

RESEARCH IN CONTEXT

## Climate shapes the seed germination niche of temperate flowering plants: a meta-analysis of European seed conservation data

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- **Background and Aims** Interactions between ecological factors and seed physiological responses during the establishment phase shape the distribution of plants. Yet, our understanding of the functions and evolution of early-life traits has been limited by the scarcity of large-scale datasets. Here, we tested the hypothesis that the germination niche of temperate plants is shaped by their climatic requirements and phylogenetic relatedness, using germination data sourced from a comprehensive seed conservation database of the European flora (ENSCOBASE).
- **Methods** We performed a phylogenetically informed Bayesian meta-analysis of primary data, considering 18 762 germination tests of 2418 species from laboratory experiments conducted across all European geographical regions. We tested for the interaction between species' climatic requirements and germination responses to experimental conditions including temperature, alternating temperature, light and dormancy-breaking treatments, while accounting for between-study variation related to seed sources and seed lot physiological status.
- **Key Results** Climate was a strong predictor of germination responses. In warm and seasonally dry climates the seed germination niche includes a cold-cued germination response and an inhibition determined by alternating temperature regimes and cold stratification, while in climates with high temperature seasonality opposite responses can be observed. Germination responses to scarification and light were related to seed mass but not to climate. We also found a significant phylogenetic signal in the response of seeds to experimental conditions, providing evidence that the germination niche is phylogenetically constrained. Nevertheless, phylogenetically distant lineages exhibited common germination responses under similar climates.
- **Conclusion** This is the first quantitative meta-analysis of the germination niche at a continental scale. Our findings showed that the germination niches of European plants exhibit evolutionary convergence mediated by strong pressures at the macroclimatic level. In addition, our methodological approach highlighted how large datasets generated by conservation seed banking can be valuable sources to address questions in plant macroecology and evolution.

**Key words:** Climate, ENSCONET, evolution, germination, macroecology, plant regeneration, seed dormancy, seed trait.

### INTRODUCTION

Seed germination occurs as a response to a combination of environmental cues constituting the 'seed germination niche' (Grubb, 1977; Donohue *et al.*, 2010; Larson and Funk, 2016). The germination niche is defined as the range of environmental conditions in which a plant can complete a successful transition from seed to seedling (Grubb, 1977), including dormancy-breaking conditions and germination requirements (Baskin and Baskin, 2014). The germination niche of any given plant species ensures that the transition from seeds to seedlings occurs at the appropriate time and place for successful seedling

establishment in that species (Jurado and Flores, 2005; Finch-Savage and Leubner-Metzger, 2006; Baskin and Baskin, 2014). Observed correlations between seed germination requirements and climatic conditions (Fenner and Thompson, 2005; Donohue *et al.*, 2010; Baskin and Baskin, 2014) suggest that the optimal season for seed germination varies according to plant geographical distribution and life cycle and, consequently, so does the response to environmental cues that regulate seed dormancy breaking and promote germination (Baskin and Baskin, 2014; Dürr *et al.*, 2015; Fernández-Pascual *et al.*, 2021a). These correlations between climate and species germination

requirements suggest that macroclimate imposes ecological filters and evolutionary pressures which shape the species seed germination niche. This is particularly relevant for plants from seasonal climates, such as those at the middle latitudes (Walter, 1979), where, in contrast to the tropics, there is a marked annual variation in environmental conditions such as temperature and rainfall (Baskin and Baskin, 2014).

As reviewed by Baskin and Baskin (2014), there is a wealth of studies investigating the influence of climatic variables on seed germination. At the same time, there is an urgent need for a macroecological synthesis that: (1) formally tests the relationship between climate and seed germination; and (2) explicitly accounts for phylogenetic relatedness between species. Seed germination responses to environmental cues have been found to be non-randomly distributed across phylogenies (Carta et al., 2016a; Arène et al., 2017; Zhang et al., 2021), although similar germination responses can also be shared among phylogenetically distant species (Vandelook et al., 2019), due to convergence in seed germination syndromes in plants adapted to specific climates (Baskin and Baskin, 2014; Fernández-Pascual et al., 2021a). Thus, it is difficult to evaluate the consistency of general assumptions about the influence of climate on seed germination, and to disentangle it from shared evolutionary histories.

Whilst a large amount of data are available for plant vegetative traits (Kattge et al., 2020), regeneration traits have received less attention (Larson and Funk, 2016). This has limited macroecological research of the seed germination niche (Saatkamp et al., 2019). However, *ex situ* conservation seed banks of wild species, which routinely carry out research to identify seed dormancy breaking and germination requirements (Hay and Probert, 2013), are increasingly becoming a valuable data source for large-scale studies of seed germination (e.g. Vandelook et al., 2018; Sentinella et al., 2020; Fernández-Pascual et al., 2021a). At the European level, ENSCOBASE (the European Native Seed Conservation Consortium database; Rivière et al., 2018) is the most comprehensive database of germination data for the European flora, covering all European geographical regions and major plant families (Fig. 1). ENSCOBASE contains publicly available primary records of laboratory germination experiments from multiple seed banks across Europe, with information on experimental germination conditions (germination temperature, diurnal temperature regime, light and dormancy-breaking treatments), plus seed viability and the associated seed lot metadata, including the biogeographical region. As such, ENSCOBASE represents a valuable source of information to understand the macroecology of seed germination. Yet, there are challenges to the analysis and interpretation of the data, arising from the inherent heterogeneity of this dataset related to seed bank processing and seed lot physiological status (i.e., storage time and dormancy status, Baskin et al., 2007). This between-study variation, in term of meta-analysis theory (Koricheva et al., 2013), can be addressed by applying recent developments in phylogenetic meta-analytical methods (Mengersen et al., 2013; Garamszegi, 2014), as previously tested by Vandelook et al. (2018), Gioria et al. (2020, 2021) and Fernández-Pascual et al. (2021a, b).

Here, building on the comprehensive ENSCOBASE dataset, we tested the hypothesis that the seed germination niche of

plant species from temperate regions is shaped by climate and phylogenetic relatedness. We performed a phylogenetically informed Bayesian meta-analysis of primary data (Mengersen et al., 2013) to assess whether seed germination responses to key germination conditions (Table 1) are related to species' climatic requirements. This meta-analysis approach allowed us to identify, and visualize through a multivariate ordination, macroecological patterns across the whole continental dataset while accounting for the non-independence caused by a shared evolutionary history and to control between-study variation.

## MATERIALS AND METHODS

### Data sources

**Germination records.** We conducted a meta-analysis of primary data records (Mengersen et al., 2013), that is analysing together original records from different experiments (in our case seed bank germination tests) to synthesize their conclusions at the macroecological level. We retrieved primary germination records from the ENSCOBASE (<http://enscobase.maich.gr/>, accessed June 2019), an online repository that has compiled data on native seed collections and their related germination tests from different seed banks across Europe since 2005 (Eastwood, 2009; Rivière et al., 2018).

Here, a primary record is defined as the result (i.e. the final germination percentage, considering germination as radicle protrusion of 1–2 mm, ENSCONET, 2009) of a germination experiment conducted on a specific seed lot (i.e. a collection of seeds of a plant species obtained from a specific wild population at a specific date) and under specific germination conditions. We gathered 21 136 records of laboratory germination tests conducted in 12 seed banks (Supplementary Data Table S1) for 7458 seed lots from 3073 species. We removed 390 records because they lacked information either on experimental germination conditions or on the number of seeds sown. We also removed from the dataset those species for which all their records had less than 50% of final germination, considering that, for those species, none of the experimental conditions tested in the database represented favourable germination conditions (see Sentinella et al., 2020 for a similar approach). The final dataset included 18 762 germination records from 6869 seed lots and 2418 species (Fig. 1; Fig. S1, Tables S1 and S2).

For these records, no information was available on the duration of each germination experiment, on after-ripening as a seed dormancy-breaking treatment, or on the storage time that passed between the collection of each seed lot and the germination experiment. However, following the standard ENSCONET protocol (Eastwood, 2009; ENSCONET, 2009), it is likely that most experiments lasted from 4 to 6 weeks and were conducted soon after banking. We are aware that this means that different records could refer to seed lots at different stages of drying and/or dormancy release (Baskin et al., 2007), and to account for this between-study source of variation we included seed lot number and institution as random factors of the meta-analysis models (see below). We must also stress that this meta-analysis of primary records does not intend to identify the optimal germination conditions or dormancy type of any of the

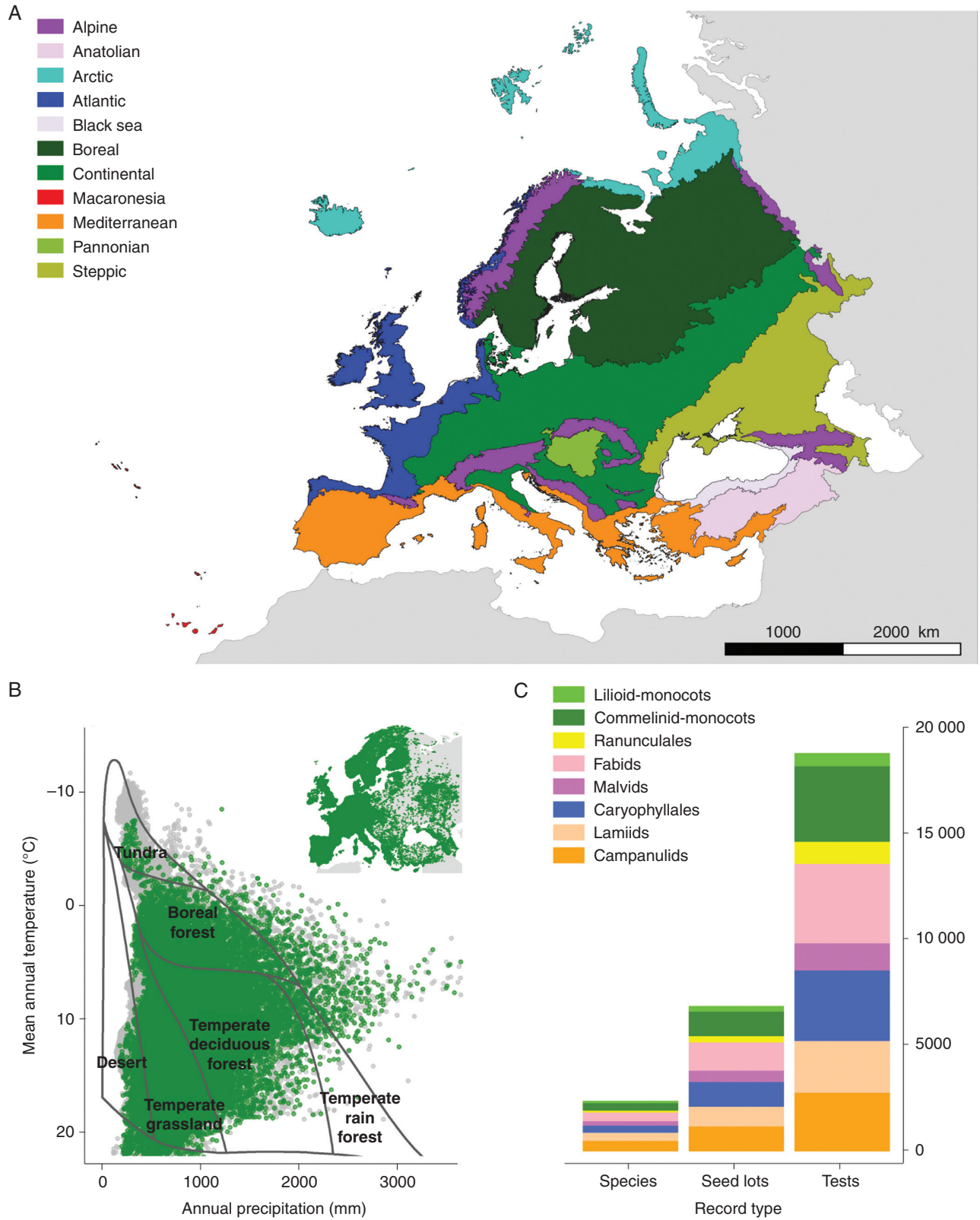


FIG. 1. Study area and dataset composition. (A) Map of European Biogeographical Regions (source: EEA, [www.eea.europa.eu](http://www.eea.europa.eu)). (B) Occurrences of species listed in the dataset (green points), versus those of all European angiosperms (grey points) (source: GBIF, <http://www.gbif.org>), in climate and geographical space. Major biomes are mapped onto climate space. (C) Dataset composition by clade grouped by number of species, seed lots and germination tests. For a detailed description of the database see [Supplementary Data Fig. S1](#) and [Table S2](#).

TABLE 1. Seed germination experimental conditions, seed mass and their functional role in the natural environment.

Experimental cue	Description	Unit/type of variable	Functional significance
Germination temperature	Weighted average of the day and night temperatures, weighted by the duration of each phase	°C	Macroclimate and season detection (Baskin and Baskin, 2014)
Alternating temperature regime	Different temperatures applied during the day and night, in diurnal cycles	Binary (yes/no)	Soil persistence, gap detection in natural habitats, soil depth, water table level (Thompson and Grime, 1983; Pons, 2000; Saatkamp et al., 2011)
Light	Seeds exposed to light during some part of the diurnal cycle	Binary (yes/no)	Soil persistence, gap detection in natural habitats, soil depth and dryness signalling (Pons, 2000; Carta et al., 2017)
Stratification	Seeds went through cold-wet stratification (<5 °C) or to warm-wet stratification (>20 °C)	Binary (yes/no)	Macroclimate and season detection (Vleeshouwers et al., 1995; Finch-Savage and Leubner-Metzger, 2006)
Scarification	Abrasion of the seed coat to allow water imbibition and/or to reduce puncture force to break through the seed coat	Binary (yes/no)	Macroclimate and season detection (Jayasuriya et al., 2009)
Seed mass	Dry mass of an average dispersal unit	mg	Dispersal distance (Tamme et al., 2014); seed persistence (Thompson et al., 1993; Gioria et al., 2020); light detection (Milberg et al., 2007; Carta et al., 2017); seedling establishment (Moles and Westoby, 2004)

given species, but aims to test macroecological patterns (climate and phylogeny) in the germination responses across the whole dataset.

Records included information on number of sown and germinated seeds, and the associated seed lot meta-data: species, institution (seed bank) where the test was carried out, country of collected seed lots and biogeographical region (as defined by the European Environment Agency, EEA, [www.eea.europa.eu](http://www.eea.europa.eu)) of collection. Germination conditions (see below) were not equally distributed across biogeographical regions and major angiosperm clades (Fig. 1; Supplementary Data Fig. S1, Table S2), but most regions and major clades were well represented (Fig. 1; Fig. S1).

**Germination conditions.** Each record reported information about the experimental conditions at which the germination test was conducted [germination temperature, diurnal temperature regime (alternating vs. constant), light (vs. darkness) and dormancy-breaking treatments (stratification, scarification)]. Germination temperature (i.e. the average of the day and night temperatures, weighted by the duration of each phase) ranged from 2 to 40 °C. There were 13 637 records at constant temperatures (i.e. germination test at the same temperature during its entire duration) and 5125 records using alternating temperatures in diurnal cycles (i.e. experiments where different temperatures were applied during the day and the night). Seeds were exposed to light during some part of the diurnal cycle in 17 472 records and kept in total darkness in 1290 records. The experiments were performed with non-treated seeds in 9413 records, while cold (<5 °C) and warm stratification (>15 °C) were applied in 1643 and 1163 records, respectively. As a widely accepted standard in many seed banks, the stratification pre-treatment (cold or warm stratification) lasted on average 8 weeks (Eastwood, 2009), but the exact duration of this pre-treatment was not reported. Scarification (i.e. an abrasion of the seed coat to allow water imbibition) was performed in 4425 records.

**Phylogenetic tree.** A phylogenetic tree for the 2418 angiosperm taxa in the germination dataset was compiled using the R package V.PhyloMaker (Jin and Qian, 2019). V.PhyloMaker contains a mega-tree based on the GBOTB phylogeny for seed

plants (Smith and Brown, 2018), with updates, corrections and expansions (Jin and Qian, 2019). Taxa absent from the mega-tree were attached to their designated relatives using the ‘bind.relative()’ function based on different sources (Tutin et al., 1993; Durka and Michalski, 2012; Janssens et al., 2020).

**Climatic requirements of the species.** We used geographical distribution data provided by GBIF (Global Biodiversity Information Facility) to characterize climatic requirements for each species. Curated GBIF data were gathered from Carta et al. (2022). We obtained average climatic data for each species from the CHELSA v.1.2 database (Karger et al., 2017). We selected climatic variables representing annual trends (mean annual temperature, annual precipitation) and annual ranges (temperature seasonality, precipitation seasonality) because in previous studies they have been shown to be among the most influential climatic variables usually related to seed germination (e.g. Carta et al., 2016b; Sentinella et al., 2020).

**Seed mass of the study species.** To take into account the potential effects of seed mass on seed germination, we included seed mass as a covariate in the models. Seed mass is considered a key driver of the seed germination niche (Thompson and Grime, 1983; Pons, 2000; Moles and Westoby, 2004) and is a proxy of plant size, which makes up the first axis of variation of the global spectrum of plant form and function (Díaz et al., 2016). Seed mass data were extracted from the Seed Information Database (Royal Botanic Gardens Kew, 2019). For 121 species for which seed mass values were missing, these were calculated as genus averages.

#### Statistical analyses

**Meta-analysis models.** To test whether the seed germination niche is shaped by species’ climatic requirements, we estimated the overall interactive effects between key germination conditions (Table 1) and species’ climatic requirements on seed germination proportions. We performed a meta-analysis of primary germination data (Mengersen et al., 2013) by fitting binomial phylogenetic generalized mixed models with Bayesian estimation using the Markov chain Monte Carlo (MCMC) method, as

implemented in the R package MCMCglmm (Hadfield, 2010), following the approach previously used in related studies (Vandelook *et al.*, 2018; Gioria *et al.*, 2020; 2021b; Fernández-Pascual *et al.*, 2021a, b). This technique allowed us to consider multiple observations per species (i.e. each germination test as a single, separated observation) while simultaneously accounting for the phylogenetic relatedness among species (Garamszegi, 2014) and for the between-study variation due to different storage time or different stages of dormancy release between seed lots. The final germination proportion of each germination test was the response variable in all the models. The fixed effects of the models (i.e. the predictors) were the experimental germination conditions [i.e. germination temperature, alternating temperature regime, light and dormancy-breaking treatments (cold stratification, warm stratification and scarification)]; see above and Table 1 for a description of these conditions] and their interaction with species' climatic requirements or seed mass. The interaction between germination conditions and climatic requirements allowed us to test our specific hypothesis that climate shapes the germination responses of species (see below). The random effects considered in the models were: (1) the phylogeny accounting for the statistical non-independence of data points due to shared evolutionary history among related species; (2) species identity accounting for within-species variation in germination responses and possible measurement errors; and (3) seed lot, country of collection and germination institution to account for between-study variation among seed lots in their physiological status, e.g. dormancy, storage time as well as the processing and experimental conditions of different laboratories (seed banks). All variables were centred and scaled to unit variance so effect sizes could be compared. All models were run with weakly informative priors, 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 and Nakagawa, 2014), resulting, on average, in 9000 posterior distributions. From the resulting posterior distributions, we calculated mean parameter estimates and 95% credible intervals (CIs). The significance of model parameters was estimated by examining CIs: parameters with CIs overlapping zero were considered not significant. The phylogenetic signal of seed germination responses over all experimental conditions was calculated using Pagel's lambda ( $\lambda$ ) (Pagel, 1999).  $\lambda$  was estimated simultaneously with the regression by calculating the mean of the posterior distribution and the 95% CI of  $\lambda$  as indicated by de Villemereuil and Nakagawa (2014). When  $\lambda = 0$ , related taxa are not 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).

All analyses were run across the full dataset including all the species in the phylogeny (2418), as well as separately, for the largest clades, based on the APG IV classification (The Angiosperm Phylogeny Group, 2009): lilioid-monocots, commelinid-monocots, Ranunculales, fabids, malvids, Caryophyllales, lamiids and campanulids (Supplementary Data Fig. S1). Whilst all models accounted for the species phylogenetic relatedness (returning the phylogenetic signal as a measure of clustering in seed germination responses), running the same

models separately for each clade provided an indication of whether the seed germination responses were the same in all clades vs. lineage-specific subsets.

*Principal component analysis.* We used multivariate ordination to visualize the relationship between seed responses to germination conditions, seed mass and species' climatic requirements, and to assess these patterns for each geographical region. Multivariate ordination was carried out by means of principal component analysis (PCA) as implemented in the package FactoMiner (Lê *et al.*, 2008). The ordination was performed at the seed lot level, calculating a series of continuous traits for each seed lot. We first reduced climate variation to two axes based on a PCA of the four climatic variables. Then, we predicted germination proportions by fitting binomial generalized mixed models (with the same random effects as the MCMCglmm above) using the interaction between each experimental germination condition and the two climate axes. We then transformed the predicted germination proportions to create a continuous variable for each experimental germination condition [i.e. germination temperature, temperature regime, light and dormancy-breaking treatments (stratification and scarification)]. To do so, for each seed lot, we calculated a weighted average of the condition levels, weighting by the predicted germination proportion at each level [see Fernández-Pascual *et al.* (2021a) for a similar approach]. In the case of temperature, the weighted germination temperature is simply the germination temperature weighted by germination proportion; for the other germination conditions the weighted average at each condition level was used to calculate the relative indices of germination as follows (using the relative light index as an example): RI = weighted averaged germination in the light / (weighted averaged germination in the light + weighted averaged germination in the dark). Only experimental germination conditions significantly related to climate in the meta-analytical models were retained in the ordination (warm stratification was not included). These continuous seed traits were used in the ordination, whilst the other continuous variables (climatic variables and seed mass), as well as the categorical variables clade and geographical region of seed collecting (as in Fig. 1), were included as supplementary variables.

## RESULTS

### *Meta-analysis models*

In the following sections we describe the results of the meta-analysis of the relationship between species' responses to germination conditions and their climatic requirements, explaining the general pattern (Fig. 2) and how the different clades comply with the general pattern. For the detailed results per clade, see Supplementary Data Fig. S2. Detailed numerical summaries for all models across all species and all clades are available in Tables S3 and S4. Model summaries include information on the fixed and random effects (Tables S3 and S4). Fixed effects represent how the predictive variables affect the response variable (i.e. final germination proportion). Specifically, we tested for an interaction between germination conditions and species' climatic requirements on seed germination proportions: a negative

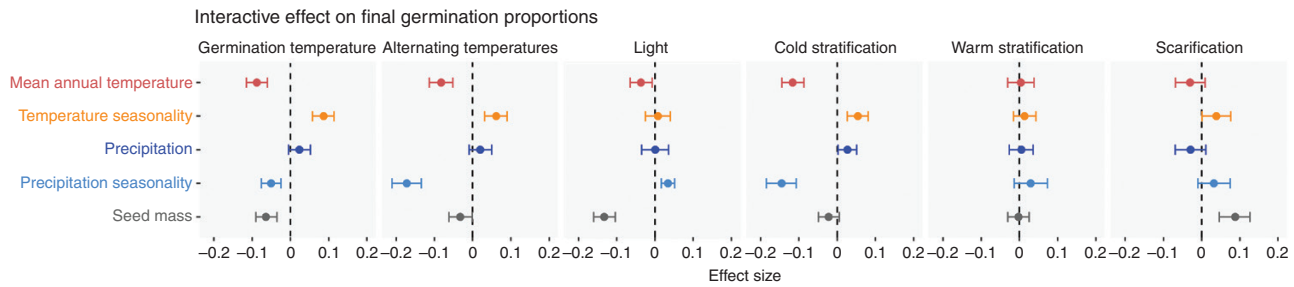


FIG. 2. Meta-analysis of the seed germination niche in relation to climate. Interactive effect of experimental germination conditions (see Table 1) with species' climatic requirements and seed mass on the final seed germination proportions according to the binomial phylogenetic mixed models with Bayesian estimation (MCMCglmm). Dots indicate the posterior means of the interaction effect size. The horizontal bars represent the 95% credible intervals. The line of zero effect is shown. When the credible intervals overlap with the zero-effect line, the interactive effect is not significant. A negative interaction indicates that, when the species climatic requirement has a high value, the effect of the germination condition on germination becomes more negative; for example, when mean annual temperature (climate) is high, the germination response to warm germination conditions (experimental condition) decreases.

interaction indicates that, when the species' climatic requirement has a high value, the effect of the germination condition on germination becomes more negative, e.g. when the mean annual temperature (climate) is high, the germination response to warm germination (experimental condition) decreases.

**Germination temperature.** Across all species, the interactive effect of germination temperature with species' climatic requirements on germination proportions was: (1) significantly negative for mean annual temperature and precipitation seasonality; and (2) significantly positive for temperature seasonality (Fig. 2). According to these results, species from warm and seasonally dry climates tended to show higher germination proportions when germinating in cooler experimental conditions (i.e. cold-cued germination). This general pattern was also significant for lilioid-monocots, Caryophyllales and campanulids (Supplementary Data Fig. S2). At the same time, species from climates with large thermal differences between summer and winter (e.g. continental climates) displayed a warm-cued germination (Fig. 2). This pattern was significant for commelinid-monocots, Caryophyllales, lamiids and campanulids (Fig. S2). The interaction between germination temperature and annual precipitation was not significant at the general level but rather was clade-specific: humid climates were related to cold-cued germination in commelinid-monocots, and to warm-cued germination in Ranunculales, fabids and campanulids (Fig. S2).

**Alternating temperature regime.** The general pattern for alternating temperatures followed the one detected for germination temperature, with interactions being: (1) significantly negative for mean annual temperature and precipitation seasonality; and (2) significantly positive for temperature seasonality (Fig. 2). Thus, species from warm and seasonally dry climates tended to germinate better under constant temperature regimes. This pattern was significant for commelinid-monocots, lamids and campanulids (Supplementary Data Fig. S2). On the other hand, species from climates with high temperature seasonality germinated better under alternating temperatures, a pattern significant for commelinid-monocots and fabids (Fig. S2). Annual precipitation was only significant for the commelinid-monocots, in which group species from humid climates responded better to alternating temperatures (Fig. S2).

**Light.** Regarding the germination response to light, the general pattern of interaction with species climate was: (1) significantly weak negative for mean annual temperature; and (2) significantly weak positive for precipitation seasonality (Fig. 2). In other words, the germination of species from warmer climates was reduced when exposed to light. This general pattern was also significant in lilioid-monocots and Caryophyllales (Supplementary Data Fig. S2). Conversely, species from seasonally dry climates germinated better in light, a general pattern that was significant for Ranunculales, fabids, lamiids and campanulids (Fig. S2). Temperature seasonality did not show a general trend but was clade-specific: higher temperature seasonality was related to higher germination in the light for lilioid-monocots, commelinid-monocots and Caryophyllales, but was related to lower germination in the light for campanulids (Fig. S2). Also, the interaction of germination with annual precipitation was clade-specific, with humid climates related to higher germination in the light for lilioid-monocots and to lower germination in the light for fabids (Fig. S2).

**Dormancy-breaking treatments.** The general pattern of interaction of cold stratification was the same as for germination temperature and alternating temperatures: (1) significantly negative for mean annual temperature and precipitation seasonality; and (2) significantly positive for temperature seasonality (Fig. 2). Therefore, cold stratification tended to reduce germination in species from warm and seasonally dry climates, a trend that was significant for commelinid-monocots, fabids, malvids and campanulids (Supplementary Data Fig. S2). Cold stratification was instead beneficial to the germination of species from climates with more seasonal temperatures, a trend that was significant in lilioid-monocots, commelinid-monocots and Caryophyllales (Fig. S2). The interaction of annual precipitation was again clade-specific: cold stratification promoted germination of species from humid climates in commelinid-monocots and fabids but reduced it in Caryophyllales (Fig. S2).

When analysing all taxa together, warm stratification did not show a significant interaction with climatic variables or with seed mass (Fig. 2). However, warm stratification promoted germination of commelinid-monocots from humid climates, Ranunculales from seasonally dry climates and fabids from climates with high temperature seasonality (Supplementary Data Fig. S2).

In addition, no significant general trend was found between scarification and climate (Fig. 2). Within clades, however, scarification was more beneficial for species from colder climates in lamiids and Caryophyllales (Supplementary Data Fig. S2). In fabids, responses to scarification were stronger in species from dry and seasonally dry climates (Fig. S2).

*Effect of seed mass.* Seed mass had a significant negative interaction with germination temperature and light, and a positive interaction with scarification (Fig. 2). Thus, the germination of heavier seeds was reduced at higher temperatures and in the light but was more responsive to scarification.

*Random effects and phylogenetic signal.* The random effects captured other sources of variance not considered by the fixed predictors. Specifically, here we considered: (1) phylogeny accounting for the statistical non-independence of data points due to shared evolutionary history; (2) species identity accounting for within-species variation and possible measurement errors; and (3) seed lot, country of collection and germination institution to account for between-study variation.

Random effects (phylogeny, species identity, seed lot, country of collection and germination institution) were related to variation in the germination response to the experimental conditions, with phylogeny being stronger, on average, than species identity, the country of collection or the seed lot (Supplementary Data Tables S3 and S4). In turn, the phylogenetic signal of seed germination in response to the experimental conditions was always significantly different from zero (Tables S3 and S4). Detailed values of the phylogenetic signal for all models across all species and all clades are available in Tables S3 and S4.

#### Principal component analyses

We applied a PCA ordination to visualize the main axes of variation in the seed germination niche and their relationship with climate. The first PCA axis explained 57 % of the total variation (Fig. 3). The quantitative variables with the largest contribution to this first axis were germination temperature, alternating temperatures and cold stratification. This horizontal axis ordered species from those with cold-cued germination occurring in warm and highly seasonally dry climates at the left (mostly coinciding with seed lots collected in the Mediterranean region), to those exhibiting warm-cued germination and positive germination responses to cold stratification and alternating temperature regimes occurring in cool and/or humid climates at the right (mostly coinciding with seed lots collected in the Alpine, Atlantic and Continental regions). The second PCA axis explained 33 % of the total variability. The main contributing variables along axis 2 were scarification and seed germination in the light. This axis ordered species from those with light seeds whose germination was promoted by light at the bottom, to those species that responded to scarification and had heavy seeds at the top. Note that whilst the variable light is mostly aligned to this vertical axis, it is right-orientated along the horizontal axis; that is, both light and scarification constitute an independent axis of the germination niche of temperate plants, while light shows some degree of relationship with the

climate. Seed mass is left-oriented, suggesting a relationship with warm and seasonally dry climates: Mediterranean seed lots had heavier seeds than those from all the other regions (Mediterranean =  $6.53 \pm 0.9$  mg), while Alpine seed lots had lighter seeds (Alpine =  $2.71 \pm 0.4$  mg); Atlantic and Continental seed lots had intermediate seed mass (Atlantic =  $3.64 \pm 0.39$  mg, Continental  $4.37 \pm 0.46$  mg).

In general, the ordination of seed germination responses to experimental conditions and species' climatic requirements suggests common germination responses within geographical regions. In particular, seed lots from the Mediterranean region are almost exclusively on the left side of the ordination, while those from the Alpine region are on the right side of the ordination (Fig. 3). By contrast, the ordination does not allow us to identify specific germination responses within clades (Supplementary Data Fig. S3). This result in combination with the clade model results (see above) suggests that, under similar climates, species share seed germination responses regardless of the clade they belong to.

## DISCUSSION

#### *The germination niche of temperate flowering plants*

Our meta-analysis supports the hypothesis that the seed germination niche of temperate plants is shaped strongly by climate. In warm and seasonally dry climates the seed germination niche includes a cold-cued germination response and an inhibition determined by alternating temperatures and cold stratification, while in climates with high temperature seasonality opposite responses can be observed. Furthermore, the phylogenetic signal in seed responses to experimental conditions confirms our expectation that the germination niche is constrained by evolutionary relatedness and probably conservatism. Nonetheless, the overall relationship between climate and germination is subject to convergent evolution mediated by strong pressures at the macroclimatic level as we found common responses in phylogenetically distant lineages under similar climates. Here, we discuss the ecological significance of these findings and the role of the evolutionary processes that probably shaped them.

A positive and significant phylogenetic covariation showed that the probability of germination at warm conditions and after a period of cold stratification was higher for species from cold regions with marked temperature seasonality, notably from the Alpine but also from the Continental and Atlantic regions (Fig. 3). This germination niche has been theorized to favour seed germination in spring/summer, after overwintering (Grime *et al.*, 1981), i.e. the cold-adapted temperate germination syndrome (Fernández-Pascual *et al.*, 2021a). On the other hand, plants occurring in the Mediterranean sites were characterized by germination at low temperatures and constant temperature regimes, a germination niche that purportedly favours regeneration during winter when water stress is lower, i.e. the Mediterranean germination syndrome (Thanos *et al.*, 1995). Finding these macro-ecological patterns in an explicitly phylogenetic meta-analysis confirms the general trends that have been previously suggested in the literature (Baskin and Baskin, 2014) and provides new evidence for evolutionary convergence behind these patterns.

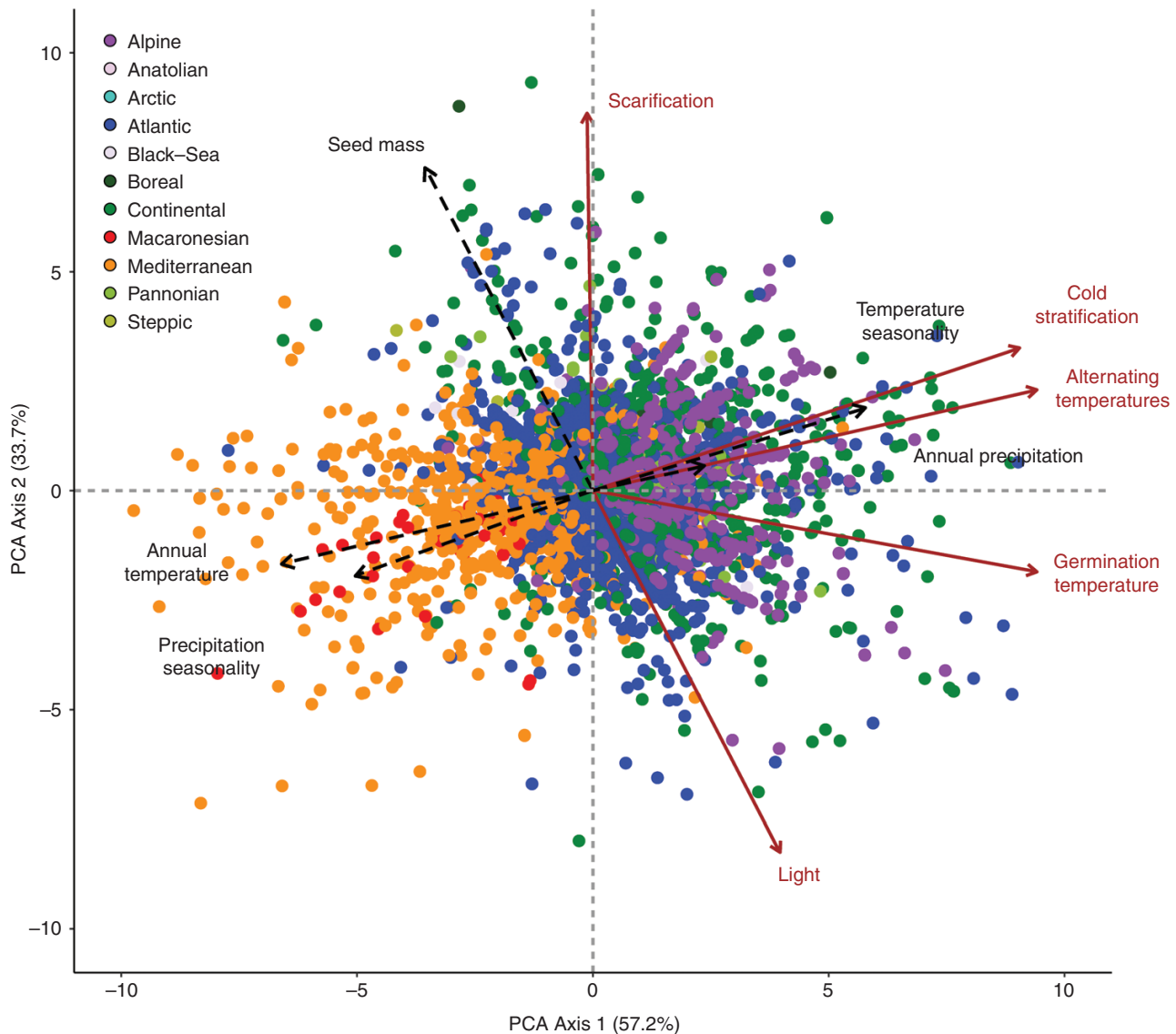


FIG. 3. Visualization of the seed germination niche of the European flowering plants. Principal component analysis (PCA) ordination summarizing the cross-covariance between seed germination traits, seed mass and species' climatic requirements along the first two axes. Each dot corresponds to a seed lot coloured by biogeographical region (as indicated). Labels in red correspond to loadings of the seed germination experimental conditions (see Table 1) used to construct the ordination. Labels in black correspond to supplementary variables, not used to construct the ordination.

Seed germination response to light constituted an independent axis of the germination niche of temperate plants, only weakly related to climate. Indeed, light acts as an environmental cue detecting safe sites and short-term regeneration windows for seedling establishment such as canopy openings or depth of seed burial (Thompson and Grime, 1983; Pons, 2000; Finch-Savage and Leubner-Metzger, 2006; Carta *et al.*, 2017). Our meta-analysis confirms that the responses of seeds to light constitute a trade-off with seed mass (Milberg *et al.*, 2007; Rubio de Casas *et al.*, 2017; Santana *et al.*, 2020). Similarly, seed germination responses to scarification were decoupled from climatic variables and, like the responses to light, were driven by seed mass (Leishman *et al.*, 2000; Donohue *et al.*, 2010; Zhang *et al.*, 2014).

By repeating all analyses separately across the major clades, we showed that the germination responses were not

lineage-specific and rather similar across all clades. However, we detected subtle but meaningful differences among clades. For example, the effect of scarification was particularly strong for fabids, since physical dormancy due to a water-impermeable seed coat characterizes several families with many species in this clade (Baskin and Baskin, 2014). Seed germination response to light was strongly negative in lilioid-monocots (Vandelook *et al.*, 2018), whilst graminoids (Commelinid-monocots) were more likely to germinate at warm conditions [see Baskin and Baskin (2014) and literature therein]. Nevertheless, these findings show consistent germination responses to climate across clades, in agreement with the responses across the full dataset. Clustering of germination responses under similar climatic conditions, exhibited by phylogenetically distant lineages, suggests that the observed patterns are likely to be the result of evolutionary convergence mediated by strong pressures at



the macroclimatic level. Furthermore, the phylogenetic signal in seed germination responses may indicate that phylogenetic constraints contributed to the observed patterns. Thus, it is likely that extant diversity in the seed germination responses resulted from processes such as niche conservatism and independent convergent adaptations to the environment (Prinzinger *et al.*, 2001; Swenson *et al.*, 2006; Crisp *et al.*, 2009). However, more in-depth studies are needed to disentangle the exact role of phylogenetic constraints and evolutionary convergence at the macroecological scale. In addition, the role of local environment (habitat scale) and plant life history traits should be also considered to better understand all the factors shaping the germination niche and determining the exact timing of germination in the natural environment (Thompson and Grime, 1983; Baskin and Baskin, 2014; Zhang *et al.*, 2014).

#### Study strengths and limitations

Modelling the seed germination niche across broad taxonomic and geographical scales is difficult because the availability of curated and preserved seed germination data is limited (Saatkamp *et al.*, 2019). To our knowledge, our meta-analysis has used the largest dataset among published studies of plant regeneration from seed [but see Sentinella *et al.* (2020) and Fernández-Pascual *et al.* (2021a)] to pursue this aim. In doing so, we added a phylogenetic perspective to the idea that climate is a strong predictor of the seed germination niche.

Nevertheless, the germination data we analysed here present challenges related to the conservation purpose of the dataset, which was created by *ex situ* seed banks to identify seed dormancy-breaking and germination requirements and monitor the viability of the stored seed lots (Hay and Probert, 2013; Rivière *et al.*, 2018). Specifically, it was not feasible to retrieve specific information on the storage status (i.e. ‘fresh’ or ‘stored’) and time of testing in the original database (<http://enscobase.maich.gr/>), highlighting an issue associated with the use of seed lots with different moisture levels (Baskin *et al.*, 2007). Thus, we worked under the assumption that all seed lots had experienced some degree of storage before testing. Therefore, results on the effects of treatments applied to overcome physiological dormancy (e.g. cold stratification) should be taken with caution as storage could also have affected the dormancy status of the seeds (Baskin *et al.*, 2007). ‘Exceptional species’ *sensu* Pence *et al.* (2022), i.e. those plant species that cannot effectively be stored in conventional seed banks, due to limitations that hinder their collection, processing, storage and recovery (Pence *et al.*, 2022), are likely – by definition – not to be included in the original dataset. Although recalcitrant plant species are overall a negligible component of the temperate floras, many dominant tree species (e.g. *Quercus* sp. pl.) do have recalcitrant seeds (Tweddle *et al.*, 2003), and this could have contributed to an underrepresentation of woody species in our dataset. Finally, seed lots and germination records were not equally distributed across the European regions.

However, the Bayesian meta-analytical approach used here, and in previous research (Vandelook *et al.*, 2018; Fernández-Pascual *et al.*, 2021a, b), allowed us to overcome these limitations and provides a robust framework to address macroecological questions. As our meta-analysis models explicitly accounted

for the above-mentioned between-study sources of variation, the conclusion of our macroecological study that the seed germination niche is shaped by species’ climate is robust enough to these potential sources of bias.

## CONCLUSIONS

This is the first quantitative meta-analysis of the seed germination niche at a continental scale, highlighting how seed banking can be a valuable source to address questions in plant macroecology and evolution. Our findings provide phylogenetic support for the hypothesis that the seed germination niche of plants from temperate regions is shaped by climate. The climate–germination relationship, plus the evidence of convergent evolution at the macroclimatic level, highlights how the shape of the seed germination niche is vital for the survival of plant species and is thus subject to natural selection. Specifically, germination niche patterns were aligned along two opposite gradients of temperature and precipitation seasonality, and strongly mediated by phylogenetic relatedness and seed mass.

## SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Figure S1. Dataset description: number of species, seed lots, germination tests, and germination test per species by clade and within geographical regions. Figure S2. Meta-analysis of the seed germination niche in relation to climate across clades. Figure S3. Visualization of the seed germination niche of European flowering plants. Table S1. Institute germination data providers. Table S2. Summary of germination data included in <http://enscobase.maich.gr/> across four main regions and germination conditions. Table S3. Summary of binomial phylogenetic mixed models with Bayesian estimation examining the interactive effect of experimental germination conditions with species’ climatic requirements and seed mass on the final seed germination proportions, across the full dataset. Table S4. Summary of binomial phylogenetic mixed models with Bayesian estimation examining the interactive effect of experimental germination conditions with species’ climatic requirements and seed mass on the final seed germination proportions, across each major clade. Also available are the R codes used in the study to fit the MCMCglmm models.

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authors read and approved the final version of the manuscript. Original germination data are available via the European Native Seed Conservation Consortium database (ENSCOBASE; <http://enscobase.maich.gr/>). Codes for the analyses used in the paper are available in the Supplementary Data. The authors declare no conflicts of interest.

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