 0 ºC and 0.01 ºC resolution. Despite differences in the total snow cover and mean temperatures, the selected snowbed and fellfield conditions were representative of the patterns observed in the two systems. We transformed the two reference data series for calculating maximum (T max) and minimum daily temperatures (T min) and calculated the number of days with snow cover, estimated as days with less than 1 ºC temperature variation around zero degrees (Zhang *et al.*, 2005). These conditions were then used to setup a weekly-resolution program in two incubator chambers to conduct a continuous seasonal experiment (Fig. 1d). The chambers were programmed with daily temperature ramps between the Tmax and Tmin observed in the field. The experiment was set to mimic field conditions on a weekly basis, using monthly-resolution photoperiod regimes. Each incubator was configured in Aralab incubators (Aralab climatic chamber Fitoclima S600 PL, equipped with 4 led modules 11W 350mA) using Fitolog 9000 software (version 9308, Aralab Pharmaceutical Stability software). The “fellfield” incubator was programmed with a snow-free winter period below 0 ºC temperatures. with daily photoperiod and temperature fluctuation for 144 days. The “snowbed” scenario was programmed with a long snow period with constant 0 ºC temperature and darkness for 196 days. More detailed information about weekly programs is available in supporting information Table S2.

Germination experiments were conducted sequentially after field collection. Each seed lot was placed in both incubators simultaneously, sowing four replicates of 25 seeds in 9 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 3 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 period, 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, no germination scores were done in that period.

We removed seeds from the petri dishes once germination occurred (radicle > 1.5 mm long). At the end of the experiment, we cut open non-germinated seeds under the binocular loupe to visually assess if they were empty, infected, or seemed normal. We considered seeds with white and firm embryos viable, i.e. potentially germinable (Baskin and Baskin, 2014). We removed empty or infected seeds as well as populations with zero germination or with 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) for further analysis. The experiment was terminated after 14 months (July 2021 - September 2022). The final dataset (Supporting information Table S1) consisted of the raw scoring data for 95 seed lots of 54 species from 21 taxonomic families. A total of 10,816 viable seeds were used in the experiment.

## 2.4 Germination traits

We defined seven traits to describe germination phenology (**Table 1**) and to synthesize the patterns observed in the experiments. The first four traits contemplate the phenological season: autumn and summer germination consider specific periods of time measured in Julian calendar dates, and they are equal between incubators. Winter and spring germination are defined by specific thermal thresholds and they differ between incubators; winter germination period includes from the last germination score before winter (T mean < 3.5 ºC) until T mean > 2 ºC, from when the period changes to spring germination until summer solstice (germination score the 24th of June) (see Fig. 2a bottom: germination phenology periods). We also calculated two traits related to germination speed: time to reach 50% germination (T50) and Environmental heat sum (EHS) to reflect how many days and accumulated degrees (in ºC) the seeds experienced when reaching 50% germination (N = 68). Both measures were calculated by fitting a linear model between the two checks before and after reaching 50% germination to calculate the exact date and to compute the number days from sowing to T50. We finally considered total germination, calculated as the accumulated germination at the end of the experiment.

## 2.5 Statistical analysis

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).

We analyzed each study system separately and modelled, with MCMCglmm, every germination trait as response variable and incubator as explanatory variable (fixed factor), using phylogeny and sampling site (nested within species) as random factors (germination trait~ incubator). We also tested each germination trait as response variable with both incubator and system as explanatory variables (fixed factors) paying special attention to their interaction. Random factors remained the same as the first model (germination trait ~ incubator \* system). Phylogeny was included using a reconstructed tree for the 54 species, created with V.PHYLOMAKER R package (Jin and Qian, 2019) using phylosignal and phylobase R packages (Keck *et al.*, 2016; R Hackathon et al., 2020). 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).

To further explore the relationship between species and germination traits we divided the raw data in 2 subsets, one per each incubator and perform a PCA with FactoMineR package (Le, Josse and Husson, 2008). To select non redundant traits, we first did a correlation analysis with corrplot (Wei and Simko, 2021) of all seven traits (supporting information Fig. S3). Since t50 and autumn germination were highly correlated (- 0.94) we decided to keep the later.

## 2.6 Field sowing

We complemented the laboratory experiments with the sowing of seeds for monitoring germination phenology in the field. For each study system, we selected six species which are relatively dominant in the communities and represent different taxonomic families. The seeds were sown in two sampling sites for each study system, selecting local microclimatic conditions representing snowbed and fellfield conditions within each site. To do this, we used temperature data from an additional sampling of 20 data loggers (iButton, Thermochron, …) placed in the sourroundings of each target community from 2021 to 2022. The two microclimatic conditions were easily recognizable from these data since snowbed microsites showed long snow cover and fellfield microsites had freezing temperatures in winter. In each microsite ( n= 8; 2 conditions x 2 sites x 2 systems), we allocated 30 seeds from each species into mesh bags and buried them 3-5 cm deep in the soil. We sowed the seed bags in late September (Mediterranean system) and early October (temperate system) and programmed two retrieval times after winter period: one in early spring (one month within snowmelt) and one in late autumn (within one month of first snowfall). After retrieval, we counted the germinated seeds under the binocular loupe in the laboratory and estimated their germination timing in the field.

## 3. Results

## 3.1 Phenological patterns

The cumulative germination curves obtained from the experiment showed a divergent pattern between incubators (**Fig. 2a**). Indistinctively of the system, fellfield conditions promoted germination earlier and the germination in snowbed conditions was delayed. This general trend differed in the temperate and Mediterranean system, where germination peaks took place either in summer or autumn, respectively. The temperate system showed the highest germination period in spring for the fellfield scenario, while in the snowbed scenario the germination peak was in summer. On the contrary, the Mediterranean system showed the highest germination in autumn for both incubators. The two study systems showed a certain degree of interspecific variation. In the fellfield conditions (**Fig. 2B**), the species from the temperate system showed germination peaks in autumn (31.6%) and spring (44.7%) while in the Mediterranean species, a majority of the germination curves peaked in autumn (71%). Meanwhile, in the snowbed conditions (**Fig. 2C**), species of the temperate system changed their phenology and mostly peaked in summer (36.8%), while in the Mediterranean system most species germinated autumn (57.1 %). Detailed individual species germination peak periods and delay to reach 50% germination are shown in supporting information Table S4.

The delay experienced by each species between incubators was measured as a phenological germination shift, i.e., the space between germination curves of each incubator (species germination curves are provided in supporting information Fig. S6). In a potential scenario of fellfield at the expense of snowbed conditions, most species would anticipate their germination, indicated by negative values in the germination shift (**Fig. 3A**). The only exceptions were two annual species (*Spergula morisonii* and *Cerastium ramossisimum*) and the local endemic *Helianthemum urrielense*. The other species differed in their degree of germination shift, with phylogenetically related species showing similar values in most cases (**Fig. 3**B).

## 3.2. Phenological traits

For all traits, we found the same germination responses to microclimatic conditions in the two study systems (**Fig. 4**). The fellfield conditions produced significantly higher autumn and spring germination, while the snowbed conditions promoted germination in summer and winter. Total germination was slightly higher in the fellfield conditions, but differences were only significant in the temperate system. EHS did not statistically differ between conditions (**Fig. 4A**) and T50 values were consistently higher in the snowbed incubator (**Fig. 4B**). The effect sizes were relatively larger in the temperate system, meaning that the differences between scenarios were stronger, in agreement with the observed germination shifts (detailed germination trait values per species are shown in supporting information Table S4).

When comparing traits between systems, we found significant differences in most cases (details of incubator\*system model in supporting information Table 8). As expected, autumn germination was significantly higher in the Mediterranean rather than in the temperate system. Germination during winter and summer did not differ between systems, but in both cases the seeds only germinated in the snowbed conditions. Spring germination showed significant differences with higher values in the temperate system. At the end of the experiment, total germination was higher in the Mediterranean system., the average T50 was higher in the temperate system, and EHS was lower in species from the temperate system subjected to snowbed conditions. According to Pagel’s Lambda, we found a strong phylogenetic signal in both systems (supporting information Table S8). All traits had mean lambda values above 0.8, while traits related to germination speed (T50 and EHS) showed lower values around 0.4 In both systems, we found significant effects of phylogeny and intraspecific variability (random factors) for all traits. In T50 and EHS traits we found lower or no significant effect of phylogeny, while intraspecific variation had still a significant effect.

We found a significant interaction term in all germination traits except total germination, being the temperate system in snowbed scenario showing the most distinct responses, with either higher or lower germination values than the rest (Fig. 6, note the different trajectory in germination phenology).

The PCAs of trait variation (**Fig. 5**) showed that species variability in the fellfield scenario responded concordantly in the two study systems. The first axis (explaining 42% of variation) was mainly driven by autumn germination, while the second axis (27%) was explained by summer germination. Contrastingly, species variability in the snowbed scenario responded differently. The first axis (39% of variation) was mainly correlated to EHS and summer germination, while the second axis (27% of variation) was mainly explained by winter germination. (trait contributions and axis eigenvalues are show in supporting information Table S7).

## 3.3. Germination in the field

The germination phenology recorded in the field largely agreed with the laboratory experiments (**Table 2**). In the fellfield conditions, all species germinated in spring or autumn, irrespectively of being sown in the incubator or in the field. In some cases, germination in the field was recorded in the second autumn because we couldn´t test ¿¿¿In fellfield natural conditions, higher germination values were observed in the spring retrieval (germination could have happen the first autumn just after sowing or the first month after snowmelt ….??? In the snowbed conditions, most species… In two species from the temperate system (*Androsace villosa* and *Festuca glacialis*) the laboratory experiment failed and we couldn´t compare the phenology in the incubators. Detailed individual graphs are shown in supporting information Fig. S5)). ¿In snowbed natural conditions, higher germination values were observed in the autumn retrieval (the temperatures required were not reached until summer)?

## 4. Discussion

## 4.1 Microclimatic effects on germination phenology

As we predicted, the microclimatic scenarios drove significant differences in the germination phenology of all studied species. 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. 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 (REF), but only if seedlings can survive winter conditions as seen by (Mondoni *et al.*, 2015) 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 and 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 Macroclimatic influence on germination phenology

As we expected, the temperate system diverged significantly from the Mediterranean system. The temperate system followed the “alpine germination syndrome” (Baskin and Baskin, 2014; Fernández-Pascual *et al.*, 2021) with low germination before cold stratification and higher germination once the incubators reach warm temperatures. The temperate system followed the previously described alpine germination syndrome (Baskin and Baskin, 2014; Fernández-Pascual *et al.*, 2021) corroborating the findings by many authors (Cavieres and 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 system 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, Marcante and Erschbamer, 2010).

The Mediterranean system showed the highest germination in autumn and earlier in the growing season, following the previously described “Mediterranean germination syndrome” (Giménez-Benavides, Escudero and Pérez-García, 2005). The Mediterranean system followed the previously described Mediterranean germination syndrome (Giménez-Benavides, Escudero and Pérez-García, 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 system are well adapted to germinate at cooler temperatures. The higher values of total germination reached in the Mediterranean system 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 systems 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 system in snowbed scenario suggests that there are species with stricter germination requirements that will 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 systems from the same biogeographical area. The two systems 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). Although the microclimatic scenarios were based in the temperate system field data; the Mediterranean system 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 and Baskin, 2014; Körner, 2021); the results of the Mediterranean system 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 and 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 and 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 and Mooney, 1968).

## 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 (Mondoni *et al.*, 2015; 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 systems 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, Morgan and Lord, 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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## Competing interests

None declared.

## Authors contributions

CEA, EFP and BJA designed the research. CEA collected the data. CEA and EFP analysed the data. CEA wrote the first draft of the manuscript. All authors read and revised the manuscript and agreed on the final version.

## Data availability

The data that support the findings of this study is available in the Supporting Information of this article and GitHub together with R scripts.

## References

Baskin, C. C. and Baskin, J. M. (2014) *Seeds. Ecology, Biogeography and Evolution of Dormancy and Germination*. 2nd Editio, *Seeds*. 2nd Editio. San Diego, CA, USA: Academic Press. doi: 10.1016/B978-0-12-416677-6.00001-9.

Bernareggi, G. *et al.* (2016) ‘Seed dormancy and germination changes of snowbed species under climate warming: The role of pre-And post-dispersal temperatures’, *Annals of Botany*, 118(3), pp. 529–539. doi: 10.1093/aob/mcw125.

Billings, W. D. and Mooney, H. A. (1968) ‘The ecology of arctic and alpine plants’, *Biological Reviews*, 43(4), pp. 481–529. doi: 10.1111/j.1469-185X.1968.tb00968.x.

ten Brink, H., Gremer, J. R. and Kokko, H. (2020) ‘Optimal germination timing in unpredictable environments: the importance of dormancy for both among- and within-season variation’, *Ecology Letters*, 23(4), pp. 620–630. doi: 10.1111/ele.13461.

Cavieres, L. A. and Arroyo, M. T. K. (2000) ‘Seed germination response to cold stratification period and thermal regime in Phacelia secunda (Hydrophyllaceae): Altitudinal variation in the mediterranean Andes of central Chile’, *Plant Ecology*, 149(1), pp. 1–8. doi: 10.1023/A:1009802806674.

Donohue, K. (2005) ‘Seeds and seasons: interpreting germination timing in the field’, *Seed Science Research*, 15(3), pp. 175–187. doi: 10.1079/ssr2005208.

Donohue, K. *et al.* (2010) ‘Germination, postgermination adaptation, and species ecological ranges’, *Annual Review of Ecology, Evolution, and Systematics*, 41, pp. 293–319. doi: 10.1146/annurev-ecolsys-102209-144715.

Dürr, C. *et al.* (2015) ‘Ranges of critical temperature and water potential values for the germination of species worlwide: contribution to a seed trait database’, *Agricultural and Forest Meteorology*, 200, pp. 222–232. doi: 10.1016/j.agrformet.2014.09.024.

Fernández-Pascual, E. *et al.* (2017) ‘Comparative seed germination traits in alpine and subalpine grasslands: higher elevations are associated with warmer germination temperatures’, *Plant Biology*, 19(1), pp. 32–40. doi: 10.1111/plb.12472.

Fernández-Pascual, E. *et al.* (2021) ‘The seed germination spectrum of alpine plants: a global meta-analysis’, *New Phytologist*, 229(6), pp. 3573–3586. doi: 10.1111/nph.17086.

Giménez-Benavides, L., Escudero, A. and Pérez-García, F. (2005) ‘Seed germination of high mountain Mediterranean species: Altitudinal, interpopulation and interannual variability’, *Ecological Research*, 20(4), pp. 433–444. doi: 10.1007/s11284-005-0059-4.

Graham, E. *et al.* (2012) ‘Fine-scale patterns of soil and plant surface temperatures in an alpine fellfield habitat, white mountains, California’, *Arctic, Antarctic, and Alpine Research*, 44(3), pp. 288–295. doi: 10.1657/1938-4246-44.3.288.

Graham, J. K., Smith, M. L. and Simons, A. M. (2014) ‘Experimental evolution of bet hedging under manipulated environmental uncertainty in Neurospora Crassa’, *Proceedings of the Royal Society B: Biological Sciences*, 281(1787). doi: 10.1098/rspb.2014.0706.

Gremer, J. R. *et al.* (2020) ‘Variation in the seasonal germination niche across an elevational gradient: the role of germination cueing in current and future climates’, *American Journal of Botany*, 107(2), pp. 350–363. doi: 10.1002/ajb2.1425.

Hadfield, J. D. (2010) ‘MCMCglmm: MCMC Methods for Multi-Response GLMMs in R’, *Journal of Statistical Software*, 33(2), pp. 1–22. Available at: http://www.jstatsoft.org/.

Hopp, R. J. (1974) ‘Plant Phenology Observation Networks’, in Lieth, H. (ed.) *Phenology and Seasonality Modeling. Ecological Studies, vol 8.* Berlin, Heidelberg: Springer. doi: https://doi.org/10.1007/978-3-642-51863-8\_3.

Hoyle, G. L. *et al.* (2015) ‘Seed germination strategies: An evolutionary trajectory independent of vegetative functional traits’, *Frontiers in Plant Science*, 6(OCTOBER), pp. 1–13. doi: 10.3389/fpls.2015.00731.

Huang, Z. *et al.* (2016) ‘The contribution of germination functional traits to population dynamics of a desert plant community’, *Ecology*, 97(1), pp. 250–261. doi: 10.1890/15-0744.1.

Jiménez-Alfaro, B. *et al.* (2014) ‘Biogeographic deconstruction of alpine plant communities along altitudinal and topographic gradients’, *Journal of Vegetation Science*, 25(1), pp. 160–171. doi: 10.1111/jvs.12060.

Jiménez-Alfaro, B. *et al.* (2021) ‘Checklist of the vascular plants of the Cantabrian Mountains’, *Mediterranean Botany*, 42, pp. 1–60. doi: 10.5209/MBOT.74570.

Jin, Y. and Qian, H. (2019) ‘V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants’, *Ecography*, 42(8), pp. 1353–1359. doi: 10.1111/ecog.04434.

Keck, F. *et al.* (2016) ‘phylosignal: an R package to measure, test, and explore the phylogenetic signal’, *Ecology and Evolution*, 6(9), pp. 2774–2780. doi: 10.1002/ece3.2051.

Kimball, S. *et al.* (2011) ‘Differences in the timing of germination and reproduction relate to growth physiology and population dynamics of sonoran desert winter annuals’, *American Journal of Botany*, 98(11), pp. 1773–1781. doi: 10.3732/ajb.1100034.

Körner, C. (2021) *Alpine Plant Life*. 3rd edn. Edited by Springer Nature Switzerland AG 2021. Springer Cham. doi: 10.1007/978-3-030-59538-8.

Le, S., Josse, J. and Husson, F. (2008) ‘FactoMineR: A Package for Multivariate Analysis’, *Journal of Statistical Software*, 25(1), pp. 1–18. doi: 10.18637/jss.v025.i01.

Levine, J. M., Mceachern, A. K. and Cowan, C. (2011) ‘Seasonal timing of first rain storms affects rare plant population dynamics’, *Ecology*, 92(12), pp. 2236–2247.

M. Pagel (1999) ‘Inferring the historical patterns of biological evolution’, *Nature*, 401(October), pp. 877–884.

Mondoni, A. *et al.* (2009) ‘Germination requirements of the alpine endemic Silene elisabethae Jan: Effects of cold stratification, light and GA3’, *Seed Science and Technology*, 37(1), pp. 79–87. doi: 10.15258/sst.2009.37.1.10.

Mondoni, A. *et al.* (2012) ‘Climate warming could shift the timing of seed germination in alpine plants’, *Annals of Botany*, 110(1), pp. 155–164. doi: 10.1093/aob/mcs097.

Mondoni, A. *et al.* (2015) ‘Climate warming could increase recruitment success in glacier foreland plants’, *Annals of Botany*, 116(6), pp. 907–916. doi: 10.1093/aob/mcv101.

Poschlod, P. *et al.* (2013) *Seed Ecology and Assembly Rules in Plant Communities*, *Vegetation Ecology: Second Edition*. doi: 10.1002/9781118452592.ch6.

R Hackathon et al. (2020) ‘phylobase: Base Package for Phylogenetic Structures and Comparative Data’. Available at: https://cran.r-project.org/package=phylobase.

Rosbakh, S. *et al.* (2022) ‘Alpine plant communities differ in their seed germination requirements along a snowmelt gradient in the Caucasus’, *Alpine Botany*, 132(2), pp. 223–232. doi: 10.1007/s00035-022-00286-x.

Rosbakh, S. and Poschlod, P. (2015) ‘Initial temperature of seed germination as related to species occurrence along a temperature gradient’, *Functional Ecology*, 29(1), pp. 5–14. doi: 10.1111/1365-2435.12304.

Scherrer, D. and Körner, C. (2011) ‘Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming’, *Journal of Biogeography*, 38, pp. 406–416. doi: https://doi.org/10.1111/j.1365-2699.2010.02407.x.

Schwienbacher, E. *et al.* (2011) ‘Seed dormancy in alpine species’, *Flora: Morphology, Distribution, Functional Ecology of Plants*, 206(10), pp. 845–856. doi: 10.1016/j.flora.2011.05.001.

Schwienbacher, E. *et al.* (2012) ‘Correspondence of seed traits with niche position in glacier foreland succession’, *Plant Ecology*, 213(3), pp. 371–382. doi: 10.1007/s11258-011-9981-4.

Schwienbacher, E., Marcante, S. and Erschbamer, B. (2010) ‘Alpine species seed longevity in the soil in relation to seed size and shape - A 5-year burial experiment in the Central Alps’, *Flora: Morphology, Distribution, Functional Ecology of Plants*, 205(1), pp. 19–25. doi: 10.1016/j.flora.2008.10.007.

Segrestin, J. *et al.* (2018) ‘When is the best time to flower and disperse? A comparative analysis of plant reproductive phenology in the Mediterranean’, *Functional Ecology*, 32(7), pp. 1770–1783. doi: 10.1111/1365-2435.13098.

Segrestin, J., Navas, M. L. and Garnier, E. (2020) ‘Reproductive phenology as a dimension of the phenotypic space in 139 plant species from the Mediterranean’, *New Phytologist*, 225(2), pp. 740–753. doi: 10.1111/nph.16165.

Shimono, Y. and Kudo, G. (2005) ‘Comparisons of germination traits of alpine plants between fellfield and snowbed habitats’, *Ecological Research*, 20(2), pp. 189–197. doi: 10.1007/s11284-004-0031-8.

Simons, A. M. (2011) ‘Modes of response to environmental change and the elusive empirical evidence for bet hedging’, *Proceedings of the Royal Society B: Biological Sciences*, 278(1712), pp. 1601–1609. doi: 10.1098/rspb.2011.0176.

Thomson, Di. M., King, R. A. and Schultz, E. L. (2017) ‘Between invaders and a risky place: Exotic grasses alter demographic tradeoffs of native forb germination timing’, *Ecosphere*, 8(10). doi: 10.1002/ecs2.1987.

Tudela-Isanta, M., Fernández-Pascual, E., *et al.* (2018) ‘Habitat-related seed germination traits in alpine habitats’, *Ecology and Evolution*, 8(1), pp. 150–161. doi: 10.1002/ece3.3539.

Tudela-Isanta, M., Ladouceur, E., *et al.* (2018) ‘The seed germination niche limits the distribution of some plant species in calcareous or siliceous alpine bedrocks’, *Alpine Botany*, 128(1), pp. 83–95. doi: 10.1007/s00035-018-0199-0.

Venn, S., Morgan, J. W. and Lord, J. M. (2013) ‘Foliar freezing resistance of Australian alpine plants over the growing season’, *Austral Ecology*, 38(2), pp. 152–161.

Verdú, A. and Traveset, A. (2005) ‘EARLY EMERGENCE ENHANCES PLANT FITNESS: A PHYLOGENETICALLY CONTROLLED META-ANALYSIS’, *Ecology*, 86(6), pp. 1385–1394. doi: 10.1890/04-1647.

Wagner, I. and Simons, A. M. (2009) ‘Divergence in Germination Traits among Arctic and Alpinepopulations of Koenigia islandica: Light Requirements’, *Plant Ecology*, 204(1), pp. 145–153. doi: 10.1007/sl 1258-009-9578-3.

Wei, T. and Simko, V. (2021) ‘R package “corrplot”: Visualization of a Correlation Matrix’. Available at: https://github.com/taiyun/corrplot.

Zhang, Y. *et al.* (2005) ‘Soil temperature in Canada during the twentieth century: Complex responses to atmospheric climate change’, *Journal of Geophysical Research D: Atmospheres*, 110(3), pp. 1–15. doi: 10.1029/2004JD004910.

## Supporting information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 Raw germination data

Table S2 Detailed incubator programs

Table S3 Complete species germination traits

Table S4 PCA traits axis contributions

Table S5 Phylogenetic signals and random factors significances

Fig. S1 Germination traits correlation plots

Fig. S2 Field and laboratory germination comparison

Fig. S3 Individual species germination curves per sampling site and incubator

Methods S1 R code with comments

# Tables and figures



**Table 1.** Description of the germination phenology traits 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 Tmean > 2ºC 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 at the end of the experiment. | 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. |

Table2. Comparison of laboratory and field experiment highest germination peak for both microclimatic conditions.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| System | Species | Fellfield germination peak | | Snowbed germination peak | |
| Laboratory | Field | Laboratory | Field |
| Mediterranean | *Armeria duriaei* | Autumn | 2nd Autumn | Autumn | 2nd Autumn |
| *Dianthus langeanus* | Autumn | 1st Autumn  Spring | Autumn | 1st Autumn  Spring |
| *Luzula caespitosa* | Autumn | 1st Autumn  Spring | Spring | 1st Autumn  Spring |
| *Phyteuma hemisphaericum* | Spring | Spring | Summer | Spring  2nd Autumn |
| *Plantago holosteum* | Autumn | Spring  2nd Autumn | Autumn | Spring  2nd Autumn |
| *Silene ciliata* | Spring | Spring | Summer | Spring  2nd Autumn |
| Temperate | *Armeria cantabrica* | Spring-Summer | Spring  2nd Autumn | Summer | Spring  2nd Autumn |
| *Carex sempervirens* | Spring | Spring | Summer | 2nd Autumn |
| *Gypsophila repens* | Autumn-Spring | 1st Autumn  Spring | Summer | None |
| *Jasione cavanillesii* | Spring | 1st Autumn  Spring | Summer | 2nd Autumn |

Table 3. Model incubator\*system results

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Incubator | | System | | Incubator\*system | |
| Trait | L\_95% CI | U\_95% CI | L\_95% CI | U\_95% CI | L\_95% CI | U\_95% CI |
| Autumn | -1.68 | -0.93 | -5.27 | -1.60 | -2.18 | -0.94 |
| Winter | 4.36 | 6.32 | -5.43 | 0.64 | 0.02 | 5.65 |
| Spring | -2.01 | -0.96 | 0.72 | 3.60 | -2.54 | -1.04 |
| Summer | 1.30 | 2.52 | -0.09 | 2.29 | 0.47 | 2.06 |
| Total germination | -0.55 | 0.17 | -2.81 | -0.38 | -0.85 | 0.13 |
| T50 | 0.17 | 0.42 | 0.40 | 1.08 | 0.21 | 0.59 |
| EHS | -0.33 | 0.01 | -0.02 | 0.82 | 0.00 | 0.53 |

Fig. 1 Study system description. (a) Map of the study sites in northwest Spain, within the Cantabrian Mountain and the location of our two systems: Mediterranean (yellow) and Temperate (green). (b) Boxplots show respectively Mean annual air temperature (bio1) and summer precipitation (bio17) calculated from CHELSA 2.1 (averages from 1981 - 2010) based on 47 locations per each study site. (c) 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 MLog5W, Geoprecision datalogger used in the field. (d) 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 C.

Gráfico

Descripción generada automáticamente

Fig. 2 Representation of the cumulative germination curves of our two study systems. (a) Cumulative germination based on all target species sowed from each system 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. Density plots within each system represents the calculated area between individual species cumulative germination curves. At the bottom horizontal bars represent the phenology periods calculated. (b) Cumulative germination curves for each individual species in the fellfield incubator from both systems. (c) Show cumulative germination curves for each individual species in the snowbed incubator from both systems.

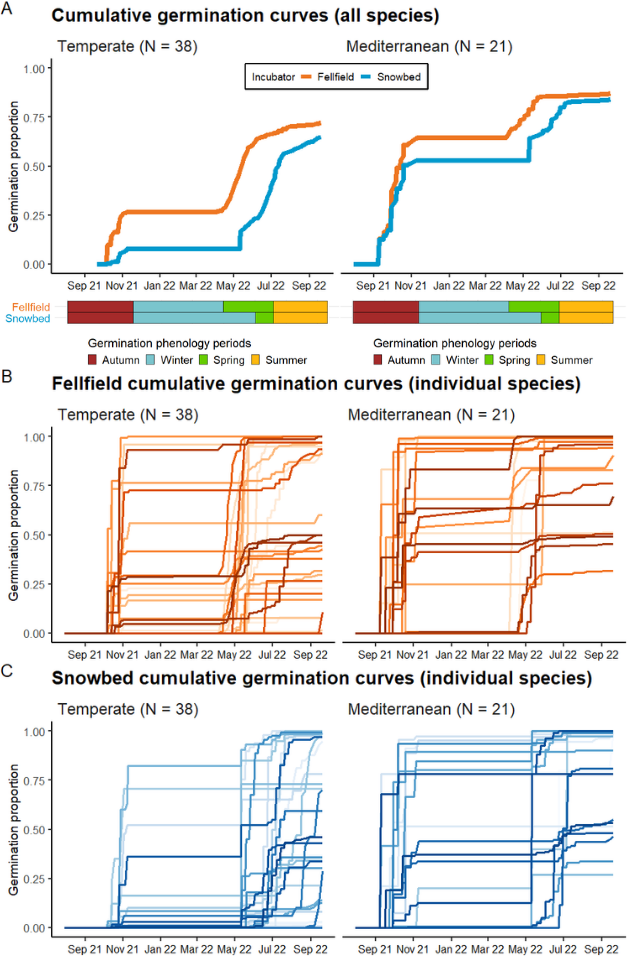


Fig. 3 Germination shift as response to microclimatic conditions. (a) Density plot in representation of the germination shift for each system. (b) Phylogenetical tree with each species calculated germination shift. Orange bars represent germination shift towards early season (higher germination in fellfield incubator in comparison to snowbed incubator, i.e bigger differential area), blue bars represent germination shift towards late season (higher germination in snowbed incubator in comparison to fellfield incubator).

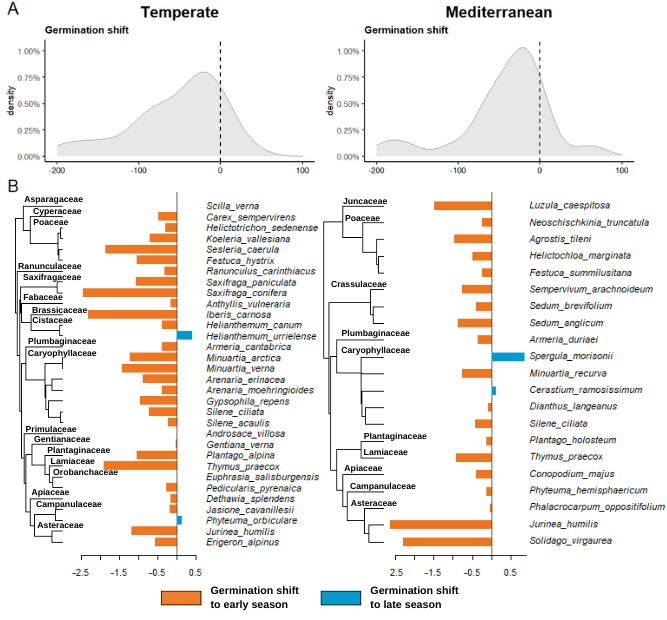


Fig. 4 Germination phenology traits responses for both incubators in each systems. (a) Model size effects of incubator according to the MCMC-glmm analysis of the data. Dots indicate mean effect size and whiskers are 95 % credible intervals (CI). The vertical dashed line marks the zero effect: when the 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). (b) Mean germination values for the seven traits at each scenario for both systems. Notice the different scales in y-axis. 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.

Gráfico, Gráfico de barras, Gráfico de rectángulos

Descripción generada automáticamente