

Seed germination ecology of alpine plants: a global meta-analysis of primary data

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Contents

1	Introduction	1
2	Materials and methods	3
2.1	Data collection	3
2.2	Description of the dataset	3
2.3	Germination indices	3
2.4	MCMC analysis	4
2.5	FAMD ordination	4
3	Results	4
3.1	Dormancy classes	4
3.2	Seed mass and embryo:endosperm	5
3.3	Germination temperature	5
3.4	Alternating temperatures	5
3.5	Light	5
3.6	Scarification	5
3.7	Stratification and GA ₃	5
3.8	Random effects and phylogenetic signal	5
3.9	FAMD ordination	6
4	Discussion	6
5	Figures	6
	References	7

1 Introduction

Alpine environments are those that occur above the maximum elevation at which trees can grow, and are characterized by low temperatures, strong winds, unstable substrates, and short growing seasons (Körner, 2003). The short alpine summer is a major barrier for plant recruitment, as it constrains the period favorable for seedling establishment (Chambers *et al.*, 1990; Forbis, 2003). Alpine seedlings must survive extreme environmental stress and yet grow to a critical biomass by the end of the growing season, to withstand the harsh and long-lasting winter (Schütz, 2002). The physiological process of seed germination is the essential, yet most vulnerable, start of seedling establishment. Because it is an irreversible process, germination must be timed to occur when the environment is favourable for subsequent seedling survival and growth (Poschlod *et al.*, 2013). Thus, the mechanisms regulating the timing of the seed-to-seedling transition are expected to be under strong selective pressure (Angevine & Chabot, 1979). Natural selection should favour seed germination requirements that reduce the probability of facing environmental conditions that are not appropriate for seedlings. The main physiological drivers of germination, water availability and temperature (Bewley *et al.*, 2013), are also two main features of climate. In addition, many plant species have developed seed dormancy,

by which germination is prevented during periods that are only ephemerally favourable, ensuring germination in the right season (Baskin & Baskin, 2014). Different degrees of dormancy also ensure the distribution of offspring emergence across time, as bet-hedging against unpredictable environments (Venable, 2007). Other germination cues, such as the response to light (Carta *et al.*, 2017) and alternating temperatures (Thompson, 1977), allow for a fine-scale detection of germination niches and safe sites (Jumpponen *et al.*, 1999). In the alpine environment, the diversity of microhabitats has apparently resulted in variable germination ecologies across species, making it difficult to define a common *alpine germination syndrome* (Körner, 2003; Schwienbacher *et al.*, 2011).

Early studies on the germination ecology of alpine plants demonstrated that freshly collected seeds of most arctic and alpine species required relatively high temperatures for germination (Bliss, 1958; Amen, 1966; Billings & Mooney, 1968). High-temperature germination has been considered to be an adaptation to prevent seed germination at the timing of seed dispersal (autumn), when temperatures are low and there is a high risk of frost (Cavieres & Arroyo, 2000). Indeed, germination of alpine seeds tends to occur after exposure to winter in early summer (Körner, 2003; Mondoni *et al.*, 2015); at this stage the temperature window for germination usually widens towards lower values (Nishitani, 1996). Nevertheless, there is an increasing number of studies highlighting the germination of freshly collected seeds at cool incubation temperatures or even during cold stratification treatments (Schwienbacher *et al.*, 2011; Hoyle *et al.*, 2015; Fernández-Pascual *et al.*, 2017; Cavieres & Sierra-Almeida, 2018). Low-temperature germination could be an adaptation to germination under snow or at snowmelt, which could presumably allow seedlings to develop a deeper root system before topsoil desiccation in summer (Kammer & Möhl, 2002), as well as to attain an optimal size for overwintering (Billings & Mooney, 1968).

Many alpine species have been described as having deep physiological dormancy (Schwienbacher *et al.*, 2011; Sommerville *et al.*, 2013; Baskin & Baskin, 2014). Dormancy in freshly-dispersed seeds would prevent precocious germination under autumn conditions, when appropriate soil moisture and temperature 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 timing germination to a posterior period, more appropriate for seedling survival and growth. Thus, it can be expected that a cold stratification period would be a common requirement for seed germination in alpine plants. Nonetheless, in an early review, Amen (1966) concluded that cold stratification was not a common requirement for the seed germination of several alpine species from different mountains in the USA (see also Sayers and Ward (1966); Marchand and Roach (1980); Kaye (1997)). More recently, Sommerville *et al.* (2013) and Hoyle *et al.* (2015) showed that in 19 and 54 Australian alpine plant species, respectively, a cold stratification period significantly increased seed germination only in half of the species tested. In contrast, Söyrinki (1938, cited in Körner (2003)), experimenting with 91 alpine species from the Alps, found that storage at winter temperatures (i.e. cold stratification) increased seed germination in the great majority of cases. Shimono and Kudo (2005) reported that cold stratification increased seed germination over a range of temperatures in most of the 27 plant species studied in the alpine zone of Japan. Cavieres and Sierra-Almeida (2018) reported that, 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 still did not germinate after cold stratification. Therefore, how important cold stratification is for seed germination in alpine plant species remains unclear and requires a global assessment.

The response of alpine seeds to light and alternating temperatures can provide further information on their capacity to detect fine-scale environmental variation. The preference of some species to germinate in light (Densmore, 1997; Mondoni *et al.*, 2009) could favour the creation of a persistent soil seed bank (Jaganathan *et al.*, 2015), advantageous in temporally and spatially unpredictable alpine environments (Kalin Arroyo *et al.*, 1999; Cavieres & Arroyo, 2001). Some species seem to prefer dark germination (Schwienbacher *et al.*, 2011), a behaviour interpreted by some as detecting safe sites in rock crevices (Arslan *et al.*, 2011). Regarding alternating temperatures, a study of 445 species from the Qinhai-Tibet plateau detected that species from high elevation alpine meadows did not show a significant response to diurnal temperature oscillations (Liu *et al.*, 2013).

2 Materials and methods

2.1 Data collection

We have conducted a meta-analysis of primary data (Mengersen *et al.*, 2013). To gather data, we contacted research groups who have performed experiments on the germination of alpine seeds, asking them to send 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 from the Cantabrian Mountains (Fernández-Pascual *et al.*, 2017), the Alps [Mondoni *et al.* (2009); Mondoni *et al.* (2012); Tudela-Isanta *et al.* (2018a); Rosbakh, unpublished], the Apennines (Mondoni, unpublished), the Caucasus [Rosbakh, unpublished], the Qinhai-Tibet Plateau (Bu *et al.*, 2007, 2008; Liu *et al.*, 2013), the Andes [Cavieres & Arroyo (2000); Cavieres & Sierra-Almeida (2018); Briceño, unpublished] and the Australian Alps [Venn (2007); Venn & Morgan (2009); Sommerville *et al.* (2013); Satyanti, unpublished]. We also received data on European alpine species from *EnscoBase* (<http://enscobase.maich.gr/index.html>). Once received, we standardized the species names using *The Plant List* (The Plant List, 2013) with the package *Taxonstand* (Cayuela *et al.*, 2019) in *R* (R Core Team, 2019). For each species, we checked its elevation range in local floras (Hegi, 1906; Pignatti, 1982; Castroviejo, 1987; Brach & Song, 2006; Parolly & Rohwer, 2019), catalogues (Rodríguez *et al.*, 2018) and herbaria (*Australian National Herbarium*). We used the elevation ranges to (i) remove from the dataset species that do not grow above the treeline; and (ii) classify the rest of the species as *strict alpine* (i.e. species that only grow above the subalpine) or *generalist* (i.e. species that can grow above the subalpine but also in the lowlands). For each species, we also compiled the following traits: life form and life span from the references used for the elevation, plus some extra references (Cabrera, 1982; Oberdorfer, 2001; RN4745; Shetekauri & Jacoby, 2009; Zavala-Gallo *et al.*, 2010; Al-Shehbaz, 2018) and online sources (<https://www.infoflora.ch/de/>; <http://plantnet.rbgsyd.nsw.gov.au/search/simple.htm>; <http://buscador.floraargentina.edu.ar/>; <https://patagoniawildflowers.org/>); seed dormancy class (Baskin & Baskin, 2014; Rosbakh *et al.*, 2020); seed mass (Bu *et al.*, 2007, 2008; Liu *et al.*, 2013; Royal Botanic Gardens, Kew, 2017) and embryo to endosperm ratio (Vandelook, unpublished). For the species missing seed mass or embryo values, we used genus or family means.

2.2 Description of the dataset

The final dataset contains 9,793 records (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 generalists). Seed lots had been collected in 8 alpine regions of the world (**Fig. 1**), in both hemispheres. The total number of seeds used in the experiments is 365,508. The range of germination temperatures (weighted average of the daily thermoperiod) goes from 0 to 36 °C, with 7,515 records of constant temperatures and 2,278 of alternating temperatures. Light was used in 8,927 records, darkness in 866. The experiments were performed with unstratified seeds in 7,291 records, and of the rest, the majority (2,436) went through cold stratification. Scarification was applied to 119 records, and GA₃ to 651. Germination incubations had ran for different periods of time, we established a cut-off time of 8 weeks to calculate the final germination percentages, in order to have an homogeneous comparison of germination.

2.3 Germination indices

As a response variable for the germination treatments, we used the final germination proportion and, in addition, we calculated the mean time to germination (MGT) and the germination uncertainty index (UNC) with the package *GerminaR* (Lozano-Isla *et al.*, 2019). MGT indicates the time it takes for half of the seed lot to germinate, while UNC estimates how scattered germination is through time. To calculate these indices, we used only records that had (i) more than 50% final germination *check with Angelino*; and (ii) less than 4 weeks of MGT; we established these limits to prevent the results being altered by a modification of seed dormancy status during the germination incubation.

2.4 MCMC analysis

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 MCMCglmm, while for MGT and UNC we used gaussian MCMCglmm. Models had, as fixed effects, the experimental conditions (temperature, alternating temperature, light, scarification, stratification and GA₃), plus their interaction with seed mass and embryo:endosperm, and the strict alpine or generalist character of the species. Random effects included a reconstructed phylogenetic tree for the 661, species identity, seed lot, lab and alpine region. To create the phylogeny, we used the R package *V.PhyloMaker* (Jin & Qian, 2019). *V.PhyloMaker* contains a mega-tree which relies on GBOTB for the seed plants (Smith & Brown, 2018), with updates, corrections and expansion. We binded taxa absent from the mega-tree to the genus-level basal node. In all models, all variables were scaled. 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 (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 (Pagel, 1999), estimated simultaneously with the models by calculating the mean of the posterior distribution and the 95% CI of lambda as indicated by (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 traits evolution that does not fully follow a Brownian motion model (Pagel, 1999).

2.5 FAMD ordination

To visualize the alpine seed germination spectrum, we performed a Factorial Analysis of Mixed Data (FAMD) as implemented in the package *FactoMineR* (Le *et al.*, 2008). Roughly, FAMD ordination is a mix between PCA and MCA that allows to include continuous and categorical variables. We calculated the ordination at the species level, i.e. for each species we calculated a series of continuous and categorical traits. We created a continuous variable for each germination cue (i.e. temperature, alternating temperatures, light, scarification, stratification and GA₃). To do so, for each cue and species, we calculated a weighted average of the cue levels (cue levels were the temperature treatments in the case of temperature; 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 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. For each species, we also calculated a single MGT (the min, i.e. the time taken at the most favourable treatment) and UNC (the mean). We conducted the FAMD only with the 293 species for which we had MGT and UNC values. We also included the continuous variables seed mass and embryo:endosperm, as well as the categorical variables dormancy class, distribution (alpine vs. generalist), life form and life span.

3 Results

3.1 Dormancy classes

Most of the species had some type of seed dormancy (**Fig. 2a**), the most common one being physiological (PD). A minority of species were non-dormant (ND), and ND was slightly more frequent in generalist species. The most noticeable difference between generalist and strict species was in the morphological (MD) and morphophysiological (MPD) classes, which were more frequent in the strict alpine species. Physical dormancy (PY) was rare in both strict alpine and generalists.

3.2 Seed mass and embryo:endosperm

Both generalist and strict alpine species had a similar range of values for seed mass (**Fig. 2b**) and embryo to endosperm ratio (**Fig. 2c**). The values of seed mass ranged from 0.02 to 58 mg, with a median of 0.56. Embryo:endosperm 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.

3.3 Germination temperature

Temperature had a positive effect on the final germination proportion (**Fig. 3a**), indicating a preference for warmer temperatures. Increasing temperatures also decreased germination time (**Fig. 3b**) and uncertainty (**Fig. 3c**). The effect of warmer temperatures was more intense in strict alpine than in generalist species. Seed mass and embryo:endosperm reduced the response to temperature: heavier and less endospermic seeds increased less their germination proportion and decreased less their germination time in warmer temperatures, although uncertainty did not show an interaction with mass or embryo:endosperm.

3.4 Alternating temperatures

Alternating temperatures had a positive effect on the germination proportion (**Fig. 3a**), but not in germination time (**Fig. 3b**) or uncertainty (**Fig. 3c**). The positive effect on the germination proportion was slightly higher in the generalist species. Again, higher seed mass and embryo:endosperm reduced the positive effect of alternating temperatures.

3.5 Light

Light enhanced the germination proportion (**Fig. 3a**), with no differences between strict alpine and generalist species. It did not affect the germination time (**Fig. 3b**), but it did increase the germination uncertainty of generalist species (**Fig. 3c**). Heavier and less endospermic seeds responded less to light.

3.6 Scarification

Scarification promoted germination (**Fig. 3a**) and reduced germination time (**Fig. 3b**), but it did not affect germination uncertainty (**Fig. 3c**). Strict alpine species responded slightly more to scarification. Heavier seeds responded more to stratification, while seeds with smaller embryos responded less.

3.7 Stratification and GA₃

Stratification increased the germination proportion (**Fig. 3a**), had a small negative effect on germination time (**Fig. 3b**) and reduced germination uncertainty (**Fig. 3c**). The positive effect on the germination proportion was higher on the strict alpine species. Seed mass did not interact with stratification, but species with smaller embryos had a smaller response to stratification in their germination proportion, and reduced less their germination time and uncertainty. GA₃ had similar effects to stratification, with the main difference being that seed mass did reduce the response to GA₃.

3.8 Random effects and phylogenetic signal

Random factors had an effect on the germination response to the environment (**Fig. 4**). The final germination proportion and the mean germination time were affected more strongly, on average, by the seed lot and the species identity. Alpine region and lab had a lower average effect, but more variability. Germination uncertainty showed the opposite pattern, with a stronger effect of lab and alpine region, which might be representing different germination scoring schedules among research groups. The phylogenetic signal in the response to all germination parameters (**Fig. 5**) was positive for the final germination proportion and the mean germination time. For the germination uncertainty it was closer to zero, indicating a weak effect of phylogeny, which perhaps is also caused by a stronger effect of different scoring schedules.

3.9 FAMD ordination

The first FAMD axis explained 15% of the variation. The quantitative variables with the largest contribution to this first axis were germination temperature, germination uncertainty, GA₃ and alternating temperatures. Among the qualitative factors, strict, generalist, physiological dormancy and annual contributed to axis 1. In summary, the axis separated (i, left) generalist and annual species with physiological dormancy, a positive response to alternating temperatures and more germination uncertainty from (ii, right) strict alpine species with a preferences for warmer temperatures and a positive response to GA₃ (**Fig. 6**). Axis 2 explained 11% of the variability. The main contributing variables were embryo:endosperm, mean germination time, seed mass and scarification; and the main categorical factors were physical dormancy, graminoid life form and morphophysiological dormancy. This axis separated (iii, bottom) morphophysiological dormant and graminoid species with longer mean time to germination from physically dormant species that responded to scarification and had heavier, less endospermic seeds.

4 Discussion

The influence of environmental conditions as drivers of these contrasting germination responses to temperature is gaining recognition. For example, alpine species show higher optimal temperatures for germination than either subalpine species (i.e. species that live close to the treeline, Fernández-Pascual *et al.* (2017)) or congeneric counterparts from below the treeline (Walder & Erschbamer, 2015). Differences in germination traits have been attributed also to species successional niche, with pioneer species germinating better at colder temperatures than later successional species (Schwienbacher *et al.*, 2012). Species from calcareous and siliceous alpine grasslands show a slow overwinter germination or high germination under all conditions, respectively (Tudela-Isanta *et al.*, 2018a,b). Other factors related to species germination characteristics include slope (Xu *et al.*, 2017) and biogeographical origin (Giménez-Benavides *et al.*, 2005). Nevertheless, no habitat-related germination strategies were identified when comparing a major divide in alpine microhabitats, as is the one between fellfields and snowbeds (Shimono & Kudo, 2005).

5 Figures

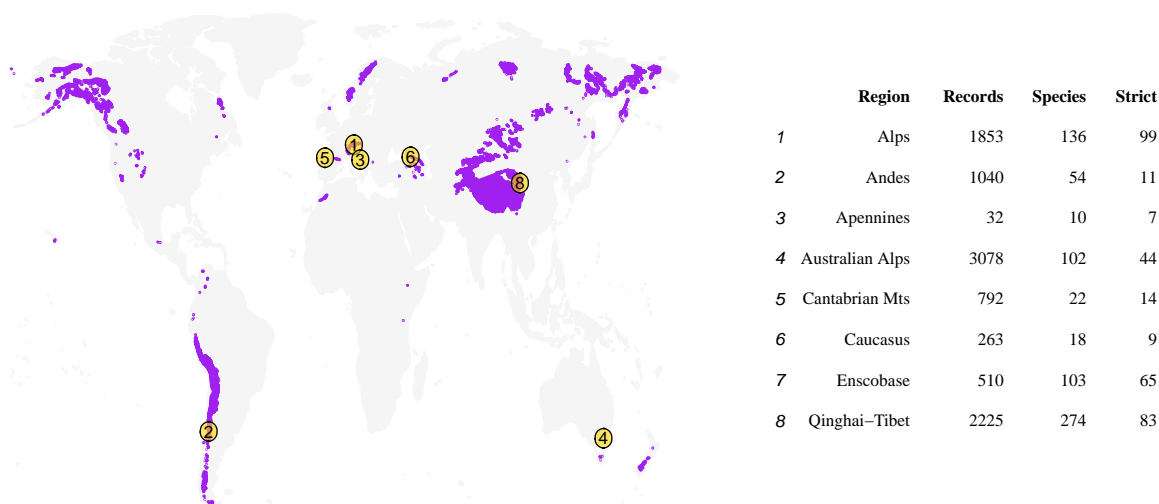


Figure 1: Geographical origin of the germination data with the number of records, species and strict alpine species per alpine region. Ensconet is not plotted because its records come from alpine regions throughout Europe. The purple areas correspond to the global extension of alpine environments according to Testolin *et al.** [-@RN4750].

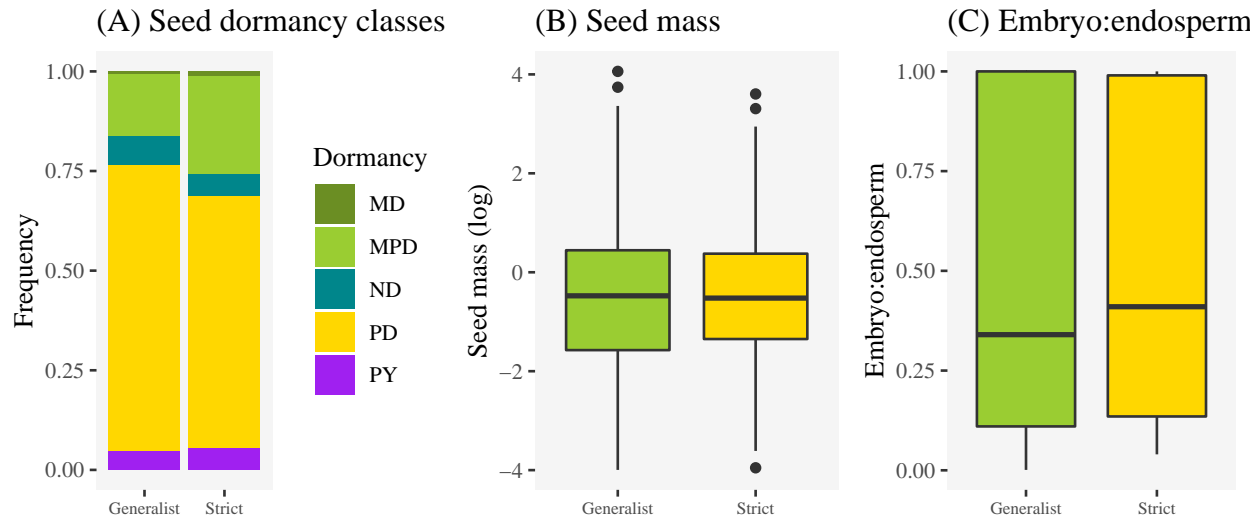


Figure 2: Seed dormancy classes, seed mass and embryo to endosperm ratio in generalist and strict alpine species. Seed dormancy classes are abbreviated as follows: MD (morphological), MPD (morphophysiological), ND (non dormant), PD (physiological), PY (physical).

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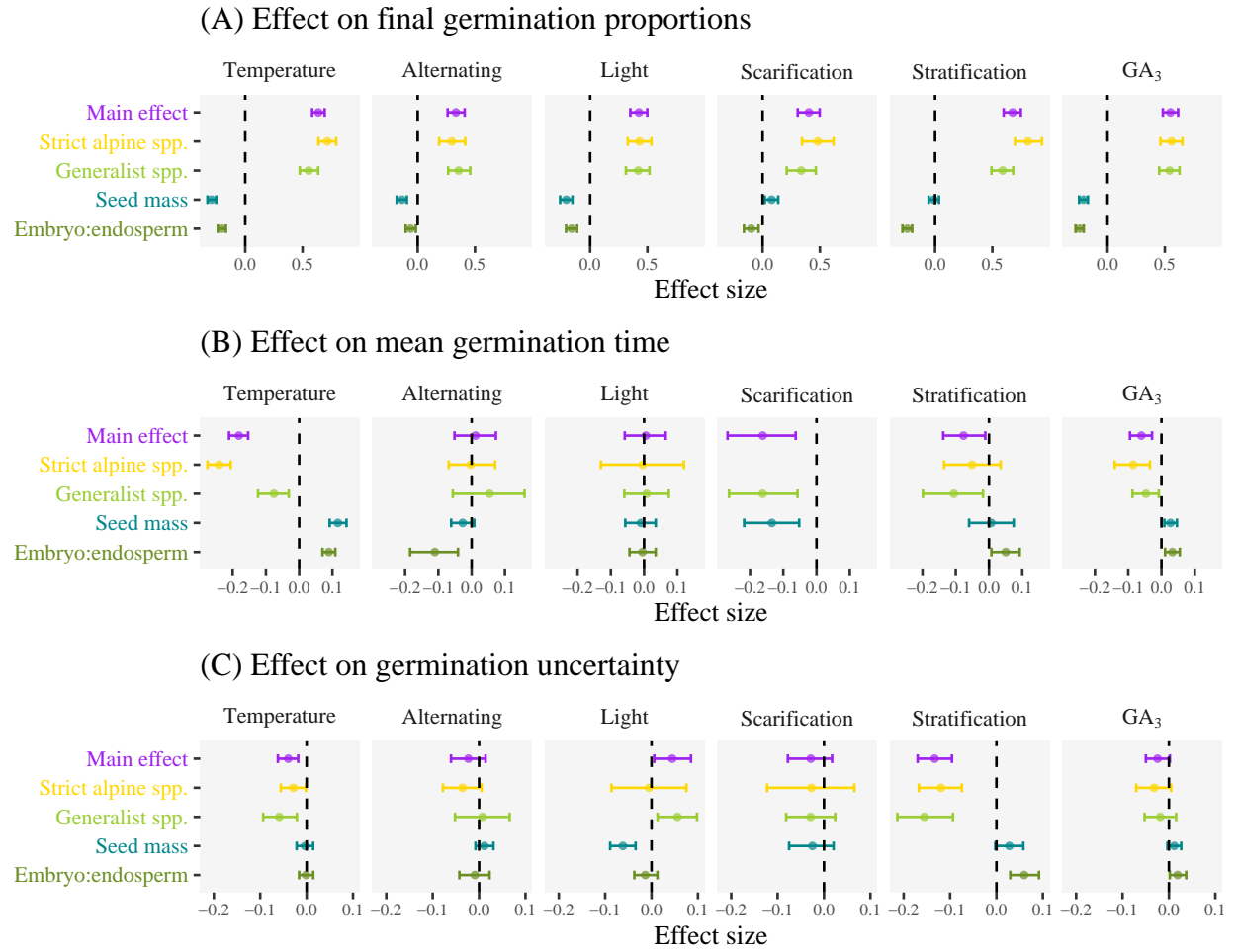


Figure 3: Effect of the germination environment on germination, according to the MCMC meta-analysis of the primary data.

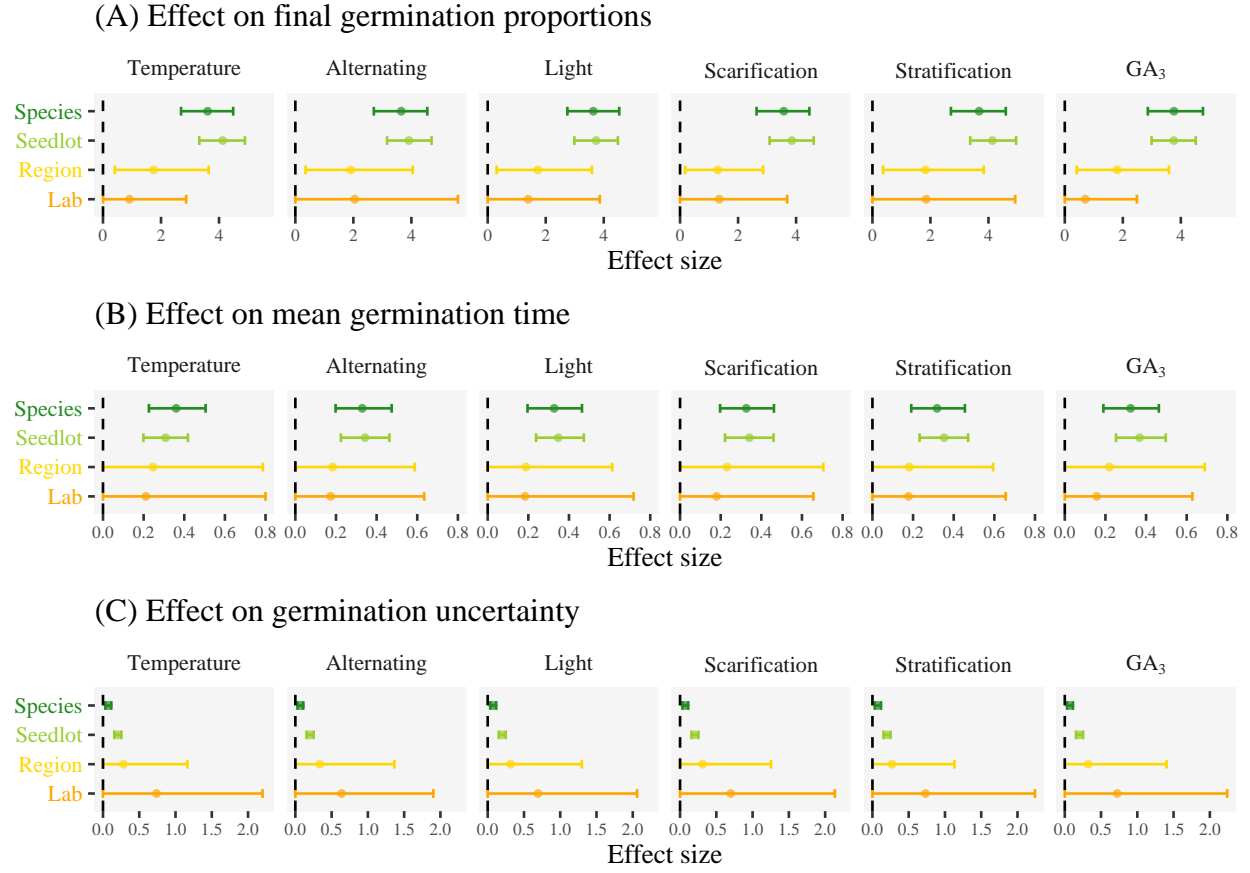


Figure 4: Effect of the random factors on germination, according to the MCMC meta-analysis of the primary data.

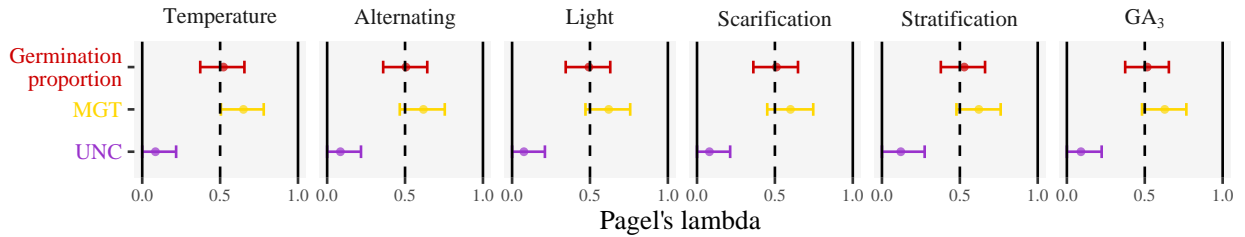


Figure 5: Phylogenetic signal in the response to the germination environment.

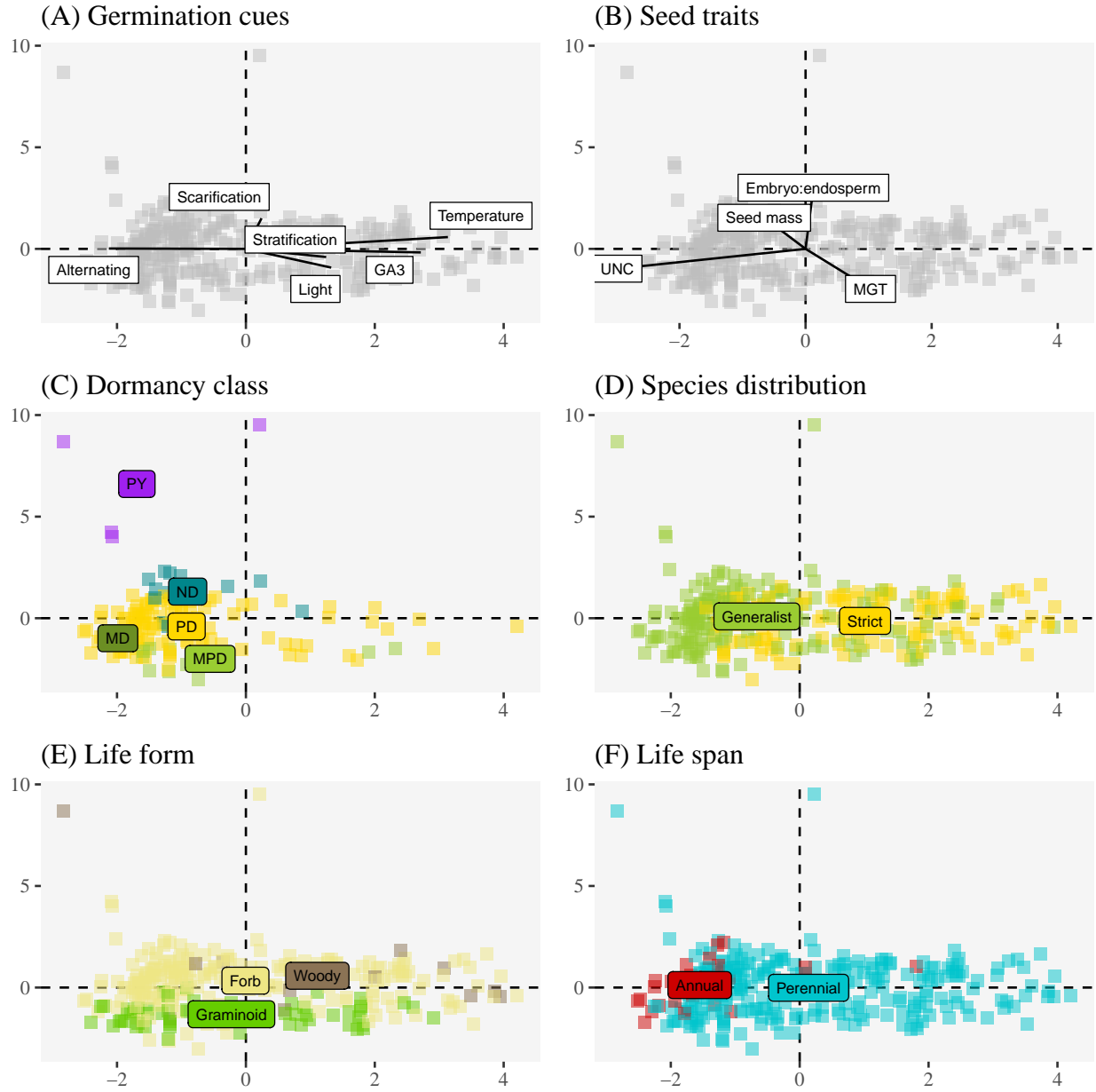


Figure 6: FADM ordination of the seed variables and the species distribution, life form and life span.

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