



## The seed germination spectrum of alpine plants: a global meta-analysis

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# 1    **The seed germination spectrum of alpine plants: a global meta-**

## 2    **analysis**

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### Summary

- We present a meta-analysis of the alpine seed germination spectrum based on primary data from germination experiments conducted in four continents with 661 plant species, with the aim of testing the generality of alpine germination patterns at the global level.
- We use phylogenetic Generalized Linear Mixed Models to estimate the influence of six environmental cues on seed germination proportion, mean germination time and germination synchrony; accounting for possible effects of seed morphology (mass, embryo:seed ratio) and phylogeny.
- Alpine plants are characterized by physiological seed dormancy, strong need for cold stratification, warm-cued germination and positive germination responses to light and alternating temperatures. Species with a distribution limited to the alpine belt have a higher preference for warm temperatures and a stronger response to cold stratification than species whose distribution extends also to the lowlands. Seed mass, embryo size and phylogeny have strong constraining effects on germination responses to the environment.
- Overwintering and warm-cued germination are key drivers of germination in alpine habitats. The interplay of seed morphological traits and germination physiology reflects pressures to avoid frost or drought stress. These results indicate the convergence, at the global level, of the seed germination spectrum of alpine species.

## 54    **Keywords**

55    alpine; alternating temperature; cold stratification; embryo endosperm ratio; light  
56    germination; seed dormancy; seed germination; seed mass

## 57    **Introduction**

58    Alpine environments occur worldwide, above the maximum elevation at which trees  
59    can grow naturally (Körner *et al.*, 2011; Testolin *et al.*, 2020). These treeless  
60    habitats are characterized by low temperatures, strong winds, unstable substrates  
61    and short growing seasons (Körner, 2003). Their dependence on extreme and  
62    strict climatic conditions (Körner & Paulsen, 2004), coupled with the relatively small  
63    terrestrial area they occupy (Testolin *et al.*, 2020), makes alpine environments  
64    disproportionately vulnerable to climate change (Huss *et al.*, 2017; Verrall &  
65    Pickering, 2020). This threatens the survival of the world's rich and specialized  
66    mountain biodiversity (Perrigo *et al.*, 2020). It also endangers the sustainability of  
67    the ecosystem services that alpine environments provide for hundreds of millions  
68    worldwide, including the provisioning of natural resources, the regulation of  
69    environmental hazards and the maintenance of cultural and recreational activities  
70    (Körner & Ohsawa, 2005; Egan & Price, 2017). Successful management of climate  
71    change and of its consequences will depend on an adequate understanding of  
72    alpine biodiversity.

73    Specially, plant regeneration by seed is a key process that determines whether  
74    species will persist in their current habitat or will be able to migrate to new sites  
75    (Walck *et al.*, 2011); and it is also fundamental for active efforts in plant  
76    conservation (Li & Pritchard, 2009) and seed-based ecological restoration (Merritt  
77    & Dixon, 2011; Ladouceur *et al.*, 2018). Although most alpine plants can reproduce  
78    clonally (Körner, 2003), sexual reproduction by seed is the main strategy to  
79    maintain genetic diversity and colonize suitable new sites in response to  
80    environmental changes. However, the short reproductive season of the alpine

habitat constrains the phenological timing of flowering, pollination, seed development and seed dispersal. For regeneration by seed to be successful, dispersed propagules must germinate in the most appropriate period to ensure the survival of seedlings under environmental stress (Chambers *et al.*, 1990; Schütz, 2002; Forbis, 2003). The physiological process of seed germination is therefore an essential life stage that must be timed to occur when the environment is favourable for subsequent seedling survival and growth (Poschlod *et al.*, 2013). In alpine habitats, seed germination will be a crucial test for plant populations coping with climate change, determining whether they will persist or go into extinction.

Natural selection is expected to favour seed germination requirements that reduce the probability of facing environmental conditions which are not appropriate for seedling survival and growth (Angevine & Chabot, 1979). Thus, germination is mostly regulated by environmental cues related to water availability and soil temperature (Bewley *et al.*, 2013). The propagules of many plant species have also developed seed dormancy, by which germination is prevented during periods that are only ephemerally favourable, like a short warm spell in the middle of winter (Baskin & Baskin, 2014). Different degrees of dormancy within a seed population work to ensure the distribution of seedling emergence across time, thereby bet hedging offspring survival against unpredictable environments (Venable, 2007). Other germination cues, such as the response to diurnal alternating temperatures (Thompson, 1977) and the need for light or darkness (Carta *et al.*, 2017), allow for a fine-scale detection of germination micro-niches and safe sites (Jumpponen *et al.*, 1999). Given the comparatively high heterogeneity of alpine climates and plant lineages adapted to different regions, and the wealth of local studies on alpine seed ecology (reviewed in the following paragraphs), a current challenge is to synthesize, at the global level, the seed ecological spectrum of alpine plants while accounting for the evolutionary relatedness among taxa. The seed ecological spectrum (Saatkamp *et al.*, 2019) is defined as a set of seed traits that determines the ability of plants to disperse, persist, germinate, and establish in different

habitats. A major goal for trait-based seed ecology is to study the relationships and trade-offs between different aspects of the seed ecological spectrum (Saatkamp *et al.*, 2019), such as the physiological drivers of germination versus key morphological traits like seed mass (Moles *et al.*, 2005) and the embryo to seed ratio (Vandelook *et al.*, 2012).

In the available literature, many alpine species have been described as having seeds with deep physiological dormancy, i.e. a type of dormancy that is caused by the seed's internal balance of phytohormones and requires a long exposure to dormancy-breaking treatments to be terminated (Schwienbacher *et al.*, 2011; Sommerville *et al.*, 2013; Baskin & Baskin, 2014). This physiological dormancy would prevent precocious germination of recently dispersed seeds during autumn, when appropriate conditions are not likely to persist for more than a few weeks or days (Meyer & Monsen, 1991). A requirement for cold stratification to break dormancy would allow seeds to sense the snow season, thereby postponing germination to a more favourable period for seedling survival and development. Thus, it can be expected that a cold stratification period is a common requirement for seed germination in alpine plants. Nonetheless, an early review (Amen, 1966) suggested that cold stratification was not a requirement for the seed germination of several alpine species from different mountain ranges in the USA, a finding that has been reported by subsequent studies (Sayers, 1966; Marchand & Roach, 1980; Kaye, 1997). More recently, research on Australian alpine plants found that a cold stratification period only increased germination in half of the species tested (Sommerville *et al.*, 2013; Hoyle *et al.*, 2015). In contrast, cold stratification increased seed germination over a range of temperatures in most of the species studied in the alpine zone of Japan (Shimono & Kudo, 2005). Along an elevational gradient in the central Chilean Andes, cold stratification was an important requirement for seed germination in species from lower elevations, while species from higher sites did not germinate even after cold stratification (Cavieres & Sierra-Almeida, 2018). Finally, in a comparative study on germination of unstratified

seeds from different habitats of the Austrian Alps, species from alpine grasslands had the lowest final germination proportion, suggesting that they had the highest level of dormancy (Margreiter *et al.*, 2020).

Seed dormancy is not the only trait that can prevent, in practice, autumn germination. Early studies on the germination ecology of alpine plants demonstrated that in most species recently dispersed seeds require relatively high temperatures for germination (Bliss, 1958; Amen, 1966; Billings & Mooney, 1968). Warm-cued germination has been considered as an adaptation to prevent seed germination at the time of seed dispersal (autumn) when temperatures are relatively low and there is a high risk of frost (Cavieres & Arroyo, 2000). Indeed, germination of alpine seeds tends to occur after winter, mainly in early summer (Körner, 2003; Mondoni *et al.*, 2015). In recent times, an increasing number of studies reported that fresh seeds of some alpine plants also germinate at cool incubation temperatures or during cold stratification treatments (Schwienbacher *et al.*, 2011; Hoyle *et al.*, 2015; Fernández-Pascual *et al.*, 2017a; Cavieres & Sierra-Almeida, 2018). This cold-cued germination could be an adaptation to germinate under snow or during snowmelt, which could presumably allow seedlings to develop a deeper root system before topsoil desiccation in summer (Kammer & Möhl, 2002), or to attain an optimal size for overwintering (Billings & Mooney, 1968). Yet, the generality of warm-cued germination across different alpine regions and habitats has never been studied systematically, and the relative importance of cold stratification versus warm-cued germination remains unclear. A central question is whether physiological seed dormancy plays a relevant role in postponing alpine germination during autumn and winter, or the warm-cued germination is enough to prevent germination under cool autumn temperatures. The response to this question becomes pertinent under a warming climate, which could result in non-dormant seeds germinating readily in autumn. Non-dormant seeds could possibly have an advantage as the growing seasons become longer, if seedlings have enough time to grow and become sufficiently large to survive the



winter snow season. Potentially, having a non-dormant or less dormant seed could be a better strategy for alpine plants to thrive under future climate (Verdú & Traveset, 2005; Mondoni *et al.*, 2015). However, we might also expect that seedlings from these species will be exposed to frost damage if snow starts to melt earlier and insulation during winter disappears (Venn *et al.*, 2013) and therefore a mechanism that enables diverse germination timing (i.e. low germination synchrony) should be preferred.

Besides patterns of seed dormancy and germination temperature, the response of alpine seeds to diurnal alternating temperatures and light can provide further information on their capacity to detect fine-scale environmental cues. Fluctuations of diurnal temperature decrease with increasing burial depths; below 10 cm soil temperature might be too stable to trigger germination in species requiring temperature alternation (Van Assche & Vanlerberghe, 1989). Solar irradiance in physiologically significant quantities penetrates only the first millimetres of the soil (Tester & Morris, 1987). Therefore, these two cues can indicate whether seeds are buried deep in the soil, in rock crevices or under snow. The depth of seed burial is crucial for seedling emergence, as small seeds lack the resources to survive until they reach the soil surface (Bond *et al.*, 1999). A study of 445 species from the Qinghai-Tibet plateau found that species from high elevation alpine meadows did not show a significant response to diurnal temperature oscillations (Liu *et al.*, 2013). This is intriguing given that alpine habitats typically have a strong day-night climatic variation during the growing season. Regarding light and darkness, some local studies have found alpine species to have a preference for germinating in light (Densmore, 1997; Mondoni *et al.*, 2009). This trait could favour the creation of a persistent soil seed bank (Venn & Morgan, 2010; Jaganathan *et al.*, 2015) which is advantageous in the temporally and spatially unpredictable alpine environments (Kalin Arroyo *et al.*, 1999; Cavieres & Arroyo, 2001). Indeed, alpine soil seed banks are more frequent than previously supposed, as consistently reported in recent years (Venn & Morgan, 2010; Hoyle *et al.*, 2013; Jaganathan *et al.*, 2015).

Nevertheless, other alpine species seem to prefer dark germination (Schwienbacher *et al.*, 2011), which may be interpreted as a strategy for detecting safe sites in rock crevices (Arslan *et al.*, 2011). Although some germination studies report laboratory experiments conducted with constant and alternating temperatures, or light and dark conditions, they are very much case-dependent, and therefore it is difficult to evaluate whether these factors show a consistent pattern across global alpine ecosystems.

In this work, we make a global collection of primary germination data from laboratory experiments conducted with seeds of alpine plant species. The assembled dataset represents eight alpine regions belonging to four continents, and we use it to investigate the germination response of alpine plants to key environmental factors. These factors include dormancy-breaking treatments (cold stratification, GA<sub>3</sub> and scarification), average germination temperature, diurnal alternating temperatures and light (Bewley *et al.*, 2013; Baskin & Baskin, 2014). Given the heterogeneity of alpine species lineages adapted to different regions, we account for the shared evolutionary history using a phylogenetic comparative approach (Garamszegi, 2014). We also analyse the relationship between germination ecology and two morphological traits which are key drivers of the seed ecological spectrum: seed mass and the embryo to seed ratio (Saatkamp *et al.*, 2019). Our main aim in conducting this work is to test the consistency of general assumptions about the influence of major environmental cues on seed germination of alpine plants. Specifically, we determine at the global scale whether alpine seeds: (1) have physiological dormancy; (2) require cold stratification to break dormancy; (3) need relatively warm temperatures to germinate; (4) do not require alternating temperatures for germination; and (5) respond positively to light. To understand the ecological constraints of our meta-analysis on alpine species pools, we analyse how the germination responses differ between strict alpine species (that occur exclusively above the treeline) and generalist species (that occur above the treeline but also in the lowlands). We can expect that the former group will

show a more convergent alpine germination syndrome, while the latter will be more plastic in their response.

## Materials and Methods

### *Data collection*

We conducted a meta-analysis of primary data (Mengersen *et al.*, 2013), which consists of pooling together original data from different local studies to synthesize their conclusions at the global level. All data processing, analysis and manuscript production has been performed in *R* (R Core Team, 2019). The original data, plus *R* code for the analysis and creation of the manuscript using Rmarkdown, can be accessed at the GitHub repository <https://github.com/efernandezpascual/alpineseeds>. (The repository will be made open when the manuscript is accepted for publication, a zip version has been uploaded to <https://drive.google.com/file/d/12Usqi7fOAbOoZ9Uu9wkJt2FANB629LFP/view?usp=sharing> for peer-review). To gather data, we contacted research groups which have performed experiments on seed germination of alpine plants, asking them to provide raw data from laboratory germination experiments. The submitted data had to report the studied species, the germination treatments, the number of seeds sown, and the number of seeds germinated. We received data (Table 1) from the Cantabrian Mountains of Spain, the European Alps, the Italian Apennines, the Northern Caucasus, the Qinghai-Tibet Plateau of China, the Chilean Andes, and the Australian Alps. We also received data on European alpine species from *EnscoBase*, the database of the European Native Seed Conservation Network (<http://enscobase.maich.gr/index.tml>).

Once received, we standardized the species names according to *The Plant List* (The Plant List, 2013) using the package *Taxonstand* (Cayuela *et al.*, 2019) in *R*. For each species, we recorded its elevation range from local floras (Hegi, 1906;

Pignatti, 1982; Castroviejo, 1987; Brach & Song, 2006; Parolly & Rohwer, 2019), catalogues (Rodríguez *et al.*, 2018) and herbaria (*Australian National Herbarium*, <https://www.anbg.gov.au/cgi-bin/anhsir>). We used the elevation ranges (i) to remove from the dataset outlier species that do not grow above the treeline; and (ii) to classify the rest of the species as *strict alpine* (i.e. species that only grow above the treeline) or *generalist* (i.e. species that can grow above the treeline but also in the lowlands). For each species, we compiled three additional traits. First, seed dormancy class obtained from Baskin & Baskin (2014) and Rosbakh *et al.* (2020a). We simplified the original dormancy classes to five categories: physiological (germination prevented by the seed's internal balance of phytohormones), morphological (germination prevented by an embryo which is underdeveloped at the time of dispersal), morphophysiological (both physiological and morphological dormancy present), physical (germination prevented by a water-impermeable seed coat) or non-dormant. Second, seed mass as provided by the Royal Botanic Gardens Kew Seed Information Database (2017) and some additional sources (Bu *et al.*, 2007, 2008; Liu *et al.*, 2013). Third, the embryo to seed surface ratio. Embryo to surface area values were based on measurements of the surface area of the embryo and seed from drawings and photographs retrieved mainly from Martin (1946) and the Royal Botanic Gardens Kew Seed Information Database (2017), supplemented with own measurements (Vandelook, unpublished). For some species that were missing seed mass or embryo values, we calculated genus or family averages.

#### *Germination response variables*

We used the final germination proportion (i.e. the number of seeds germinated out of seeds sown) at 8 weeks as the main response variable for the germination treatments. We further calculated the mean germination time and the germination uncertainty index with the package *GerminaR* (Lozano-Isla *et al.*, 2019). Mean germination time is the time that it takes for half of the seed lot to germinate, indicating the germination speed in each experimental condition. The germination

uncertainty index estimates how scattered germination is through time, and gives an idea of whether germination is synchronous (i.e. most seeds germinate around the mean germination time) or asynchronous (i.e. germination events are separated through time during the germination experiment). Lower values in the germination uncertainty index indicate higher germination synchrony. The uncertainty index is analogous to the synchrony index and we used it because, unlike the latter, its values are not constrained between 0 and 1 (Lozano-Isla *et al.*, 2019). To calculate these indices, we used only records that met two conditions: (i) more than 50% final germination percentage; and (ii) a mean germination time under 4 weeks. We established these limits to prevent the results being altered by a modification of the seed's dormancy status during the germination incubation (e.g. a fraction of the seed lot is non-dormant at the beginning of the incubation and germinates shortly after the start of the experiment; while another fraction is originally dormant, loses dormancy in response to the incubation conditions, and germinates in a second wave).

### *Statistical analyses*

We meta-analysed germination data by fitting generalized mixed models with Bayesian estimation (Markov Chain Monte Carlo generalized linear mixed models, MCMCglmm) using the R package *MCMCglmm* (Hadfield, 2010). To model final germination proportion, we used binomial MCMCglmms, while for mean germination time and the germination uncertainty index we used gaussian MCMCglmms. Models had, as fixed effects, the experimental conditions (stratification, GA<sub>3</sub>, scarification, temperature, alternating temperature and light), plus their interaction with seed mass and embryo:seed, and the strict alpine or generalist character of the species. Random effects included a reconstructed phylogenetic tree for the 661 species, and species identity, seed lot, lab (i.e. data provider), and alpine region (Table 1). To create the phylogeny, we used the R package *V.PhyloMaker* (Jin & Qian, 2019) which contains an updated mega-tree of the seed plants based on Smith & Brown (2018). We placed taxa absent from the

mega-tree at the genus-level basal node. In all models, all variables were scaled so their contribution to the effect sizes could be compared. We used weakly informative priors in all models, with parameter-expanded priors for the random effects. Each model was run for 500,000 MCMC steps, with an initial burn-in phase of 50,000 and a thinning interval of 50 (De Villemereuil & Nakagawa, 2014), resulting, on average, in 9,000 posterior distributions. From the resulting posterior distributions, we calculated mean parameter estimates and 95% Highest Posterior Density (HPD) and Credible Intervals (CI). We estimated the significance of model parameters by examining CIs, considering parameters with CIs overlapping with zero as non-significant. To estimate the phylogenetic signal of seed germination over all variables we used Pagel's lambda ( $\lambda$ ) (Pagel, 1999), estimated simultaneously with the models by calculating the mean of the posterior distribution and the 95% CI of  $\lambda$  as indicated by De Villemereuil et al. (2014). When  $\lambda = 0$ , related taxa are no more similar than expected by chance, while when  $\lambda = 1$ , the trait is evolving following a constant variance random walk or Brownian motion model; intermediate values of  $\lambda$  indicate a phylogenetic correlation in trait evolution that does not fully follow a Brownian motion model (Pagel, 1999).

### *Visualization of the alpine seed germination spectrum*

To visualize the seed germination spectrum of alpine plants, we employed a Factorial Analysis of Mixed Data (FAMD) as implemented in the package *FactoMineR* (Le et al., 2008). FAMD ordination combines the properties of PCA and MCA to jointly measure the variation of continuous and categorical variables. The ordination was performed at the species level, i.e. calculating a series of continuous and categorical traits for each species. We transformed the final germination proportions to create a continuous variable for each germination cue (i.e. stratification, GA<sub>3</sub>, scarification, temperature, alternating temperatures and light). To do so, for each cue and species, we calculated a weighted average of the cue levels (in the case of temperature, cue levels were the temperature treatments; for the other cues the levels were 0 = absence and 1 = presence), weighting by the

germination proportion at each level. This approach underrepresents the importance of the levels that were not tested for a given species, but can serve as a proxy of the response to the germination cues when visualized across the whole dataset; it must be stressed that this stage of the analysis serves only for visualization and not hypothesis testing. We also included germination timing traits by calculating single values for the mean germination time (the minimum, i.e. the time taken at the most favourable treatment) and the germination uncertainty index (the mean). We conducted the FAMD with only the 293 species for which we had mean germination time and germination uncertainty index values. We finally included the continuous variables seed mass and embryo:seed, as well as the categorical variables dormancy class (physiological, morphophysiological, morphological, physical or non-dormant) and distribution (strict alpine vs. generalist species).

## Results

### *Description of the dataset*

The final dataset used in our meta-analysis contained 9,799 records (i.e. germination proportions for a given seed lot of a species, recorded in a set of experimental conditions) contributed by 12 research groups, representing 62 seed plant families and 661 species (291 strict alpine species and 370 generalist species). Seed lots were originally sampled in 8 alpine regions of the world (Table 1), in both hemispheres.

Most species in the dataset were reported as having dormant seeds (Fig. 1a), but the frequency of the dormancy classes did not differ between generalist and strict alpine species. Among those species with dormant seeds, physiological dormancy was the most common dormancy class, followed by morpho-physiological and then physical. Both strict alpine and generalist species had a similar range of values for seed mass (Fig. 1b) and embryo:seed ratio (Fig. 1c). The values of seed mass



ranged from 0.02 mg (*Calceolaria purpurea*) to 58 mg (*Vicia orobus*), with a median value of 0.56 mg. Embryo:seed ratio encompassed the full range of potential values, from endospermic species with very small embryos (0.001) to non-endospermic seeds (1). The median value was 0.34.

The total number of seeds used in the experiments was 365,808. Germination temperatures (i.e. the weighted average of the day and night temperatures, weighted by the duration of each phase) ranged from 0 to 36 °C, with 7,521 records of constant temperatures (i.e. experiments that used the same temperature during all their duration) and 2,278 of alternating temperatures (i.e. experiments where different temperatures were applied during the day and the night, in diurnal cycles). Seeds were exposed to light during some part of the diurnal cycle in 8,933 records and kept in total darkness in 866 records. The experiments were performed with untreated seeds in 7,297 records, and of the rest, the majority (2,436) went through cold stratification (< 5 °C, in darkness). Scarification (i.e. an abrasion of the seed coat to allow water imbibition) was performed in 119 records, and GA<sub>3</sub> (a plant hormone that promotes embryo growth and stimulates germination) in 651 records. Since germination incubations ran for different periods of time, we established a cut-off time of 8 weeks to calculate the final germination percentages, to have a homogeneous comparison across records.

#### *Dormancy breaking treatments*

In general, stratification significantly increased the final germination proportion (Fig. 2a), as shown by a credible interval not overlapping zero. This positive effect occurred in both generalist and strict alpine species, although the effect size was larger in the strict alpine group. Stratification slightly reduced the mean germination time (Fig. 2b), which was evident in the generalist species, but not in the strict alpine species. Further, stratification reduced the germination uncertainty index as a general response (Fig. 2c), and slightly more so in generalist species. Seed mass did not interact with stratification, but species with larger embryos had a smaller response to stratification in their final germination proportion and reduced



less markedly their mean germination time and germination uncertainty index. GA<sub>3</sub> had similar effects to stratification, with the main difference being that seed mass affected the response to GA<sub>3</sub>, whereas it did not interact with the response to stratification.

Scarification promoted the germination proportion (Fig. 2a) and reduced the mean germination time (Fig. 2b), but it did not affect the germination uncertainty index (Fig. 2c). Strict alpine species were slightly more responsive to scarification than generalist species. Heavier seeds were more responsive to scarification, while seeds with larger embryos responded less.

#### *Germination temperature*

Temperature had a positive significant effect on the final germination proportion as shown by a credible interval not overlapping zero (Fig. 2a), indicating a preference for warmer temperatures. Warmer temperatures also significantly decreased mean germination time (Fig. 2b) and the germination uncertainty index (Fig. 2c). The effect of warmer temperatures was slightly higher in strict alpine than in generalist species, although the credible intervals of the two groups of species do overlap. Seed mass and embryo:seed had a negative interaction with temperature, reducing the response to temperature. In other words, heavier and less endospermic seeds had a smaller increase in germination proportion and a smaller decrease in mean germination time when germinating in warmer temperatures. The germination uncertainty index did not show an interaction with seed mass or embryo:seed, as shown by the credible interval overlapping zero.

#### *Alternating temperatures*

Alternating temperatures had a positive effect on the final germination proportion (Fig. 2a), but not in the mean germination time (Fig. 2b) or the germination uncertainty index (Fig. 2c). The positive effect on the germination proportion was slightly higher in the generalist species. As in the case of the mean germination temperature, higher seed mass and embryo:seed values reduced the positive

effect of alternating temperatures on the final germination proportion. Alternating temperatures resulted in faster germination (reduced the mean germination time) for seeds with low values of embryo:seed.

#### *Light*

Light increased the final germination proportion (Fig. 2a), with no differences between strict alpine and generalist species. It did not affect the mean germination time (Fig. 2b), but it did result in more variable germination (increased the germination uncertainty index) of generalist species (Fig. 2c). Heavier and less endospermic seeds responded less to light.

#### *Random effects and phylogenetic signal*

Random factors had a significant effect on the MCMCglmm models (Fig. 3). The final germination proportion and the mean germination time were affected more strongly, on average, by the seed lot and the species identity, suggesting that these traits are subject to intra- and interspecific variability, respectively. Alpine region and lab had a lower average effect and more variability as shown by their credible intervals. The germination uncertainty index showed the opposite pattern, with a stronger effect of lab and alpine region. The phylogenetic signal in the response to all germination parameters (Fig. 4) was significantly positive for the final germination proportion and the mean germination time. For the germination uncertainty index, it overlapped with zero, indicating a weak effect of phylogeny.

#### *FAMD ordination*

The first FADM axis explained 17% of the variation. The quantitative variables with the largest contribution to this first axis were germination temperature, germination uncertainty, GA<sub>3</sub> and alternating temperatures. Among the qualitative factors, the strict alpine / generalist categories contributed to axis 1. In summary, the horizontal axis separated (i, left) generalist species with a positive response to alternating temperatures and more germination uncertainty from (ii, right) strict alpine species

with a preference for warmer temperatures and a positive response to GA<sub>3</sub> (Fig. 5). Axis 2 explained 12% of the variability. The main contributing variables were embryo:seed, mean germination time, seed mass and scarification; and the main categorical factors were physical dormancy and morphophysiological dormancy. This axis separated (iii, bottom) morphophysiologically dormant species with longer mean time to germination from (iv, top) physically dormant species that responded to scarification and had heavier, less endospermic seeds.

## Discussion

Our meta-analysis of primary germination data shows that alpine plants from different mountains of the world tend to show specialized seed germination characteristics. For most alpine species, both dormancy and warm-cued germination combine to ensure germination occurs in the season most conducive to survival: seeds tend to germinate when, after weeks of exposure to conditions that mimic winter, they are moved to mid-summer temperatures. Specifically, the germination ecology of strict alpine species is characterized by (1) physiological seed dormancy; (2) a strong need for cold stratification or GA<sub>3</sub> to break dormancy; (3) warm-cued germination; (4) a positive response to alternating temperatures, although not so prominent as in generalist species; (5) a positive response to light; (6) slow and relatively synchronous germination; and (7) an interplay with seed and embryo size, with smaller and more endospermic seeds being more responsive to stratification, warmth, alternating temperatures and light. Here we discuss the ecological significance of the different aspects of the alpine seed germination spectrum.

### *Seed dormancy*

Our dataset indicates that seed dormancy is frequent across alpine species and plays an important role in postponing plant recruitment to favourable times. Furthermore, the frequency of dormancy is similar in strict alpine and generalist

species, suggesting that this is a general trait of cold-adapted mountain species. Seeds with the two most frequent dormancy classes, physiological and morphophysiological, require a stratification period during which certain conditions (e.g. cold and wet, although other combinations are possible) are met over a period of months (Baskin & Baskin, 2014; Rosbakh *et al.*, 2020a). Indeed, our results show that cold stratification promotes germination. The phytohormone gibberellic acid (GA<sub>3</sub>) works as a general substitute of cold stratification to overcome the inherent physiological dormancy of alpine species. Additionally, we found some species with physical dormancy. This dormancy type can be broken by mechanical scarification via freezing-thawing cycles in spring or extreme temperature fluctuations during summer, but is also capable of responding to seasonal cycles of temperature and humidity (Van Assche *et al.*, 2003).

Overall, these results confirm that overwintering is essential for promoting seed germination in alpine species, concurring with previous local studies (Cavieres & Arroyo, 2000; Schütz, 2002; Giménez-Benavides *et al.*, 2005; Shimono & Kudo, 2005; Sommerville *et al.*, 2013; Garcia-Fernandez *et al.*, 2015; Hoyle *et al.*, 2015; Fernández-Pascual *et al.*, 2017a; Cavieres & Sierra-Almeida, 2018). Since global climate change is causing major changes in snow cover duration (Beniston, 2012; Gobiet *et al.*, 2014), it could disrupt natural cold stratification cycles in alpine environments, compromising population viability and indirectly favouring species with no stratification requirement (Sommerville *et al.*, 2013). This risk will be partly alleviated by the plasticity of physiological seed dormancy in response to the seed maturation temperature (Fernández-Pascual *et al.*, 2013 ; Carta *et al.*, 2016b), a mechanism of “seed memory” that facilitates acclimatisation to changing environments (Fernández-Pascual *et al.*, 2019), and which could reduce the stratification requirements of seeds produced in a warmer climate.

#### *Thermal regulation of germination*

We found a general increase of seed germination with higher incubation temperatures. This effect was more pronounced in strict alpine compared to

generalist species, confirming the findings of local studies (Walder & Erschbamer, 2015; Fernández-Pascual *et al.*, 2017a). It was also more pronounced in small seeded and endospermic species. Small-seeded species have a lower proportion of seedling survival under drought (Leishman & Westoby, 1994) but may require warmer germination temperatures than large-seeded species, especially in seasonal climates (Arène *et al.*, 2017). Considering that risk reduction is an important selective pressure for the evolution of germination traits (Venable & Brown, 1988), a plausible explanation for these patterns is that alpine plants received selection pressure from damaging spring frosts and evolved a frost avoidance mechanism by germinating at high temperatures (Taschler & Neuner, 2004; Marcante *et al.*, 2012; Rosbakh *et al.*, 2020b). Moreover, strict alpine species may be less subjected to drought damage during establishment compared to generalist species: as elevation increases, plants face less drought risk because precipitation increases (except in Mediterranean and semi-arid mountains), but at the same time there is a higher probability of early or late season frosts (Körner, 2003; Schrier *et al.*, 2007; Beniston, 2016). Together, these results indicate that germination patterns in alpine species are driven by an interplay of seed size and germination temperature to escape either frost or drought stress; small seeds are being selected for fast germination at warm temperatures, in order to escape unfavourable early-spring frost, and large seeds are being selected for slower germination under cooler conditions, which should maximize emergence during snowmelt (when water availability is highest) and gives seedlings adequate time to develop a root system to cope with desiccation risks in summer. Supporting this view, seedlings of alpine pioneer species have a low frost resistance (Marcante *et al.*, 2012), yet high heat tolerance up to 40–50°C (Marcante *et al.*, 2014).

In our analysis, increasing temperatures also decreased germination uncertainty, showing that germination synchrony is a plastic trait driven by temperature. While asynchronous germination is thought to be a form of adaptation to unpredictable alpine environments (Wagner & Simons, 2009; Simons, 2011), our results indicate

that asynchronous germination occurs when temperatures are relatively cool, likely as a bet-hedging strategy against the risk of early-spring frost. On the other hand, a fast and synchronised germination at warm conditions (i.e. in late spring) may be another important strategy that increases alpine seedling survival by avoiding drier conditions in summer. The extreme germination uncertainty syndrome, i.e. staggering germination so that emergence occurs both before and after winter, is known in alpine species (Körner, 2003; Hoyle *et al.*, 2015; Satyanti *et al.*, 2019). Staggered germination is usually exhibited as a rapid first wave of germination followed by second wave several weeks or months later (Körner, 2003). If autumn seedlings grow faster than spring seedlings (Satyanti *et al.*, 2019), this will likely have cascading effects on individual fitness along the life of the plant (Donohue *et al.*, 2005, 2010).

#### *Alternating temperatures and light*

We found a positive germination response to alternating temperatures and light, conditions that mimic the environment in the upper soil and certain microsites during the snow-free season (Billings & Mooney, 1968; Körner, 2003; Mondoni *et al.*, 2012). Alternating temperatures had a slightly lower effect on strict alpine species, compared with generalist species, but still had an effect. This partly contradicts the findings of Liu *et al.* (2013), who reported a lack of a response to temperature fluctuation for the species distributed only at high elevations of the Qinghai-Tibet Plateau. Liu and co-workers argued that, in that area, high temperature fluctuations may occur in all months of the year and therefore fluctuating temperature alone may not be a reliable indicator of suitable conditions for seedling establishment and growth, while warm daily temperatures could be a cue that the short summer growing season has begun (Liu *et al.*, 2013). When analysed at the global level, alternating temperatures generally increase germination of alpine plants, which corresponds well with the fact that most alpine regions have a strong day-night climatic variation during the growing season. It is also not surprising that we detected a negative interaction between seed mass and

the germination response to light and alternating temperature regimes, since large seeds can afford to germinate at greater depths (where they are more protected from the alpine environment) and still reach the soil surface (Pons, 2000).

#### *The alpine seed germination spectrum*

Using the whole set of traits compiled in this study we visualize the variation in the seed germination spectrum of alpine plants. On one end of the spectrum, strict alpine species tend to have slow and synchronous germination, require warm temperatures and light to germinate, and need stratification or GA<sub>3</sub> to break physiological dormancy. On the other end, generalist species tend to have fast germination, show a bet-hedging strategy (high germination uncertainty) and germination traits suggesting possible fast germination after specific cues (scarification, alternating temperatures). The dormancy classes without a physiological component (non-dormant, physical, and morphological) appear associated with generalist species. This gradient of regenerative strategies mirrors prominent gradients of fast or slow population dynamics (Silvertown *et al.*, 1992; Nobis & Schweingruber, 2013), fast or slow developing leaf traits (Wright *et al.*, 2004), or large sets of plant ecological features (Grime, 1977). “Fast” regeneration can be understood as a plastic and opportunistic strategy to cope with frequently disturbed habitats such as avalanche ways, steep eroding slopes, regressing glaciers, and riverbeds (Pierce *et al.*, 2007; Gentili *et al.*, 2013). The “slow” regeneration of strict alpine species, on the other hand, seems to be a more specialized syndrome and might be the result of convergent evolution acting on those species that are truly restricted to the alpine vegetation belt.

A general assumption of seed trait ecology is that seed mass and embryo:seed ratios are relatively conserved across related species (Moles *et al.*, 2005; Vandeloos *et al.*, 2012). In our alpine dataset, both traits showed no differences between strict alpine and generalist species. This is in line with the ambiguity of relationships that have been found between seed mass and elevation for alpine species (Pluess *et al.*, 2005; Vandeloos *et al.*, 2012; Wang *et al.*, 2014; Bauk *et al.*,



2015). The similarity in embryo:seed size between generalist and strict alpine species confirms the absence of a correlation between embryo-seed size and elevation found in the Apiaceae (Vandelook *et al.*, 2012). In contrast with the supposed phylogenetic conservatism of these morphological traits, physiological germination responses are understood to be more plastic traits that can quickly acclimatize to new situations (Fernández-Pascual *et al.*, 2019). While phylogenetic signal in seed germination is generally found, especially in highly selective environments (Carta *et al.*, 2016a; Arène *et al.*, 2017; Fernández-Pascual *et al.*, 2017b), germination patterns can also be shared between phylogenetically distant species (Vandelook *et al.*, 2019) and may have low or absent phylogenetic signal (Rosbakh & Poschlod, 2015; Fang *et al.*, 2017; Fernández-Pascual *et al.*, 2017a). The phylogenetic signal found here indicates that evolutionary history cannot be neglected when studying alpine seed germination patterns. Furthermore, we detected close relationships between seed-embryo size and physiological responses of seeds, suggesting that both sets of traits are connected and may be subjected to co-adaptation. Previous studies have shown that non-endospermic seeds are smaller and are likely to be non-dormant at the time of dispersal and thus germinate quicker than alpine endospermic seeds (Sommerville *et al.*, 2013; Hoyle *et al.*, 2015; Satyanti *et al.*, 2019). Together, these results indicate that seed morphology and physiology are connected aspects. This connection, intertwined with their shared phylogenetic history, may constrict the potential variability of the seed ecological spectrum.

## Conclusions

Alpine species from different regions of the world have specialised germination characteristics that support successful regeneration in challenging alpine environments. Our results point to an evolutionary convergence of germination patterns in alpine species. They also provide the first global assessment of the seed germination spectrum in relation with morphological seed traits of alpine plants, suggesting potential relationships and trade-offs between sets of



regenerative traits that will need further research. New studies also will need to consider evolutionary history as an intrinsic constraint of the seed ecological spectrum. Overall, this study provides a global assessment of alpine seed germination that can be used as a reference in further studies focused on spatial or temporal variation in seed germination, their links with other plant traits, and the expected responses of alpine plants to climate change.

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## **Author Contribution**

BJA conceived the original idea. EFP, AC, AM, LC, SR, SV, AnS, LG, VB, FV, HB, KS, PP contributed data. EFP assembled and managed the database. AC and EFP analysed data. EFP led manuscript writing, with contributions from BJA, AC, AM, LC, SR, SV, AnS, LG, VB, FV, EM, ArS. All authors revised the manuscript and approved the final version.

## **Data Availability Statement**

The original data, R code for the analysis and creation of the manuscript can be accessed at the GitHub repository <https://github.com/efernandezpascual/alpineseeds>. Upon publication, a version of record of the repository will be deposited in Zenodo. (The repository will be made open when the manuscript is accepted for publication, a zip version has been uploaded to

648 <https://drive.google.com/file/d/12Usqi7fOAbOoZ9Uu9wkJt2FANB629LFP/view?usp=sharing> for peer-review)

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## Figures

**Figure 1** Seed dormancy classes, seed mass and embryo to seed ratio in the subsets of strict alpine and generalist species analysed in this study. Seed dormancy classes are abbreviated as follows: MD (morphological), MPD (morphophysiological), ND (non-dormant), PD (physiological), PY (physical).

**Figure 2** Effect of the germination environment on germination, according to the MCMC meta-analysis of the primary data. The dots indicate the posterior mean of the effect size, and the brackets its 95 % credible interval. The line of zero effect is shown. When the credible intervals overlap with the zero-effect line, the effect is not significant. The figure shows first the main effect, then the effects for the strict alpine and generalist groups, and then the interaction with seed mass and embryo:seed. A negative interaction (e.g. seed mass and light, in the case of the germination proportion) indicates that, as the interacting factor increases (e.g. seed mass) the response to the germination cue (e.g. light) decreases, in comparison with the main effect.

**Figure 3** Effect of the random factors on germination, according to the MCMC meta-analysis of the primary data. The dots indicate the posterior mean of the effect size, and the brackets its 95 % credible interval. The line of zero effect is shown.

**Figure 4** Phylogenetic signal in the response to the germination environment. When  $\lambda = 0$ , related taxa are no more similar than expected by chance; when  $\lambda = 1$ , the trait is evolving following a constant variance random walk or Brownian motion model.

**Figure 5** FADM ordination of the alpine seed germination spectrum. Each square is a species. Labels indicate the contribution of the variables to the axes. Seed

dormancy classes are abbreviated as follows: MD (morphological), MPD (morphophysiological), ND (non-dormant), PD (physiological), PY (physical).

**Tables**

**Table 1** Description of the datasets contributing primary data to this meta-analysis. The number of germination records, number of species and number of strict alpine species are given.

Source	Coverage	Records	Species	Strict
Briceño, unpublished	Andes	236	25	5
Bu et al. (2007, 2008)	Qinghai-Tibet	1766	242	68
Cavieres & Arroyo (2000), Cavieres & Sierra-Almeida (2018)	Andes	804	31	6
enscobase.maich.gr	Europe	510	124	75
Fernández-Pascual et al. (2017a)	Cantabrian Mts	792	22	14
Liu et al. (2013)	Qinghai-Tibet	465	151	42
Mondoni, unpublished	Apennines	32	10	7
Mondoni et al. (2009), Mondoni et al. (2012)	European Alps	506	101	74
Rosbakh, unpublished	Caucasus	263	18	9
Rosbakh & Poschlod (2015)	European Alps	971	21	15
Satyanti, unpublished	Australian Alps	632	91	41
Sommerville et al. (2013)	Australian Alps	1395	13	3
Tudela-Isanta et al. (2018)	European Alps	376	47	29
Venn (2007), Venn & Morgan (2009)	Australian Alps	1051	15	5

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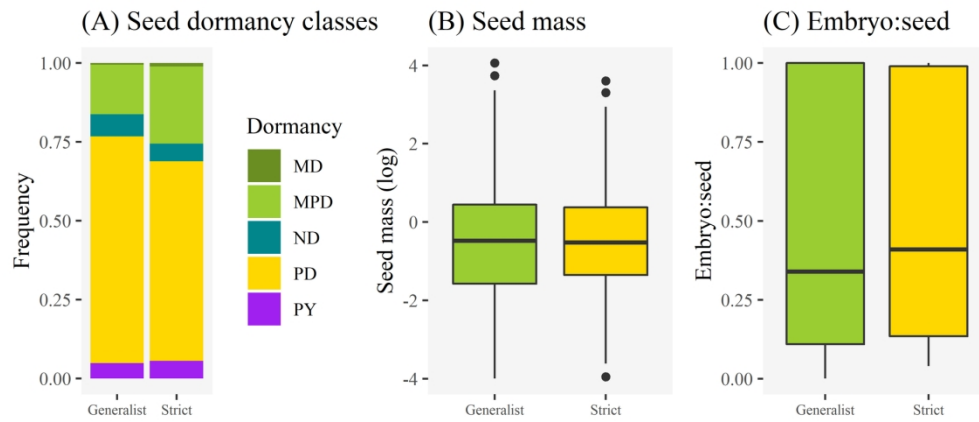


Figure 1 Seed dormancy classes, seed mass and embryo to seed ratio in the subsets of strict alpine and generalist species analysed in this study. Seed dormancy classes are abbreviated as follows: MD (morphological), MPD (morphophysiological), ND (non-dormant), PD (physiological), PY (physical).

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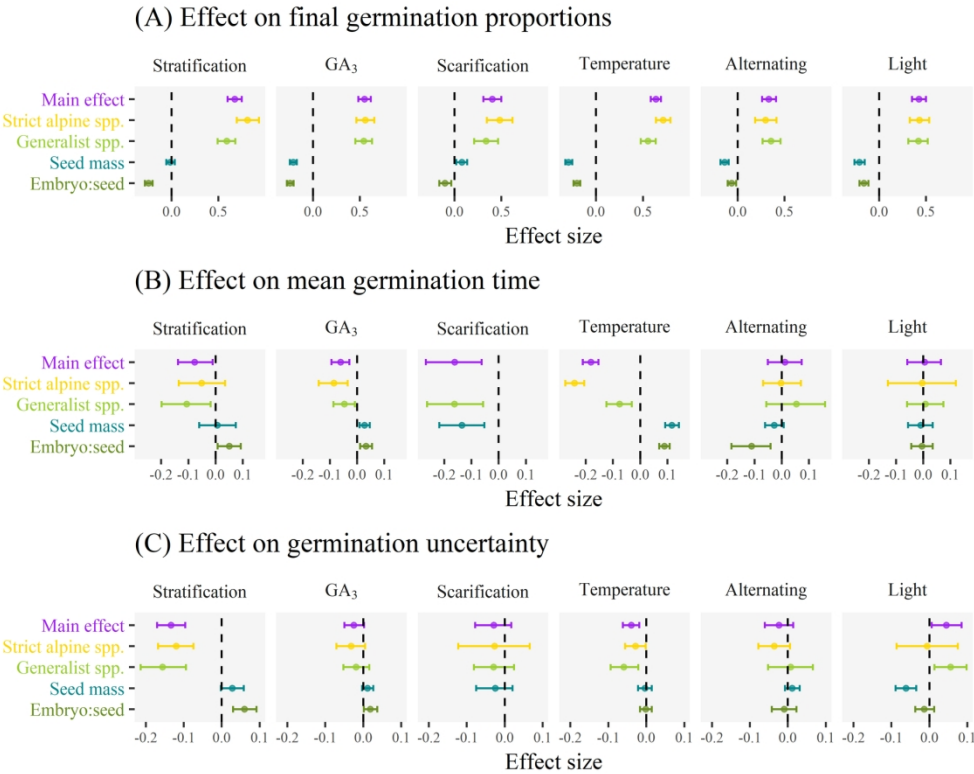


Figure 2 Effect of the germination environment on germination, according to the MCMC meta-analysis of the primary data. The dots indicate the posterior mean of the effect size, and the brackets its 95 % credible interval. The line of zero effect is shown. When the credible intervals overlap with the zero-effect line, the effect is not significant. The figure shows first the main effect, then the effects for the strict alpine and generalist groups, and then the interaction with seed mass and embryo:seed. A negative interaction (e.g. seed mass and light, in the case of the germination proportion) indicates that, as the interacting factor increases (e.g. seed mass) the response to the germination cue (e.g. light) decreases, in comparison with the main effect.

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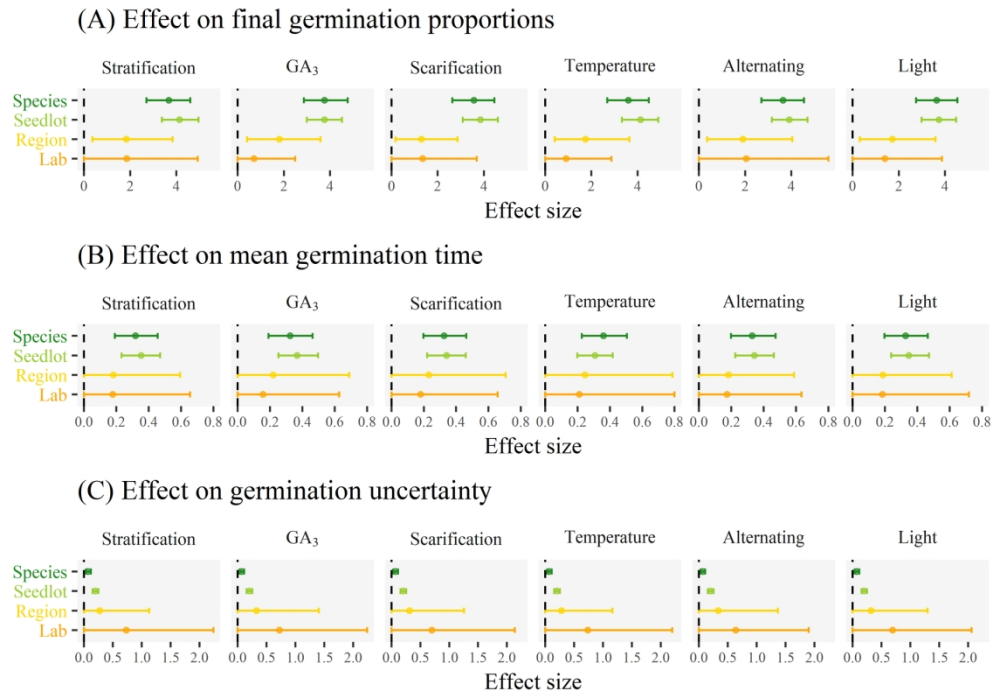


Figure 3 Effect of the random factors on germination, according to the MCMC meta-analysis of the primary data. The dots indicate the posterior mean of the effect size, and the brackets its 95 % credible interval. The line of zero effect is shown.

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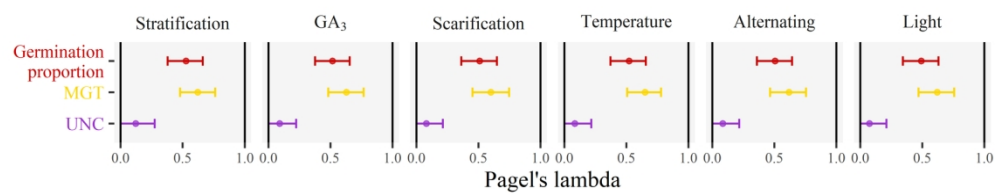


Figure 4 Phylogenetic signal in the response to the germination environment. When  $\lambda = 0$ , related taxa are no more similar than expected by chance; when  $\lambda = 1$ , the trait is evolving following a constant variance random walk or Brownian motion model.

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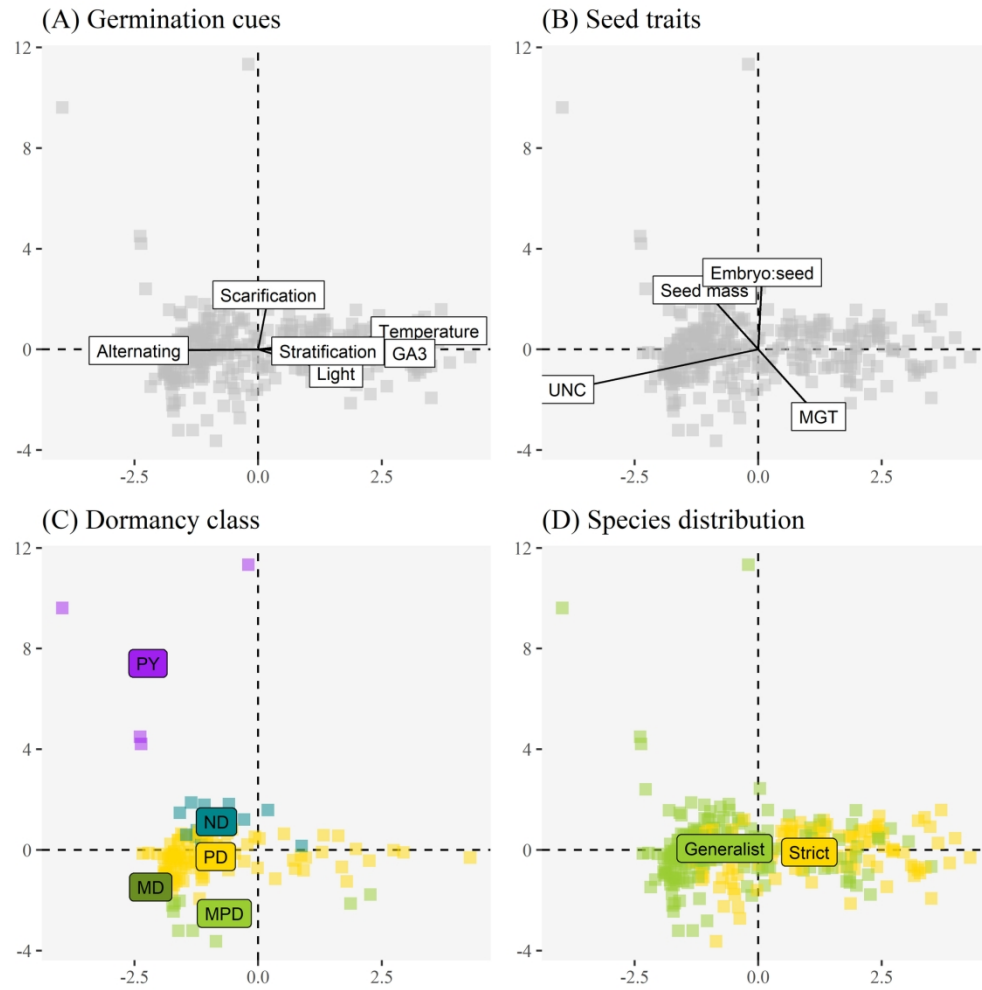


Figure 5 FADM ordination of the alpine seed germination spectrum. Each square is a species. Labels indicate the contribution of the variables to the axes. Seed dormancy classes are abbreviated as follows: MD (morphological), MPD (morphophysiological), ND (non-dormant), PD (physiological), PY (physical).

169x169mm (300 x 300 DPI)