

RESEARCH ARTICLE

Thermal risk of seed germination of UK's plant populations and implications for climate-smart ecological restoration

Efisio Mattana^{1,2} , Elena Fouce Hernandez¹, Lola Andrews¹, Leela Watt Poddar¹, Jamal Rowe-Habbari¹, Isabel S. Negri¹, Freya Cornwell-Davison¹, Juan Viruel^{1,3} , Chris Cockel¹, Charlotte E. Seal¹, Ted Chapman¹

Abstract

Introduction: Seed-based ecological restoration actions are needed to halt biodiversity loss and mitigate climate change effects. However, identifying populations to target for climate-ready seed sourcing remains a major challenge due to germination and genetic constraints.

Objectives: This study evaluates thermal tolerance of seed germination in UK populations of species of restoration interest and integrates these findings with existing genetic diversity assessments to guide climate-smart, seed-sourcing strategies.

Methods: Six species (*Achillea millefolium*, *Centaurea nigra*, *Daucus carota* s.l., *Leucanthemum vulgare*, *Rhinanthus minor*, and *Scorzoneroideis autumnalis*) were identified among those for which assessments of genetic diversity estimates and seed lots banked for long-term conservation were available. Forty-five seed lots were incubated at a range of constant temperatures and thermal niches for germination modeling. Thermal risk for germination was then assessed by comparing current and predicted environmental temperatures of each population with the corresponding thermal germination parameters.

Results: All species except *R. minor* showed wide thermal windows for germination, suggesting that environmental temperatures are unlikely to limit reproduction from seeds under future UK climates. In *D. carota* s.l., residual dormancy masked origin effects, while *R. minor* exhibited narrow germination niches, suggesting higher vulnerability to warming. Combining germination results with genetic-based restoration assessments allowed species to be classified into four climate-smart, seed-sourcing categories: no constraints; genetic constraints; germination constraints; and genetic and germination constraints.

Conclusions: This study provides a practical framework for evaluating the feasibility and urgency of climate-smart, seed-based restoration. This approach is directly applicable to other UK species and to other temperate floras.

Implications for Practice: For the investigated species, from a germination perspective, sourcing seeds from within the United Kingdom is likely to provide climate-ready material. Species and populations with high thermal risk should be prioritized for climate-smart sourcing, ensuring that both germination ecology and genetic constraints are addressed. For *Daucus carota*, genetic mixing of seed material should be avoided even among populations of the same taxonomically recognized subspecies. For *Rhinanthus minor*, interventions should be limited to areas where present and projected climates support successful germination, while appropriate site management and time of sowing maximizing exposure to cold stratification can support population persistence.

Key words: climate change, global warming, plant reproduction, seed dormancy, seed sourcing

Introduction

Since the “Great Acceleration” of the 1950s in Europe and the start of the Anthropocene (Steffen et al. 2015), the known distribution ranges of more than half of all native and archaeophyte plants in the United Kingdom (UK) have declined (Walker et al. 2023). This decline builds upon historic negative trends in species population size and distribution fragmentation, making the UK one of the most nature-depleted countries in the world (Burns et al. 2023). Urgent proactive conservation actions, including seed-based, species-level recovery and reintroduction (White et al. 2023), as well as broader ecological restoration interventions (Larson et al. 2023), are needed to halt biodiversity loss in this country and mitigate the effects of climate change.

Author contributions: EM conceived the idea and designed the research, with inputs from TC; EFH, LA, LWP, JRH. EM carried out the experiments and analyzed the data; EM drafted the manuscript; EM, EFH, LA, LWP, JRH, ISN, FCD, JV, CC, CES, TC read, contributed, edited, and approved the final manuscript.

¹Royal Botanic Gardens, Kew, Wakehurst, RH17 6TN Ardingly, West Sussex, U.K.

²Address correspondence to E. Mattana, email e.mattana@kew.org

³Technological College, University of Zaragoza, Crta. Cuarte sn, 22071 Huesca, Spain

© 2025 The Author(s). Restoration Ecology published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.

This is an open access article under the terms of the [Creative Commons Attribution License](#), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

doi: 10.1111/rec.70239

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.70239/supinfo>

Understanding the reproductive performance of native plants is important to predict the resilience of their populations to the impacts of climate change (Beveridge et al. 2024) and help identify the winners and losers as a consequence of these impacts on the persistence of their natural populations (Cochrane et al. 2011; Mattana et al. 2023; Hsu et al. 2024). In addition, information on the intraspecific variability of this performance can help identify those populations at greatest risk under a changing climate which should be targeted for conservation actions (e.g. in situ and ex situ conservation), as well as those “climate-ready” populations (sensu Breed et al. 2013; Havens et al. 2015; Broadhurst et al. 2016) whose seed material can be sourced to carry out seed-based, plant-conservation translocations (White et al. 2023) and/or restoration interventions (Larson et al. 2023). Populations with higher genetic diversity may offer greater resilience and adaptability, while genetically depauperate populations might require genetic augmentation or controlled mixing to avoid inbreeding depression (White et al. 2025b).

Seed germination occurs as a response to the combination and interaction of environmental cues which determine the successful transition from seed to seedling (Grubb 1977; Baskin & Baskin 2014). Among these environmental variables, temperature is one of the most critical factors driving seed survival, dormancy break (e.g. through cold stratification), and germination success (Baskin & Baskin 2014), particularly in temperate climates (Carta et al. 2022). Seed germination responses to temperature can be modeled by a thermal time approach based on germination rate (GR). This approach allows the identification of thermal parameters such as the accumulation through time of required thermal units (e.g. °C per day) needed to reach a defined germination percentile and the correspondent theoretical cardinal temperatures (e.g. Trudgill et al. 2000) which define the width of the thermal niche for germination. Calculating the thermal niche for germination gives a measure of the temperature sensitivity during the germination phase of a species/population, enabling an assessment of their adaptation to local climates under current and projected future scenarios (e.g. Hsu et al. 2024; Hirst et al. 2025).

Seed lots stored in conservation seed banks are increasingly being used in plant translocation activities (White et al. 2023), although care should be applied in using old collections to avoid risks of maladaptation to new environmental conditions (Mattana et al. 2025; White et al. 2025a). In addition, conservation seed banks can support ecological restoration activities by producing large amounts of data on seed traits from different origins of a species (Merritt & Dixon 2011; Kildisheva et al. 2020; Goodale et al. 2023), which could inform climate-smart approaches to seed sourcing. Climate-smart approaches recommend collecting seed material from populations that are already adapted to the projected future climatic conditions of the reforestation or restoration sites, when local populations might not adapt quickly enough to the pace of climate change (St. Clair et al. 2022). The Millennium Seed Bank of the Royal Botanic Gardens, Kew (MSB) has been collecting seeds from the UK flora since the late 1960s and now holds almost 80% of the native and archaeophyte flora, often represented by collections

from different populations, targeted to enhance intraspecific diversity across ecological gradients (Chapman et al. 2019; Clubbe et al. 2020). This systematic sampling across ecological and climatic gradients not only can help capture a broad range of germination traits, but can also safeguard a large proportion of the genetic diversity present within a species, which is essential for long-term restoration success.

White et al. (2025b) recently published the assessment of genetic diversity estimates for 52 UK native and archaeophyte plant species of conservation and ecological restoration interest. This assessment provides management and conservation recommendations for practitioners in the absence of genetic data, particularly regarding the risks of sampling, donor selection, and negative outcomes of mixing genetic material from different populations of each species. It is based on estimates of genetic parameters dependent on life history trait values (i.e., mode of reproduction, dispersal method/ability, time to maturity, reproductive output, recruitment, UK distribution, fragmentation, scattered distribution, ecological amplitude, and demography), paving the path for species-specific genetic analyses which are still needed to provide robust recommendations (White et al. 2025b). Thus, seed collections stored at the MSB of species for which the assessment of genetic diversity estimates is available represent a unique study system to investigate seed germination responses to increasing environmental temperatures and their implications for climate-smart restoration activities within the UK. By integrating genetic diversity metrics with thermal germination profiles, it becomes possible to design restoration strategies that are both physiologically and genetically robust, minimizing the risks of maladaptation and genetic homogenization.

In this study, we identified seed lots stored at the MSB from different UK origins of species of ecological restoration interest and carried out seed germination experiments along a wide range of incubation temperatures with the aim to: (1) understand population responses to temperature of these species; and (2) quantify the thermal risk of seed germination of these populations. Finally, by integrating these findings with those of (White et al. 2025b), we (3) provide insights into the use of UK native species in climate-smart, seed-based restoration activities. This integrated approach offers a framework where restoration material can be selected not only for climatic compatibility but also for maintaining or enhancing adaptive genetic variation in restored habitats.

Methods

Seed Lot Details

Six study species (Fig. 1) were selected among plants for which the assessment of genetic diversity estimates was compiled by (White et al. 2025b) and with seed lots stored at the MSB for long-term conservation available for research. All six species are of ecological restoration interest in the UK (White et al. 2025b) and form part of the European “restoration species pool” whose seeds are commercially available to practitioners (Ladouceur et al. 2018). *Achillea millefolium* L. (yarrow) is a

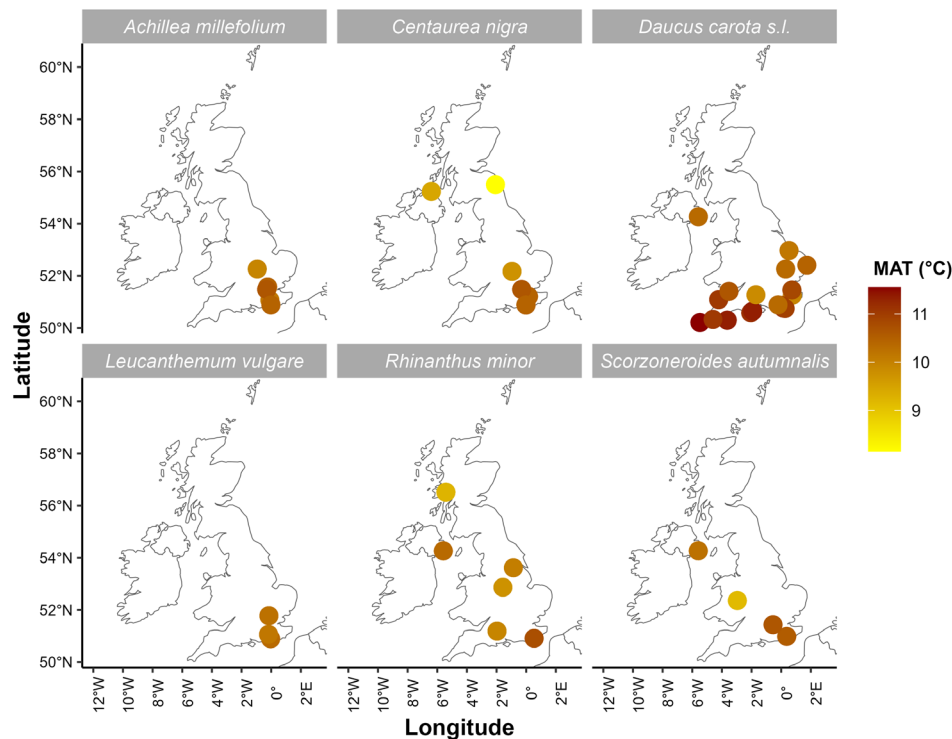


Figure 1. Distribution of the investigated seed lots for each species, showing the mean annual temperature (MAT) for each locality (see Table S1 for details). Climatic data were downloaded from the Chelsa website version 2.1 (Karger et al. 2017; Karger et al. 2021).

rhizomatous, grazing-tolerant perennial common in pastures and waysides and to a lesser degree in meadows; *Centaurea nigra* L. (common knapweed) is a robust perennial widespread in meadows, pastures, downland, floodplain meadows, waysides, and uplands used in restoration seeding; *Daucus carota* L. (wild carrot) is a mid-season biennial/winter annual of grasslands in infertile, well-drained neutral to calcareous soils; *Leucanthemum vulgare* Lam. (ox-eye daisy) is a common and widespread short-lived perennial of meadows, pastures, and waysides; *Rhinanthus minor* L. (yellow rattle) is a common and widespread obligate hemiparasitic annual, frequent in pastures and waysides, and of high interest for restoration because it helps the establishment of species-diverse meadows; and *Scorzoneroideis autumnalis* (L.) Moench (autumn hawkbit) is a rosette-forming herb of short turf and open ground, characteristic of road verges and pasture on moist fertile soil (Grime et al. 1988; MacIntyre 2024).

A total of 45 seed lots were identified, ranging from 3 to 19 per species (Table S1; Fig. 1). *D. carota* seed lots stored at the MSB are classified with and without specifying the nominal subspecies (*D. carota* subsp. *carota*; Table S1), and they also include one collection of *D. carota* subsp. *gummifer* (Syme) Hook.f. (sea carrot; Table S1), thus we refer to them as *D. carota* s.l. Seed lots were retrieved from storage at -20°C and equilibrated to 18°C and 15% relative humidity (RH) before the start of the experiments. The average mass of each dispersal unit (i.e., cypsels for *A. millefolium*, *C. nigra*, *L. vulgare*, and *S. autumnalis*; mericarps for *D. carota* s.l.; and true seeds for

R. minor) was calculated by weighing 20 dispersal units for each seed lot (Table S1).

Germination Experiments

The experimental setup and data analysis were adapted from those in Mattana et al. (2023), as detailed below. For each seed lot, three replicates of 50 seeds each were sown in plastic Petri dishes filled with 1% agar-water solution and incubated at each one of nine constant temperatures (from 0 to 40°C , with a 5°C interval), with a photoperiod of 12 hours irradiance per day, except for *R. minor* seed lots, which were incubated in the range 0 – 20°C , as this species is known to germinate only at low temperatures (Marin et al. 2017). In addition, as no germination was detected after 90 days for any of the *R. minor* seed lots at 15 and 20°C , seeds originally incubated at each of these two temperatures (hereafter referred to as “stratification”) were divided among three replicates of 16 seeds each and then also incubated at 0, 5, and 10°C to compare germination results with seeds originally incubated at those temperatures. Germination experiments were repeated after a cold stratification period of 3 months at 5°C for *D. carota* s.l. and *S. autumnalis* seed lots. Stratified seeds were then sown in three replicates of 20 seeds each at 5, 15, 20, 25, and 35°C .

Germination was recorded daily (excluding weekends), until germination reached its peak and scoring was carried out twice per week and then once per week. When no germination occurred in all three replicates at a given temperature for two

consecutive weeks after a minimum period of 30 days, the experiment at that temperature was closed and a cut test was carried out to identify any fresh non-germinated, moldy, and empty seeds. Experiments ran for up to 308 days. The final germination percentage was assessed using the “GerminaR” R package (Lozano-Isla et al. 2019), on the basis of the sown germinable seeds in each replicate (i.e., excluding empty and insect-infested seeds), after 45 days from sowing. The final germination proportion was modeled versus temperature, by performing quadratic generalized linear mixed models (Sentinella et al. 2020) with binomial error structure and replicate as a random factor, using the “glmer()” function in the R package “lme4” (Bates et al. 2015).

Cumulative analysis was carried out on the full length of the experiments. GR, that is, the time to reach 50% germination for each replicate/temperature/species/seed lot was estimated using the “drmtc()” function, with the non-parametric maximum likelihood estimator for time-to-event data (“NPMLE()” function) and then the “quantile(0.50)” function in the “drctc” R Package (Onofri et al. 2022). Calculated estimates of GR were fitted versus temperature using the “drm()” function from the “drc” R package, with the self-starting “GRT.Exb()” function for the exponential model (Masin et al. 2017) from the “drcSeedGerm” R Package (Onofri et al. 2018), for all species except for *R. minor*, for which the “GRT.Mb()” function for the polynomial model (Mesgaran et al. 2017) was used. Cardinal temperatures for 50% germination (T_b : base, T_o : optimum, and T_c : ceiling temperature) were then estimated using the “predict()” function on the fitted models.

Thermal Risk for Seed Germination

Historic climatic data (time period: 1981–2010) for each locality were downloaded from the Chelsa website (<https://chelsa-climate.org/downloads/>) version 2.1 (Karger et al. 2017, 2021). Future climatic data from the CMIP6 ISIMIP3 UKESM1-0-LL model (time period: 2071–2100) of the UK Met Office Hadley Centre (Tang et al. 2019) for the most optimistic (SSP1-2.6) and pessimistic (SSP5-8.5) Intergovernmental Panel on Climate Change (IPCC) emission scenarios were also downloaded from the Chelsa website for the same localities. Monthly mean, minimum, and maximum temperature and precipitation, and mean annual temperature were extracted using the R package “raster” (Hijmans et al. 2025).

The current and future thermal risk for seed germination for each population was calculated as follows (Mattana et al. 2023):

$$\text{Present or Future thermal risk} = T_{\text{env}} - T_o$$

with “ T_{env} ” calculated as the mean of the monthly average temperatures of the natural area of each seed lot, comprised between T_b (set to zero degrees when the actual value was negative to be ecologically meaningful) and T_c , allowing thermal units accumulation and leading to two temporal germination windows, one in the spring and one in the autumn. To calculate the thermal risk, the autumn window was considered for those species for which a cold stratification period was not applied

(*A. millefolium*, *C. nigra*, and *L. vulgare*), while the spring window was considered for those species for which a cold stratification period was applied (*D. carota* s.l. and *S. autumnalis*) or needed a long incubation at low temperatures ($>10^\circ\text{C}$) before starting to germinate under the same conditions (*R. minor*).

A principal component analysis (PCA) was carried out at seed lot level using the R package “factominer” (Lê et al. 2008) to visualize the relationship between cardinal temperatures and thermal breadth ($T_c - T_b$) for 50% germination and thermal risk indexes. Seed lot time in storage was also included in the ordination to confirm if the different ages of the collections (see Table S1) could have affected the results. The bi-plot was created with the “factoextra” R package (Kassambara & Mundt 2020).

Finally, we retrieved the genetic risk of populations mixing identified in White et al. (2025b), for the species investigated in this study.

Results

Temperature Sensitivity

While *Achillea millefolium*, *Centaurea nigra*, and *Leucanthemum vulgare* seed lots reached high germination percentages across a wide window of incubation temperatures after 45 days without any pretreatment (Fig. 2), a period of cold stratification was required for seed lots of *Daucus carota* s.l. to germinate over a wide range of incubation temperatures (Fig. S1). Cold stratification also substantially widened the germination window in one seed lot of *Scorzoneroideis autumnalis* (Fig. S2). Thus, for these two species, the presented results and subsequent analyses are for stratified seeds only. *Rhinanthus minor* seed lots

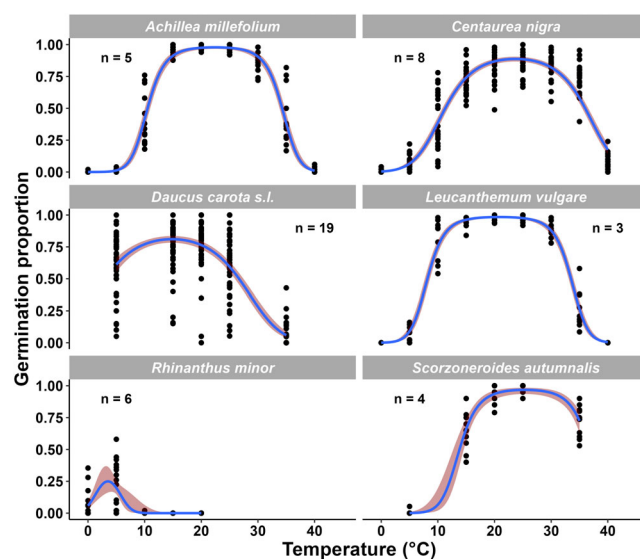


Figure 2. Seed germination responses to temperature expressed as a function of final germination proportion for the 45 seed lots of the investigated species (n) after 45 days in incubation. Points correspond to the actual values, with blue lines and red areas representing the quadratic trends and standard errors, respectively (see Tables S2 & S3 for model summaries and parameters).

reached low germination percentages (<50%) after 45 days (Fig. 2), although germination increased to percentages >75% at the end of the experiments for temperatures below 15°C (Fig. S3). However, stratification at 15 or 20°C did not improve germination performance for these seed lots (Fig. S3). Thus, the presented results and subsequent analyses for this species are only for seeds without stratification at 15 or 20°C.

The final germination proportion of all seed lots showed a Gaussian response to temperatures, which could be fitted by quadratic models (GLMMs) (Tables S3, S4). For each species, germination proportion increased as temperature increased until the optimal temperature window was reached and then decreased at warmer temperatures (Fig. 2). *R. minor* had the narrowest window of cold germination temperatures (<10°C: Fig. 2), with optimal windows gradually moving to warmer temperatures for *D. carota* s.l., *A. millefolium*, *L. vulgare*, *C. nigra*, and *S. autumnalis*, respectively (Fig. 2).

Overall, GR followed the same trend of thermal responses among species (Fig. 3), with species varying in their maximum GR value from ca. 0.6°C d⁻¹ for *A. millefolium*, *C. nigra*, and *S. autumnalis* (with a peak of almost 1.5°C d⁻¹ for the seed lot 478371) to ca. 0.020°C d⁻¹ for *R. minor*. Fitted models were statistically significant, and cardinal temperatures for 50% germination could be estimated for 33 out of the 45 tested seed lots (Table S4). For 12 seed lots, it was not possible to model the GR values versus temperature. For one of them, this was due to low overall germination, with final germination below 50% at all temperatures (*D. carota* s.l. seed lot 3573; Table S4; Fig. S1), while for seven other seed lots of *D. carota* s.l. and four of *R.*

minor, final germination reached 50% or more around optimal incubation temperatures, but the fitted models did not allow the identification of statistically significant thresholds due to the limited number of data points (Table S4; Figs. S1 & S2).

T_b ranged from the sub-zero values of *R. minor* to ca. 14°C for *S. autumnalis*; T_o ranged from less than 5°C for *R. minor* to ca. 26°C reached by both *C. nigra* and *S. autumnalis*; and T_c ranged from 10°C for *R. minor* to ca. 37°C of *C. nigra* (Table S4; Fig. 3). Thermal breadth ($T_c - T_b$) for 50% germination also varied among species. *A. millefolium*, *C. nigra*, and *L. vulgare* showed the widest thermal window for germination, followed by *D. carota* s.l. and *S. autumnalis*, while *R. minor* showed the narrowest (Table S4; Fig. 3). Overall, there was no significant effect of the temperature of the locality of origin on thermal thresholds in *A. millefolium*, *C. nigra*, and *D. carota* s.l. (the three species for which the thresholds were modeled in at least five populations; Fig. 3), except for T_b in *A. millefolium* and *D. carota* s.l. for which T_b decreased as mean annual temperature increased ($p = 0.05$; Tables S5–S13).

Thermal Risk for Germination

For species for which an autumn germination window was identified (*A. millefolium*, *C. nigra*, and *L. vulgare*), thermal risk values were all in the negative range, under current and predicted climate change scenarios, indicating that T_{env} never exceeds T_o (Fig. 4). Among the species for which a spring window was identified, *D. carota* s.l. and *S. autumnalis* populations also showed sub-zero values of thermal risk under current climatic conditions (Fig. 4). These values, however, progressively increased under the two climate change scenarios, moving toward (and exceeding for one *D. carota* s.l. population [seed lot 404859] under SSP 585 conditions) the zero threshold (Fig. 4). Finally, thermal risk values for *R. minor* were positive (i.e., T_{env} exceeds T_o) even under current conditions for both populations, leading to very high thermal risk values under global warming scenarios (Fig. 4).

The PCA ordered the seed lots mainly along its first axis (70.2%) with decreasing thermal risk and increasing thermal thresholds from left to right and along the second axis (28.4%) with decreasing values of thermal risk and T_b , and increasing values of thermal window from top to bottom (Fig. 5). On the far left, we have the two seed lots of *R. minor* with high values of thermal risks and low values of thermal breadth. In the middle are those of *D. carota* s.l. and *L. vulgare*, and on the right is the group constituted by seed lots of *A. millefolium*, *C. nigra*, and *S. autumnalis*. The ordination kept seed lots of each species grouped, although some intraspecific variability was highlighted by the ordination through the second axis, which separated one seed lot of *D. carota* s.l. (404859; Fig. S4) and one of *S. autumnalis* (53268; Fig. S4), with high values of T_b , high thermal risks, and narrow thermal breadth from the remnants of each species (Fig. 5). Time of storage was not significantly correlated to the principal dimensions.

Integrating Genetic Constraints

The germination characteristics and levels of thermal risk for seed germination previously identified, when combined with the genetic constraints in White et al. (2025b), allow for the

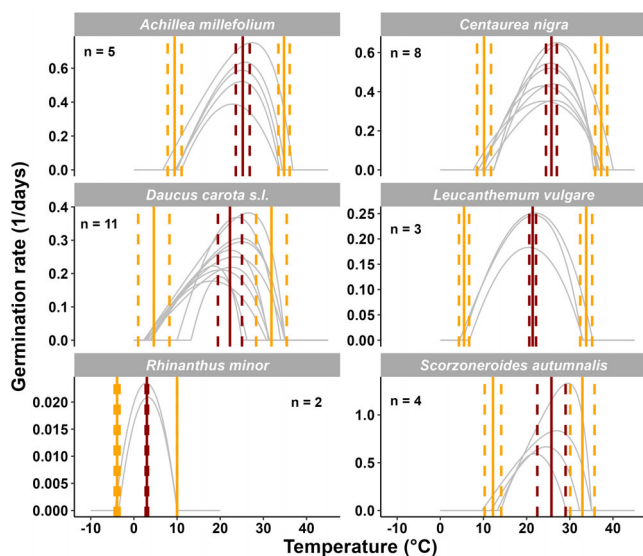


Figure 3. Seed germination responses to temperature expressed as a function of germination rate for 33 seed lots of the investigated species for which it was possible to fit the exponential models (n). Gray curves correspond to the model fitted for each seed lot. Vertical dashed lines correspond to the thermal thresholds for seed germination (see Table S4 for model parameters) for each seed lot (solid lines) ± 1 SD (dashed lines). The yellow lines correspond to base (T_b) and ceiling (T_c) temperatures, and the red line to the optimum temperatures (T_o) for seed germination.



Figure 4. Thermal mismatch for seed germination under current and predicted climate change scenarios. Negative values indicate low thermal risk since T_{env} does not exceed T_o , while positive values highlight a T_{env} higher than T_o and therefore an environmental temperature lying in the supra-optimal thermal range for germination.

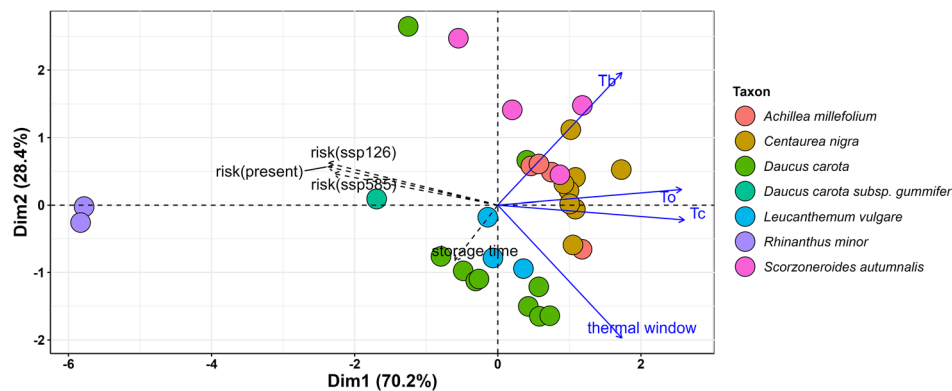


Figure 5. Principal component analysis (PCA), to visualize the relationship along the first two PCA axes between thermal thresholds: base (T_b), ceiling (T_c), and optimum temperature (T_o), and thermal window ($T_c - T_b$) for 50% germination (blue solid arrows). Thermal risk values and storage time of the seed lots were included as supplementary variables (dashed arrows).

description of three categories of climate-smart seed sourcing (Table 1). These are species with neither genetic nor germination constraints (e.g. *A. millefolium*); those with genetic constraints only (e.g. *C. nigra*); and those with genetic and germination constraints (e.g. *D. carota* s.l.). A fourth category is also here proposed for species with germination constraints and low genetic risk of populations mixing, for which climate-smart seed sourcing can be considered if seed dormancy and germination requirements are met in the target populations (Table 1).

Discussion

Germination Responses to Temperature

Plant species vary in the germination response of non-dormant seeds to temperature, differing in their optimal temperature and amplitude of their thermal window. Multiple factors, including seed physiology (Steinbrecher et al. 2025) and climate (Baskin & Baskin 2014; Sentinella et al. 2020), drive the differences in these responses which, together with seed dormancy

Table 1. Categorization of species investigated in this study according to their genetic and germination constraints for climate-smart seed sourcing.

Climate-smart, seed-sourcing category	Examples	Genetic risk of populations mixing (White et al. 2025b)	Pretreatment needed to break dormancy	Feasibility of climate-smart seed sourcing	Thermal risk for germination
No genetic or germination constraints	<i>Achillea millefolium</i> L.;	Low	No	Climate-smart seed sourcing can be considered.	Low
	<i>Leucanthemum vulgare</i> Lam.				Medium
Genetic constraints	<i>Scorzoneroide autumnalis</i> (L.) Moench	Some risk	No	Climate-smart seed sourcing can be considered if genetic studies are carried out in donor and target populations	Low
	<i>Centaurea nigra</i> L.				Low
Genetic and germination constraints	<i>Rhinanthus minor</i> L.	Some risk	Yes	Climate-smart seed sourcing should be considered only if genetic studies are carried out in donor and target populations and seed dormancy and germination requirements are met in the target populations.	High
	<i>Daucus carota</i> L.	High risk			Medium

Note: Green color corresponds to low risks and no need for dormancy breaking pretreatment; yellow color to some genetic risk of populations mixing and medium thermal risk for germination; and red color to high risks and need for a dormancy breaking pretreatment.

mechanisms, reflect different strategies in the species' reproductive ecology. In this study, all the investigated species except *Rhinanthus minor* showed a wide thermal window for germination. They are all widespread species, commonly distributed in the UK, Europe, and beyond (POWO 2025). Although there are some differences in habitat preferences among them, they are all commonly found in meadows, pastures, and other grasslands as well as in more disturbed habitats such as ruderal areas and road verges, and in the case of *Daucus carota* s.l.—in coastal areas (Grime et al. 1988). The germination thermal windows detected in this study are consistent with their ecology, allowing germination to occur across a wide range of environmental conditions and to be temporally spread during spring (for species requiring cold stratification such as *D. carota* s.l.) and/or autumn. In contrast, the thermal requirements and kinetics of germination identified in all seed lots of *R. minor* limit its germination to a very specific temporal window in late winter. Seeds of this hemiparasite (Grime et al. 1988) lose dormancy during winter (Marin et al. 2017) and germinate just before spring, when temperatures are still relatively low (Pons 1991). This germination phenology can give an ecological advantage to this species, allowing its seedlings to establish before those of other fully autotrophic species, avoiding competition for the same resources (Ter Borg 2005).

Four species (*Achillea millefolium*, *Centaurea nigra*, *Leucanthemum vulgare*, and *R. minor*) showed quite consistent responses to temperature among their seed lots, confirming trends detected by (Mattana et al. 2023) for Wakehurst (SE England)

populations of these species. However, *D. carota* s.l. and *Scorzoneroide autumnalis* showed marked variation among populations in both maximum germination percentages and width of thermal windows. While a bias exists in the number of populations and spatial distribution investigated for each species, with *D. carota* s.l. having the highest number of tested seed lots, variability in germination traits for this species is further complicated by the presence of seed dormancy at dispersal. The species produces seeds with underdeveloped embryos (Vandelook et al. 2012), and cold stratification is typically required to break this morphological dormancy (Grime et al. 1988; Baskin & Baskin 2014). However, seeds of this species vary in their level of dormancy depending not only on their origin but also on their position in the umbels and on the plant (Baskin & Baskin 2014). In addition, *D. carota* s.l. represents a taxonomically complex species group in the UK, with an uncertain classification framework at the intraspecific level, reflecting and influencing its underlying genetic structure (White et al. 2025b). Residual dormancy differences detected in this study overshadowed origin or taxonomic distinctions in germination behavior. *S. autumnalis* is an opportunistic and adaptable species which is reported to germinate both in autumn and spring at high temperatures and to form a short-term soil seed bank (Grime et al. 1988). This reproductive flexibility is reflected in our results, which show consistently high germination at elevated temperatures, both with and without cold stratification, alongside notable variability in germination performance among seed lots.

Thermal Risk for Germination and Implications for Ecological Restoration and Climate-Smart Seed Sourcing

Seed germination responses to temperature are a critical factor in selecting species and populations for restoration, as the requirements for dormancy breaking and germination must align with both current and projected environmental conditions (Mattana et al. 2023; Hirst et al. 2025). Although the results of this study require field validation, for all investigated species, except *R. minor*, the environmental temperatures expected during their main temporal windows for seed germination (i.e., autumn and spring) are unlikely to limit reproduction from seeds under either their current or predicted climates, making them strong candidates for future-proofed restoration (Mattana et al. 2023; Hirst et al. 2025). Seed germination is an important part of the regeneration and persistence of restored populations, but further studies are needed to understand if the timing of seed germination will still coincide with the most favorable season for seedling establishment (Fernández-Pascual et al. 2019). When paired with genetic diversity data, this thermal resilience strengthens their suitability, as it indicates both physiological compatibility and, in some cases, low genetic mixing risk (White et al. 2025b), suggesting high resilience of UK populations of most tested species to global warming. More studies are however needed to understand the impact of warming winter temperatures on the dormancy breaking process of *D. carota* s.l. populations, considering that high thermal risk values detected for some populations of this species are likely linked to the higher levels of residual dormancy detected for these seed lots.

In terms of seed sourcing, these findings suggest that, from a germination perspective, there is no requirement to source seed material from other countries, such as continental Europe, where the current climates match the future predictions for the UK. The findings of this study highlight how the thermal mismatch for seed germination recorded for *R. minor* is consistent among different populations. They suggest a high vulnerability for the reproduction from seeds of this annual species dependent upon successful germination each year to warming temperatures, particularly if genetic variation in phenology-related traits has been eroded by the population declines documented during the 20th century (White et al. 2025b). Moreover, *R. minor* occurs across contrasting ecological settings, which may have promoted genetic differentiation among populations; this differentiation, while potentially adaptive, introduces donor selection risks if genetically distinct populations are inadvertently mixed during restoration. Thermal responses detected for these UK populations are the same as those already reported for commercial and wild collected seed lots from Europe (Ter Borg 2005; Marin et al. 2017), although high variation in final germination proportion of commercial seed lots has previously been detected (Marin et al. 2019). Given its proven ecological value in grassland restoration, and particularly for the diversification of plant communities (Pywell et al. 2004; Westbury et al. 2006), it is urgent to carry out more in-depth studies to identify effective dormancy breaking pretreatments which could potentially widen the thermal niche for germination (Ter Borg 2005) and field validation experiments to confirm the vulnerability to global warming for its reproduction from seeds suggested by

our findings. Other management options to reduce risks to *R. minor* persistence include ensuring cutting or grazing regimes enable seed to ripen and disperse fully and create suitable areas of bare ground for germination and completing sowing in early autumn to maximize exposure to cold winter temperatures (Wagner et al. 2011; Mattana et al. 2023).

From a genetic perspective, *A. millefolium* and *L. vulgare* show no reported donor selection constraints based on life-history traits, indicating a low risk of negative genetic effects from mixing (White et al. 2025b). *C. nigra*, however, presents a more complex case: multiple ploidy levels and possible hybridization with other *Centaurea* species which create a real risk if populations are mixed without prior genetic assessment (White et al. 2025b) and hamper the application of a climate-smart approach. While the variability in seed germination among seed lots detected for *S. autumnalis* put some populations of this species more at risk, the same variability can also help identify more climate-adapted source populations. Given that this species is widespread across the UK and likely experiences substantial gene flow throughout its range, with no evidence of significant fragmentation or recent declines, the risk of mixing genetically distinct groups in restoration is considered low (White et al. 2025b). Consequently, this intraspecific variability in germination traits could be harnessed to select populations with the greatest climate resilience, without major concern for disrupting local genetic patterns. For *D. carota* s.l., high variability in germination performance is linked to dormancy rather than origin per se, but genetic mixing risk (even within taxonomically recognized subspecies) remains high due to its taxonomic ambiguity, morphological variation, patchy distribution, and short lifespan (White et al. 2025b). Finally, for *R. minor*, consistent germination responses across populations mean that any seed movement should still be restricted to areas where present and future climates support successful germination, but population genetic structure should also be considered to avoid disrupting potentially adaptive differentiation. However, it should be noted that seeds of these species are in commercially available wildflower seed mixtures which have been increasingly used in the UK. In some cases, these mixtures might be constituted of seeds imported from Europe or possibly elsewhere, making it difficult to distinguish native from alien populations (Stroh et al. 2023). Thus, even if no genetic constraints can be highlighted when applying the species life-history-data-based framework of White et al. (2025b), care should still be taken when selecting source populations to design the most genetically robust restoration strategies and—whenever possible—carry out genetic analysis.

This study provides an integrated assessment of thermal resilience of seed germination and genetic risk for six native and archaeophyte UK species of restoration interest, using banked seed lots stored for long-term conservation from different origins. Germination responses aligned closely with species ecology, with most species showing strong adaptation to predicted temperature changes, except *R. minor*, whose narrow germination niche places it at high risk from global warming. By combining germination trait data with genetic risk assessments (White et al. 2025b), we outline a framework for selecting

source populations that are both physiologically suited to future climates and genetically robust, helping to ensure that restoration efforts maintain the evolutionary potential of restored plant communities. This approach can be readily adapted for other temperate floras for which germination and genetic diversity data are available or can be experimentally derived.

Acknowledgments

This study was funded by the Players of People's Postcode Lottery through the project "Native Seeds for Restoration: diversity and resilience in the UK". The Royal Botanic Gardens, Kew receives grant-in-aid from the Department for Environment, Food and Rural Affairs (DEFRA). JV received funding from RYC2023-042611-I by MCIU/AEI/10.13039/501100011033 and FSE+. Funders had no role in study design, report writing, or article submission. We thank all partner organizations that collected the seed lots and the staff of the Royal Botanic Gardens, Kew who curated the collections at the RBG Kew Millennium Seed Bank.

Literature Cited

- Baskin CC, Baskin JM (2014) Seeds: ecology, biogeography, and, evolution of dormancy and germination. Academic Press, San Diego (USA), London (UK), and Waltham (USA)
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beveridge FC, Williams A, Cave R, Kalai Pandian S, Dayananda B, Adkins SW (2024) Interactions between seed functional traits and environmental factors and their influence on germination performance of Australian native species. *Seed Science Research* 34:56–71. <https://doi.org/10.1017/S0960258523000235>
- Breed MF, Stead MG, Ottewill KM, Gardner MG, Lowe AJ (2013) Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics* 14:1–10. <https://doi.org/10.1007/s10592-012-0425-z>
- Broadhurst LM, Jones TA, Smith FS, North T, Guja L (2016) Maximizing seed resources for restoration in an uncertain future. *Bioscience* 66:73–79. <https://doi.org/10.1093/biosci/biv155>
- Burns F, Mordue S, al Fulaij N, Boersch-Supan PH, Boswell J, Boyd RJ, et al. (2023) State of nature 2023. State of Nature Partnership. Available online at <https://www.stateofnature.org.uk/>
- Carta A, Fernández-Pascual E, Gioria M, Müller JV, Rivière S, Rosbakh S, Saatkamp A, Vandelook F, Mattana E (2022) Climate shapes the seed germination niche of temperate flowering plants: a meta-analysis of European seed conservation data. *Annals of Botany* 129:775–786. <https://doi.org/10.1093/aob/mcac037>
- Chapman T, Miles S, Trivedi C (2019) Capturing, protecting and restoring plant diversity in the UK: RBG Kew and the Millennium Seed Bank. *Plant Diversity* 41:124–131. <https://doi.org/10.1016/j.pld.2018.06.001>
- Clubbe C, Ainsworth AM, Bárrios S, Bensusan K, Brodie J, Cannon P, et al. (2020) Current knowledge, status, and future for plant and fungal diversity in Great Britain and the UK overseas territories. *Plants, People, Planet* 2: 557–579. <https://doi.org/10.1002/ppp3.10142>
- Cochrane A, Daws MI, Hay FR (2011) Seed-based approach for identifying flora at risk from climate warming. *Austral Ecology* 36:923–935. <https://doi.org/10.1111/j.1442-9993.2010.02211.x>
- Fernández-Pascual E, Mattana E, Pritchard HW (2019) Seeds of future past: climate change and the thermal memory of plant reproductive traits. *Biological Reviews* 94:439–456. <https://doi.org/10.1111/brv.12461>
- Goodale UM, Antonelli A, Nelson CR, Chau MM (2023) Seed banks needed to restore ecosystems. *Science* 379:147. <https://doi.org/10.1126/science.adg2171>
- Grime JP, Hodgson JG, Hunt R (1988) Comparative plant ecology. Springer Science+Business Media, Dordrecht Netherlands. <https://doi.org/10.1007/978-94-017-1094-7>
- Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52:107–145. <https://doi.org/10.1111/j.1469-185X.1977.tb01347.x>
- Havens K, Vitt P, Still S, Kramer AT, Fant JB, Schatz K (2015) Seed sourcing for restoration in an era of climate change. *Natural Areas Journal* 35:122–133. <https://doi.org/10.3375/043.035.0116>
- Hijmans RJ, van Etten J, Sumner M, Cheng J, Baston D, Bevan A, et al. (2025) *Raster: Geographic data analysis and modeling* (version 3.6–32) [Computer software]. <https://cran.r-project.org/web/packages/raster/index.html>
- Hirst MJ, Vázquez-Ramírez J, Rendall AR, Venn SE (2025) Thermal germination niche: implications for seed-based restoration in climate-sensitive alpine environments. *Restoration Ecology* 33:e70031. <https://doi.org/10.1111/rec.70031>
- Hsu H-W, Stuke M, Bakker JD, Kim S-H (2024) A time-to-event analysis for temperature dependence of seed germination in four conifers: ecological niche and environmental gradients. *Forest Ecology and Management* 562: 121972. <https://doi.org/10.1016/j.foreco.2024.121972>
- Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. *Scientific Data* 4:170122. <https://doi.org/10.1038/sdata.2017.122>
- Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2021) *Climatologies at high resolution for the earth's land surface areas*. *EnviDat*. <https://www.envidat.ch/dataset/2adb0c83-4653-4337-af28-f75c63ab7c74>
- Kassambara A, Mundt F (2020) *Factoextra: extract and visualize the results of multivariate data analyses* (version 1.0.7). <https://cran.r-project.org/web/packages/factoextra/index.html>
- Kildisheva OA, Dixon KW, Silveira FAO, Chapman T, Di Sacco A, Mondoni A, Turner SR, Cross AT (2020) Dormancy and germination: making every seed count in restoration. *Restoration Ecology* 28:S256–S265. <https://doi.org/10.1111/rec.13140>
- Ladouceur E, Jiménez-Alfaro B, Marin M, De Vitis M, Abbandonato H, Iannetta PPM, Bonomi C, Pritchard HW (2018) Native seed supply and the restoration species pool. *Conservation Letters* 11:e12381. <https://doi.org/10.1111/conl.12381>
- Larson JE, Agneray AC, Boyd CS, Bradford JB, Kildisheva OA, Suding KN, Copeland SM (2023) A recruitment niche framework for improving seed-based restoration. *Restoration Ecology* 31:e13959. <https://doi.org/10.1111/rec.13959>
- Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software* 25:1–18. <https://doi.org/10.18637/jss.v025.i01>
- Lozano-Isla F, Benites-Alfaro OE, Pompelli MF (2019) GerminAR: an R package for germination analysis with the interactive web application "GerminAR for R". *Ecological Research* 34:339–346. <https://doi.org/10.1111/1440-1703.1275>
- MacIntyre D (2024) *Restoring the wild*. The Crowood Press Ltd, Ramsbury, United Kingdom
- Marin M, Laverack G, Matthews S, Powell AA (2019) Germination characteristics of *Rhinanthus minor* influence field emergence, competitiveness and potential use in restoration projects. *Plant Biology* 21:470–479. <https://doi.org/10.1111/plb.12707>
- Marin M, Toorop P, Powell AA, Laverack G (2017) Tetrazolium staining predicts germination of commercial seed lots of European native species differing in seed quality. *Seed Science and Technology* 45:151–166. <https://doi.org/10.15258/sst.2017.45.1.03>
- Masín R, Onofri A, Gasparini V, Zanin G (2017) Can alternating temperatures be used to estimate base temperature for seed germination? *Weed Research* 57:390–398. <https://doi.org/10.1111/wre.12270>
- Mattana E, Chapman T, Miles S, Ulian T, Carta A (2023) Regeneration from seeds in a temperate native flora: a climate-smart and natural-capital-driven germination risk modelling approach. *Plants, People, Planet* 5:908–922. <https://doi.org/10.1002/ppp3.10378>

- Mattana E, Godefroid S, Miles S, Carta A, Ensslin A, Chapman T, Viruel J (2025) Looking back to look ahead: the temporal dimension of conservation seed bank collections. *New Phytologist* 247:1589–1598. <https://doi.org/10.1111/nph.70187>
- Merritt DJ, Dixon KW (2011) Restoration seed banks—a matter of scale. *Science* 332:424–425. <https://doi.org/10.1126/science.1203083>
- Mesgaran MB, Onofri A, Mashhadi HR, Cousens RD (2017) Water availability shifts the optimal temperatures for seed germination: a modelling approach. *Ecological Modelling* 351:87–95. <https://doi.org/10.1016/j.ecolmodel.2017.02.020>
- Onofri A, Benincasa P, Mesgaran MB, Ritz C (2018) Hydrothermal-time-to-event models for seed germination. *European Journal of Agronomy* 101:129–139. <https://doi.org/10.1016/j.eja.2018.08.011>
- Onofri A, Mesgaran MB, Ritz C (2022) A unified framework for the analysis of germination, emergence, and other time-to-event data in weed science. *Weed Science* 70:259–271. <https://doi.org/10.1017/wsc.2022.8>
- Pons TL (1991) Dormancy, germination and mortality of seeds in a chalk-grassland flora. *Journal of Ecology* 79:765–780. <https://doi.org/10.2307/2260666>
- POWO (2025) *Plants of the world online*. Facilitated by the Royal Botanic Gardens, Kew. <https://powo.science.kew.org/>
- Pywell RF, Bullock JM, Walker KJ, Coulson SJ, Gregory SJ, Stevenson MJ (2004) Facilitating grassland diversification using the hemiparasitic plant *Rhinanthus minor*. *Journal of Applied Ecology* 41:880–887. <https://doi.org/10.1111/j.0021-8901.2004.00940.x>
- Sentinella AT, Warton DI, Sherwin WB, Offord CA, Moles AT (2020) Tropical plants do not have narrower temperature tolerances, but are more at risk from warming because they are close to their upper thermal limits. *Global Ecology and Biogeography* 29:1387–1398. <https://doi.org/10.1111/geb.13117>
- St. Clair JB, Richardson BA, Stevenson-Molnar N, Howe GT, Bower AD, Erickson VJ, Ward B, Bachelet D, Kilkenny FF, Wang T (2022) Seedlot selection tool and climate-smart restoration tool: web-based tools for sourcing seed adapted to future climates. *Ecosphere* 13:e4089. <https://doi.org/10.1002/ecs2.4089>
- Steffen W, Broadgate W, Deutsch L, Gaffney O, Ludwig C (2015) The trajectory of the Anthropocene: the great acceleration. *The Anthropocene Review* 2: 81–98. <https://doi.org/10.1177/2053019614564785>
- Steinbrecher T, Voegelé A, Ignatz M, Weitbrecht K, Khan S, Graeber K, Hourston JE, Leubner-Metzger G (2025) Distinct molecular biomechanical mechanisms inhibit endosperm cell-wall weakening and seed germination at cold and warm nonoptimal temperatures. *Plant, Cell & Environment* 48:8047–8067. <https://doi.org/10.1111/pcc.70103>
- Stroh PA, Walker KJ, Humphrey TA, Pescott OL, Burkmar RJ (2023) *Plant atlas 2020: mapping changes in the distribution of the British and Irish Flora*. Princeton University Press, Princeton, United States
- Tang Y, Rumbold S, Ellis R, Kelley D, Mulcahy J, Sellar A, Walton J, Jones C (2019) MOHC UKESM1.0-LL model output prepared for CMIP6 CMIP historical. Earth System Grid Federation. Available online at <https://doi.org/10.22033/ESGF/CMIP6.6113>
- Ter Borg SJ (2005) Dormancy and germination of six *Rhinanthus* species in relation to climate. *Folia Geobotanica* 40:243–260. <https://doi.org/10.1007/BF02803238>
- Trudgill DL, Squire GR, Thompson K (2000) A thermal time basis for comparing the germination requirements of some British herbaceous plants. *New Phytologist* 145:107–114. <https://doi.org/10.1046/j.1469-8137.2000.00554.x>
- Vandelook F, Janssens SB, Probert RJ (2012) Relative embryo length as an adaptation to habitat and life cycle in Apiaceae. *New Phytologist* 195:479–487. <https://doi.org/10.1111/j.1469-8137.2012.04172.x>
- Wagner M, Pywell RF, Knopp T, Bullock JM, Heard MS (2011) The germination niches of grassland species targeted for restoration: effects of seed pre-treatments. *Seed Science Research* 21:117–131. <https://doi.org/10.1017/S0960258510000450>
- Walker K, Stroh P, Humphrey T, Roy D, Burkmar R, Pescott O (2023) Britain's changing flora: a summary of the results of plant atlas 2020. Botanical Society of Britain and Ireland. Available online at <https://doi.org/10.13140/RG.2.2.25091.99362>
- Westbury DB, Davies A, Woodcock BA, Dunnett NP (2006) Seeds of change: the value of using *Rhinanthus minor* in grassland restoration. *Journal of Vegetation Science* 17:435–446. <https://doi.org/10.1111/j.1654-1103.2006.tb02464.x>
- White FJ, Asnaghi M, Orenco M, Abeli T, Rossi G, Mondoni A (2025a) Can 20-year-old stored seeds be used for plant translocation? An investigation of the arctic-alpine specialist *Viscaria alpina*. *Restoration Ecology* 33(7): e70096. <https://doi.org/10.1111/rec.70096>
- White FJ, Ensslin A, Godefroid S, Faruk A, Abeli T, Rossi G, Mondoni A (2023) Using stored seeds for plant translocation: the seed bank perspective. *Biological Conservation* 281:109991. <https://doi.org/10.1016/j.biocon.2023.109991>
- White K, Cornwell-Davison F, Cockell C, Chapman T, Mattana E, Viruel J (2025b) Application of a biological trait-based framework for plant species conservation assessments in ecological restoration. *Restoration Ecology* 33:e14391. <https://doi.org/10.1111/rec.14391>

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Seed germination of *Daucus carota* s.l. seed lots with and without a 3-month stratification at 5°C.

Figure S2. Seed germination of *Scorzoneroideis autumnalis* seed lots with and without a 3-month stratification at 5°C.

Figure S3. Seed germination of *Rhinanthus minor* seed lots with and without a 3-month stratification at 15 or 20°C.

Figure S4. Principal component analysis (PCA), visualizing the ordination of the individual seed lots.

Table S1. Seed lot details of the Millennium Seed Bank collections tested in the experiments.

Table S2. Quadratic models (GLMM) summaries predicting final germination proportion as a function of temperature.

Table S3. Model parameters of the quadratic models (GLMMs) predicting final germination proportion as a function of temperature.

Table S4. Thermal thresholds and model parameters predicting germination rate (50%) as a function of temperature.

Table S5. Generalized linear model parameters (Gaussian family) for the responses of T_b to mean annual temperature (MAT) in *Achillea millefolium*.

Table S6. Generalized linear model parameters (Gaussian family) for the responses of T_o to mean annual temperature (MAT) in *Achillea millefolium*.

Table S7. Generalized linear model parameters (Gaussian family) for the responses of T_c to mean annual temperature (MAT) in *Achillea millefolium*.

Table S8. Generalized linear model parameters (Gaussian family) for the responses of T_b to mean annual temperature (MAT) in *Centaurea nigra*.

Table S9. Generalized linear model parameters (Gaussian family) for the responses of T_o to mean annual temperature (MAT) in *Centaurea nigra*.

Table S10. Generalized linear model parameters (Gaussian family) for the responses of T_c to mean annual temperature (MAT) in *Centaurea nigra*.

Table S11. Generalized linear model parameters (Gaussian family) for the responses of T_b to mean annual temperature (MAT) in *Daucus carota* s.l.

Table S12. Generalized linear model parameters (Gaussian family) for the responses of T_o to mean annual temperature (MAT) in *Daucus carota* s.l.

Table S13. Generalized linear model parameters (Gaussian family) for the responses of T_c to mean annual temperature (MAT) in *Daucus carota* s.l.