

***SILENE ACAULIS* EARLY-LIFE RESPONSES TO EXPERIMENTAL WARMING VARY WITH PARENT- POPULATION MICROCLIMATE**



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Abstract

Arctic ecosystems are warming at disproportionate rates, placing pressure on slow-reproducing perennial species with limited capacity for rapid evolutionary adaptation. This study examined how simulated warming affects germination probability, germination timing, early survival, and seedling growth in *Silene acaulis*, and whether population-level variation in these responses reflects microclimate-specific local adaptation. Seeds from ten populations spanning a snowmelt gradient at Latnjajaure, within the Swedish low-Arctic, were grown under control conditions based on median Latnjajaure July temperature, and a heated treatment set at +4°C above the control. Warming was broadly beneficial across all measured outcomes. Germination odds approximately tripled under heating, germination timing advanced by approximately one week, seedlings were consistently larger at all ages, and final survival rates were approximately thirteen percentage points higher under warming. However, growth rates plateaued under heated conditions, accompanied by visible desiccation in larger seedlings, suggesting that heat stress may impose constraints over longer timescales. Population-level variation in warming response was detected, most strongly for germination probability, where a significant treatment × snowmelt interaction indicated that seeds from warmer, early-snowmelt plots showed a greater relative increase in germination probability under warming than those from colder, late-snowmelt plots. Altitude independently influenced germination timing, with seeds from higher-elevation plots germinating consistently later regardless of treatment. Variance partitioning revealed that population origin explained a substantial proportion of variation in seedling size. The observed phenological differences between populations at Latnjajaure are consistent with population level variation. Although these cannot truly be distinguished from maternal effects, the evidence and literature point to at least a partial genetic component, potentially including microclimate specific adaptation. These results highlight the importance of considering intraspecific variation when predicting how Arctic species will respond to climate change, particularly for foundation species such as *S. acaulis* whose population health has cascading consequences for the broader communities they support.

Introduction

The Arctic hosts some of the most extreme environments on Earth, characterised by long winters with extensive snow cover, short growing seasons, and nutrient-poor soils. Vegetation here is dominated by slow-growing perennials, dwarf shrubs, cushion plants, grasses, and mosses; these are species that have evolved morphological and physiological strategies to withstand low temperatures and strong winds. However, because these species often occupy narrow ecological niches (Löffler & Pape, 2020; Callaghan et al., 2004), they are particularly sensitive to environmental change (Post et al., 2009).

Climate change in the Arctic region is occurring at disproportionate rates compared to the rest of the world, warming at approximately four times the global average (Rantanen et al., 2022); this is accompanied by shifts in precipitation regimes resulting in greater rainfall during the summer months (Bintanja & Andry, 2017). These changes have the potential to alter vegetation patterns, primarily with the poleward migration of boreal species, resulting in an increase in woody shrubs: a process termed shrubification (Mekonnen et al., 2021). Longer and earlier growing seasons, as described by Peng et al. (2013) and Bhatt et al. (2017), are also resulting in changes to leaf and flowering phenology (Oberbauer et al., 2013), potentially resulting in a temporal mismatch between pollinator activity and plant reproductive cycles (Redr et al., 2025). However, the extent to which these vegetation assemblage changes will occur is currently unclear, with some studies indicating that this is happening at slower rates than predicted by models (Savage & Vellend, 2015).

Seed germination in the Arctic is constrained to the relatively short summer season, with many species requiring cold stratification over winter before germinating during the following warm season (Baskin & Baskin, 2000). Germination is heavily influenced by microclimate variability, particularly by the timing of snowmelt, but also influenced by soil temperature and moisture (Bernareggi et al., 2016; Fernández-Pascual et al., 2021; Vázquez-Ramírez & Venn, 2021). With climate change expected to alter the length and conditions of the growing season, these authors suggest that germination success and timing could be impacted. Because germination represents a key demographic bottleneck in Arctic plants, small shifts in snowmelt or temperature could strongly affect recruitment success.

One of the many species characterising the low-Arctic is *Silene acaulis*, considered a foundation species, acting as an ecosystem engineer in many tundra ecosystems (Molenda et al., 2012; Reid & Lortie, 2012). It is a perennial and has a compact morphology, minimising heat loss, allowing it to survive harsh Arctic and alpine conditions. It is also long-lived with slow generation turnover (Morris & Doak, 1998), potentially limiting their capacity to adapt to climate change at a fast enough pace (Cotto et al., 2017). Climate change has already been observed to have effects on established *S. acaulis* populations such as increased competition for resources (Baruah et al., 2017) or phenological shifts resulting in reduced pollination (Tiusanen et al., 2020; Høye et al., 2021). Heat related damage and mortality have also been observed in some populations (Rai et al., 2025; Bonanomi et al., 2023). *Silene acaulis* occurs over a wide geographic range and is known to inhabit a range of microclimates and snowmelt regimes, often showing variation in life-history traits linked to its local environments (DeMarche et al., 2018). This makes the species an ideal model for examining how germination and early survival respond to climate warming, and for assessing whether it exhibits any variation between populations from different microclimates.

Arctic populations typically exhibit local adaptation to their specific microclimate (Hamann et al., 2016; Gya et al., 2023). Bjorkman et al. (2017) argue that this plays a role in the degree of change to Arctic vegetation as a result of climate change; they suggest environmental factors other than those related to climate are likely at play, giving individuals a ‘home advantage’ over outsiders, even within species. *Silene acaulis* populations have also been noted to differ between populations

from different microclimates, even between those within a close proximity to each other; Pavolotskaia (2024) observed that *S. acaulis* flowering phenology, on a population scale, is strongly associated with snowmelt timing. However, it is often unclear whether these differences arise from population-specific genetic adaptations or are a product of phenotypic plasticity responses to their microclimate. This is an important area of study as knowing the drivers behind population variability can give a better understanding of how climate change may affect Arctic populations in the near future. The responses of vegetation to these changes may depend on the extent to which morphology, physiology, and phenology are controlled by phenotypic plasticity and population genetics. This may mean that some populations may be better adapted to climate change than others.

Through this study, I will be aiming to investigate further how populations from different microclimate conditions vary in response to climate warming. This may offer a better understanding of what drives population differences and how *Silene acaulis* populations may respond to future warming. By comparing germination and early-life responses of *S. acaulis* seeds under experimental warming to their parent populations' microclimates, I aim to identify whether a degree of microclimate specific genetic diversity exists between populations. Although this research focuses on one species, this may shed light on a potentially understudied aspect within the field and could be used to direct further studies on other species.

Aims

The aims of this study are (1) to gain a better understanding of how *Silene acaulis* germination and survival is likely to be affected by climate warming, and (2) to assess whether observed phenotypic differences among *Silene acaulis* populations from different microclimates are due to genetic differentiation. Specifically, I ask:

1. How does simulated climate warming affect germination and early survival in *Silene acaulis*?
 - I expect simulated climate warming to result in higher germination rates, faster germination, and increased seedling size, but reduced early survival due to environmental stress.
2. Do plants from different microclimate populations respond differently to climate warming?
 - I expect plants from warmer early-snowmelt “home” microclimates to have an increased germination response, earlier germination timing, increased survival, and increased growth under the simulated warming treatment compared to plants from colder late-snowmelt microclimates, suggesting evolutionary adaptation to local microclimate conditions.

Materials and Methods

Study Site and Seed Processing

This study was based on the *Silene acaulis* populations situated around the Latnjajaure research station (68.35847°N, 18.49506°E) in Northern Sweden (Figure 1). This site lies within the Arctic Circle, and its vegetation is typical of low-Arctic ecosystems, mainly composed of subarctic alpine tundra. This habitat is characterised by short summer growing seasons and persistent snow cover for the remainder of the year.

This site hosts numerous populations of *S. acaulis* that experience a wide range of snowmelt timings, resulting in substantial variation in flowering phenology. Since 2023, thirteen plots have been established to monitor these populations (Pavolotskaia, 2024). In my experiment, 10 of these plots were used (Figure 2), with the rest omitted due to unavailability of seeds. Of these 10 plots, six were early-flowering and four were late-flowering. Further information on the conditions of each plot can be found in Appendix 4.

For all ten plots, seeds were collected at the end of August 2025, from several mother-plants within each plot. To control for variation in ripeness between the seeds from early and late-flowering plots, seeds collected in July were also used for the early-flowering plots; these would likely be at a comparable developmental stage to late-flowering plot seeds in August. This allows any effects of potential unripeness on germination and survival to be controlled for. An important limitation to note is that pollen provenance and the amount of between-plot pollination are unknown, and this potentially limits inference about population-level responses.

All seed samples were then cleaned, counted, and weighed. Due to space and time constraints, only a subset of the seeds collected could be sown. The highest quality seeds from each plot were chosen (assessed visually based on physical characteristics), while maintaining proportional representation and sufficient replication among plots. For mother-plants from early-flowering plots, where both July and August collections were available, an equal number of seeds from each collection event were used. A breakdown of the number of seeds used from each plot and mother-plant can be found in Appendix 2.

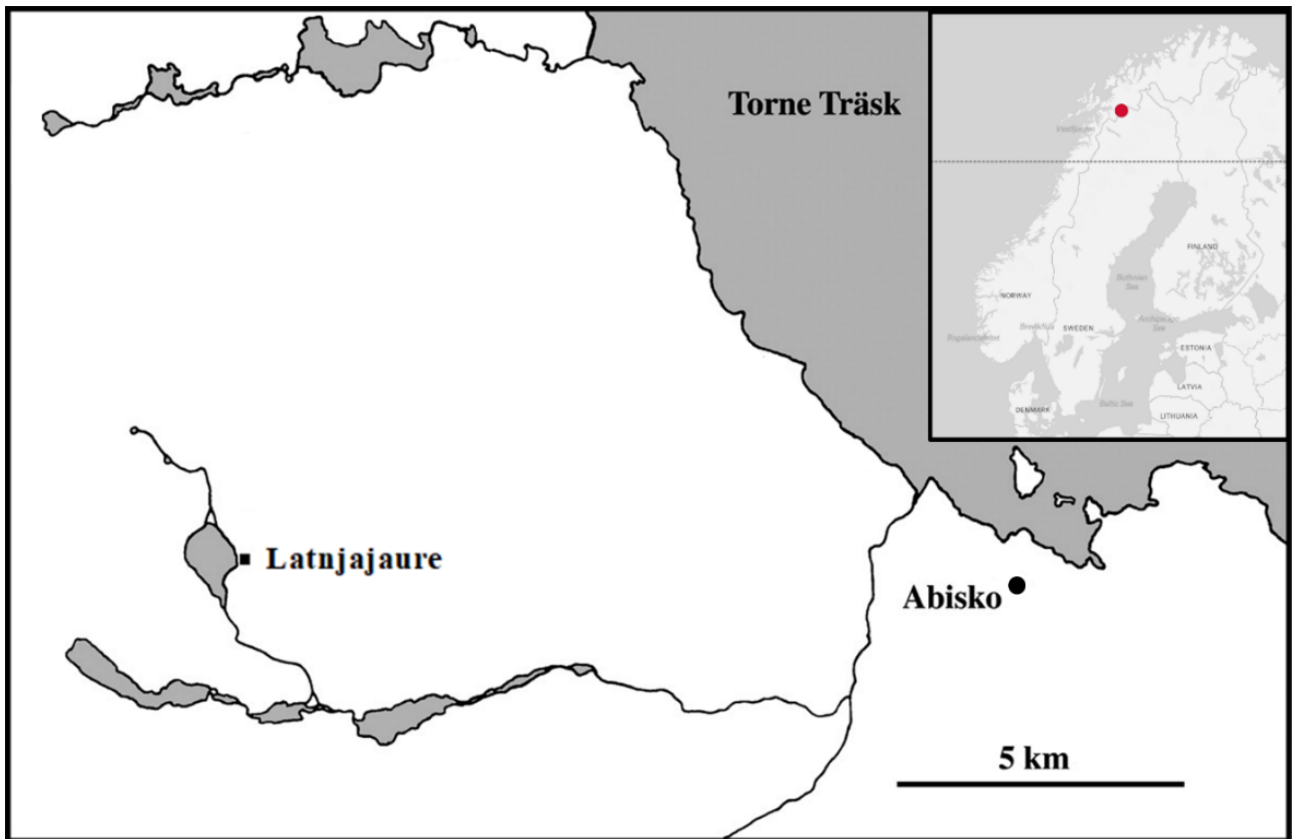


Figure 1: Position of Latnjajaure research station, with the Arctic Circle noted by the dashed line.

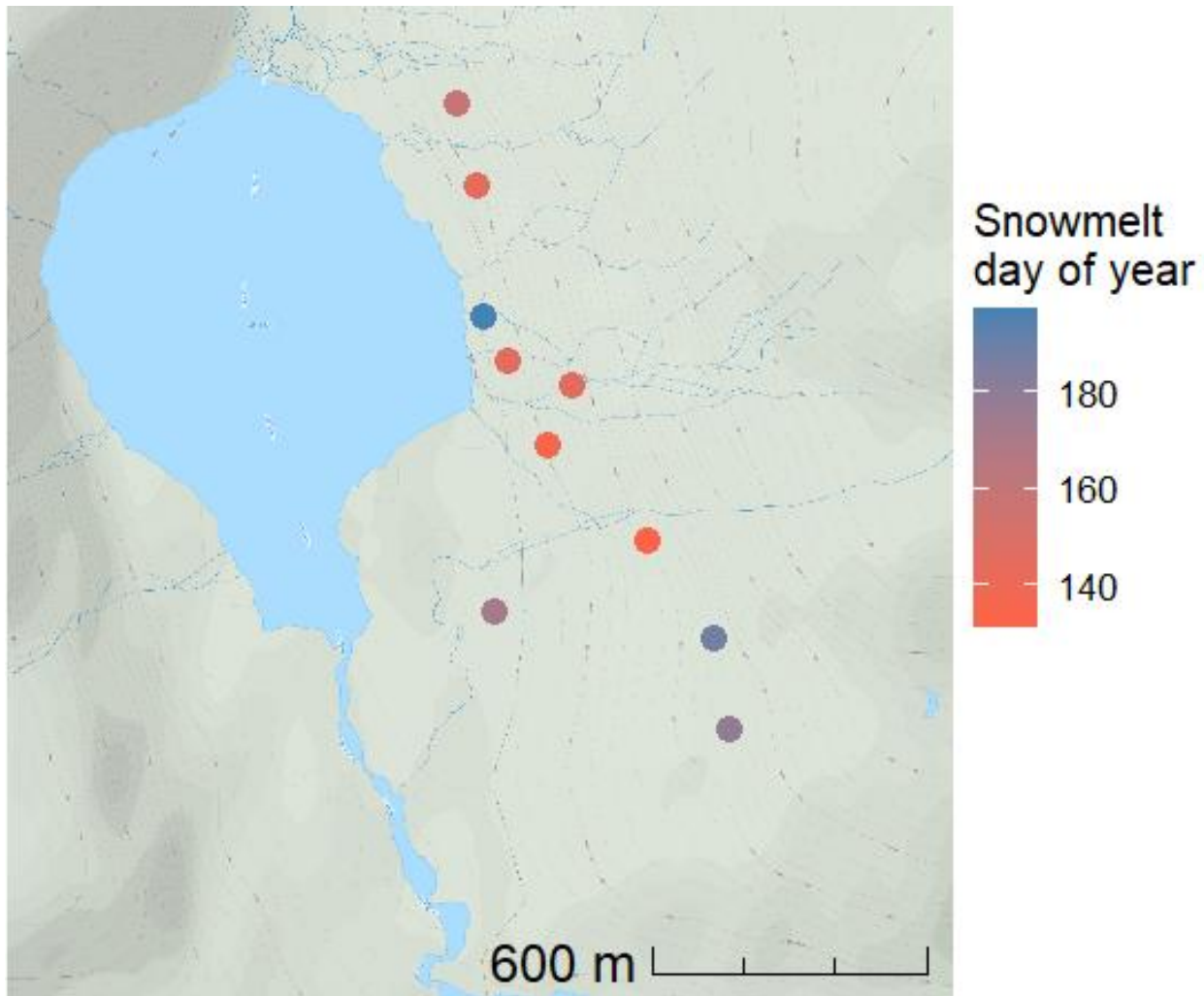


Figure 2: Location of each population studied, coloured by day of snowmelt.

Experimental Design and Setup

Climate Control Chambers

The experiment was conducted in two climate-controlled growth chambers, using a crossed experimental design, with an equal number of seeds from each mother-plant and plot represented in each chamber. One chamber served as a control. Both chambers were set at identical conditions except for temperature, with constant carbon dioxide levels, and a daily cycle for humidity and light level; the values chosen for these were based on a compromise between reflecting real-world conditions and experience from previous experiments. The temperature of the control chamber was based on climatic data from Latnjajaure; this was calculated from the median hourly temperature in July, creating the average daily temperature cycle. The 1st and 3rd quartile for each hour were also calculated, representing warm and cold days, given that daily temperature fluctuates widely. Based on these, I constructed a weekly cycle, starting with two cold days, followed by two median days, then two warm days, and another median day before repeating. As the growth chambers have a lower limit of 6°C, any value below 6°C was set to 6°C. For the experimental chamber, the same cycle was used but with 4°C added across the whole cycle. The full table of climatic variables for each chamber can be found in Appendix 3. Before the experiment began, the chamber conditions were monitored for a week; this ensured that other than temperature, all conditions were identical, in order to ensure that any variation truly represents a response to a change in temperature alone.

Sowing and Stratification

Three seeds were sown per pot and placed on the surface of the soil and covered in a thin layer of sand. The pots were wetted, and covered to prevent drying, before being placed in a dark cold-room set at 4°C for four weeks of cold stratification. This practice is commonly used to bring seeds out of dormancy and increase germination success. In total 3138 seeds were sown.

Experimental Process and Data Organisation

Experimental Process

After stratification, the pots were placed in the climate-controlled growth chambers and regularly moved and rotated to reduce potential bias of the position in the room. The pots were watered to full saturation of the soil to keep the water availability equal across all pots; this was done every five to nine days, as required.

Throughout the experiment, each pot was regularly checked for new germination or death. Initially checks were done three times a week, but as germination slowed this was reduced to twice and then once a week. In the last six weeks of the experiment, three collections of morphometric data were taken, with three weeks between each. At each collection, all live plants were measured; the measurements taken were the maximum height of the seedling, the seedling's width at its widest point, and the width perpendicular to the widest width. Cotyledons were included in the height measurement but excluded when measuring the width. Dead or drying parts of the seedling were also included in the measurements as it was not possible to make a definitive distinction between whether they were truly dead or not, with reemergence of leaves from senesced stems common.

Data Sorting and Organisation

After the start of the experiment, I recorded the date of germination and death, where applicable, for each seed. From this information, life duration was calculated as the number of days from germination to death, or to the final day of the experiment for seedlings still alive at that point. Seedlings that had not died by the end of the experiment were treated as right-censored observations, meaning their true survival time was unknown but exceeded the observation period.

The three collected values of the morphometric data were combined to represent a single unit of volume. This was done by treating the seedling as an ellipsoid ($\text{volume} = (4/3) \pi \times (\text{height}/2) \times (\text{widest}/2) \times (\text{perpendicular}/2)$), which was used as a proxy for size. Since volume scales as the cube of linear dimensions, the cuberoot of the volume was used as the primary size metric, linearising the relationship between the volume measure and the underlying linear size of the seedling. This was done for all three instances of size measurements, and at each instance, the age of the seedling was calculated, to model size trajectories over the experimental period.

For seedlings that had only produced cotyledons at the time of measurement, both width measurements were recorded as zero, resulting in a calculated volume of zero. These observations were replaced with an estimated volume based on the measured height. A width value was drawn at random from a continuous uniform distribution between 0.75 and 1.25 mm and assigned to both width measurements, assuming a circular cross-section; the cuberoot volume was then recalculated using the ellipsoid formula with the estimated width and the measured height retained. A random seed was set prior to this step to ensure that the values drawn were identical across runs. This affected 19, 29, and 22 observations at timepoints 1, 2, and 3 respectively. A random value was chosen over a fixed one to avoid introducing a spike at a single value in the response distribution, which would be inconsistent with the Gamma family assumption of a continuous positive distribution. Age at measurement was scaled across all timepoints, so that the scaling reflects the full distribution of ages across the experimental period rather than being computed separately within each timepoint.

I compiled additional data relating to the plot environment, mother-plant characteristics, and seed traits of the collected samples in order to assess the effect of these variables on variation in germination, growth, and survival.

On the plot level, altitude and climatic data were recorded, including snowmelt day, growing degree days (GDD), and soil moisture. These data were based on the daily median surface temperature and moisture collected by a TOMST TMS-4 logger at the centre of each plot. In 2025, temperature data were only available until the 29th of July, so the GDD values for 2024 were also calculated. GDD was calculated from the 1st of April until the 29th of July for 2025, and until 31st October for 2024. The baseline temperature for *S. acaulis* in the GDD calculation was set at 2°C based on previous studies (Zettlemoyer et al., 2022). The day of snowmelt was taken as the start of the first instance of five consecutive days with a mean surface temperature above 0°C. The plot soil moisture was calculated by taking the average daily value between the calculated snowmelt day of each plot until the end of the records on the 29th of July. The mean peak-flowering day for each plot was calculated based on the average of all peak-flowering dates measured in 2025 for plants from that plot. This also included plants whose seeds were not used in this experiment and excluded any plants which did not have a phenology record for 2025.

Data related to mother-plant characteristics were available from collections for previous studies. I compiled several variables related to the physical morphology and state of each plant: cushion length and width, sex (female or hermaphrodite), and whether an individual was infected by a fungal disease. Cushion length and width were combined into a single area variable using an ellipse approximation ($\pi \times (\text{length}/2) \times (\text{width}/2)$), avoiding strong collinearity between the two dimensions and providing a more biologically meaningful measure of plant size. Peak-flowering day was recorded in 2025 and 2023; when possible, the 2025 data were used, and where missing, the 2023 data were used instead. Although flowering times can vary between years, average flowering times in 2025 and 2023 followed a similar pattern. In case a particular plant had the values from both recordings missing, the average calculated for their respective plot was used in its place.

I also compiled information on each seed sample, and in addition to the average weight, I had also taken note of the collection date. I also calculated a ripeness score, aiming to have a standardised, measurable value for ripeness that can be used in analyses. This was calculated as the number of days between the peak-flowering day of each plant and the day the seeds were collected.

Statistical Analyses

The following data analyses method description is organised based on the order in which the analytical process was carried out; each step builds upon the one preceding it. The first sections focus on the selection of which variables to include and which model families should be used; the following sections are split by effector variable. This structure is, however, not replicated in the results section, with this being structured along the questions in the aims and by the response variables within each question for organisational reasons.

Data Validation and Inclusion Decisions

Seeds fell into three groups based on plot flowering phenology and collection timing: seeds from early-flowering plots collected in August (ripe), seeds from early-flowering plots collected in July (underripe), and seeds from late-flowering plots collected in August (potentially underripe). Before proceeding to formal modelling, it was necessary to evaluate whether the July collection fulfilled its intended purpose as a control for ripeness, and thus whether results from all seeds should be retained in the analyses.

To characterise how the groups differed in seed quality, ripeness score and seed weight were compared across the three groups using linear mixed models with mother-plant as a random

intercept to account for within-mother correlation across collection events. The effect of collection timing on germination probability was then examined directly by comparing July and August seeds from the same double-collected mother-plants using a binomial GLMM with plot and mother-plant as random intercepts. The corresponding effect on survival was examined using a Cox mixed-effects model with mother-plant as a random intercept, fitted on germinated seeds only.

The groups differed in ripeness score and seed weight as expected from the collection design, and collection timing had a modest but significant effect on germination probability (OR = 1.45, 95% CI: 1.13–1.86, $p = 0.003$). Collection timing had no significant effect on survival (HR = 0.896, 95% CI: 0.684–1.172, $p = 0.422$). However, the three continuous seed trait covariates (ripeness score, seed weight, and collection day of year) were included in all downstream models, capturing collection-related variation continuously and at higher resolution than the three-group classification. This was considered sufficient to account for seed quality differences between groups without requiring exclusion of the July collection. July-collected seeds were thus retained in all subsequent analyses.

Model Choice and Analytical Strategy

For each response variable (germination probability, germination timing, survival, and growth) the appropriate model family was selected based on the distributional properties and measurement scale of each response. Germination probability is binary and was modelled using a binomial GLMM with a logit link (lme4). Germination timing is continuous, strictly positive, and non-normally distributed (confirmed by Shapiro-Wilk test), and was modelled using a Gamma GLMM with a log link (glmmTMB). Survival is a time-to-event response with right-censoring and was modelled using a Cox mixed-effects model (coxme), which is semi-parametric and makes no assumption about whether mortality risk is constant, increasing, or decreasing over the course of the experiment. Growth, measured as seedling size (cuberoot ellipsoid volume) modelled against age to capture growth trajectories, is continuous and strictly positive, and was also modelled using a Gamma GLMM with a log link (glmmTMB); the log link gives a multiplicative interpretation on the response scale. Age was included both as a linear and quadratic fixed effect covariate, allowing the growth trajectory to be non-linear rather than assuming a constant proportional growth rate; this was preferred over a model with age entered as a linear term only, following empirical comparison showing substantially better fit ($\Delta\text{AIC} = 267.5$, $\text{LRT } \chi^2 = 269.5$, $p < 2.2\text{e-}16$) and a significant treatment $\times$ age² interaction indicating that the two treatments followed different trajectory shapes.

A common sequential modelling strategy was applied across all response variables. Models were built progressively, starting with seed trait predictors to characterise the effects of seed quality, before adding treatment as the primary fixed effect to test the warming hypothesis. Subsequent models extended this structure by introducing plot-level microclimate predictors and then mother-plant-level predictors as the primary fixed effects of interest, with microclimate predictors replaced by mother-plant predictors rather than accumulated alongside them. This sequential approach allows direct comparison between model steps as only the primary predictors of interest change between them, while seed trait covariates are retained throughout and the model family and link function remain consistent for each response variable. Prior to fitting each set of models, the optimal random effects structure was determined empirically by comparing alternative structures using AIC. The candidate random effects were plot, mother-plant, and seed collection group; pot was not included as a random effect as seeds were organised by collection group in the experiment, so pot-level variance is largely absorbed. Models with and without each candidate random effect were fitted and compared, and the structure with the lowest AIC was retained. This was repeated at each modelling stage as the addition of new fixed effects can alter the residual variance structure

and therefore the optimal random effects configuration. Random effects decisions and their rationale are described in the relevant analytical sections.

Prior to all modelling, binary response variables were coded as 0/1, grouping variables were converted to factors, and continuous predictors were scaled to a mean of 0 and standard deviation of 1 to make model estimates comparable across predictors. Germination probability models were fitted on the full dataset. Germination timing and survival models were fitted on germinated seeds only, as these responses are only defined for seeds that germinated. Growth models were fitted on a long-format dataset containing up to three size observations per seedling, also restricted to germinated seeds.

Seed Traits

Before testing the main hypotheses, the effects of seed traits (seed weight, collection date, ripeness score) on the experimental results were examined. This step was necessary to determine whether any observed variance in the experimental outcomes was attributable to differences in seed quality rather than variation at the plot or mother-plant level. Treatment was excluded from seed trait models as seeds were equally distributed across both chambers by design.

Prior to modelling, the three seed trait predictors were assessed for multicollinearity using Pearson correlations and variance inflation factors (VIF). Ripeness score and collection date were moderately correlated ($r = 0.604$), reflecting that seeds collected later in the season tend to be riper. Seed weight showed negligible correlation with collection date ($r = -0.005$) and moderate correlation with ripeness score ($r = 0.405$). VIF values were below 2, indicating that multicollinearity was not sufficient to warrant exclusion of any predictor, and all three were retained. Plot-level Pearson correlations between mean seed traits and the microclimate predictors were also calculated across the ten plots.

Prior to fitting the seed trait models, the optimal random effects structure was determined. For germination probability, the full structure of plot, mother-plant, and seed collection group was retained, as removing any one grouping level increased AIC by at least 4 units. The same structure was selected for germination timing, though the AIC differences were mixed; removing plot or mother-plant individually changed AIC by less than 1 unit, reflecting near-zero between-group variance in timing, while removing seed collection group worsened AIC by 3.4 units, providing the stronger justification for retaining the full structure. For survival, the Cox mixed-effects model does not reliably support more than one random effect simultaneously. Mother-plant was prioritised on biological grounds as the strongest source of non-independence in survival outcomes. Empirical testing confirmed this: models with mother-plant alone, with both mother-plant and plot, and with both mother-plant and seed collection group were essentially equivalent ($\Delta\text{AIC} < 0.02$ in all cases), with plot and seed collection group variances collapsing to near-zero when included alongside mother-plant. Mother-plant alone was therefore retained. For growth, seed collection group was excluded: initial testing showed near-zero variance ($\sigma^2 = 0.002$) and worse fit when included alongside plot and mother-plant ($\Delta\text{AIC} = +1.9$), consistent with seed trait covariates already capturing collection-level variation. Both plot and mother-plant were retained, with AIC increasing by 33.4 and 49.9 respectively when each was removed.

Using the random effects structures determined above, four models were fitted with seed weight, ripeness score, and collection date as the fixed effects of interest. Age at measurement was included as an additional continuous fixed effect covariate alongside its squared term (age^2) in the growth model, to account for variation in seedling age at each measurement occasion. Model fit was assessed using DHARMA simulated residuals for the GLMMs, and through inspection of hazard ratio plausibility and coefficient stability for the Cox model.

I also assessed whether seed quality was confounded with plot-level microclimate. Seed weight and ripeness score were each modelled as a function of snowmelt day and altitude using linear mixed models with mother-plant as a random intercept. To determine whether the effect of snowmelt on seed weight was fully explained by ripeness, (due to the effect of snowmelt on flowering time), a mediation analysis was additionally conducted. This is an acknowledged limitation of the experimental design: seed quality and population origin cannot be fully separated, and some variance attributed to plot origin in models may partly reflect seed quality differences between plots.

Treatment Effect

Prior to fitting the treatment models, the random effects structure was re-tested empirically for each response variable using AIC, as the addition of treatment as a fixed effect can alter the residual variance structure. The random effects structure from the seed trait models was retained for all four response variables, based on the results of these tests.

Treatment was added as a fixed effect to each of the seed trait models, with the control treatment set as the reference level. The three seed trait covariates were retained in all models to account for variance attributable to seed quality. The fit of each model was compared with and without treatment using likelihood ratio tests and AIC. Odds ratios and hazard ratios were obtained by exponentiating model coefficients, and 95% confidence intervals were calculated using the Wald method for all models. Treatment $\times$ age and treatment $\times$ age² interaction terms were included in the growth model to test whether the trajectory shape differed between treatments, specifically whether heated and control seedlings differed in both the rate of initial growth and the degree of deceleration with age. This is appropriate given that heated seedlings were inherently larger, and estimating proportional rather than absolute growth ensures any treatment difference in the interaction term reflects genuine growth dynamics rather than an artefact of baseline size differences. Model fit was assessed using DHARMA simulated residuals for the GLMMs and through inspection of hazard ratio plausibility and coefficient stability for the Cox model. A Kaplan-Meier survival curve was produced as a visual complement to the Cox model, showing observed survival trajectories by treatment while censoring seedlings still alive at the end of the experiment; this provides an empirical summary of mortality patterns without model assumptions.

To determine whether mortality risk was constant over time or changed with seedling age, and whether this differed between treatments, exponential and Weibull parametric survival models were fitted separately for each treatment using germinated seeds only. The exponential model assumes a constant hazard, representing age-independent mortality, while the Weibull model allows the hazard to increase or decrease with age. Models were compared using AIC, with a difference greater than 2 taken as meaningful support for the lower-AIC model. Δ AIC is defined throughout as AIC_exponential – AIC_Weibull, such that positive values indicate better fit of the Weibull model and negative values indicate better fit of the exponential. The direction and magnitude of any age-dependence was assessed through the Weibull shape parameter and its 95% confidence interval: a shape of 1 is equivalent to the exponential, values above 1 indicate increasing hazard with age, and values below 1 indicate decreasing hazard. Life duration values of zero were replaced with 0.5 days for parametric modelling only, to avoid undefined log-likelihood contributions ($n = 5$ seedlings).

Plot-Level Variables

To examine whether seeds from populations with different home microclimates differ in their germination, survival, and growth responses to simulated warming, plot-level variables were introduced into the models. Five variables were considered: plot altitude, snowmelt day, average peak-flowering day, and GDD 2024 and 2025. Soil moisture was excluded due to missing data for

plot L but is explored separately later. The five variables were first assessed for collinearity using Pearson correlations.

Snowmelt day was selected as the primary proxy for microclimate on the basis that it is typically the strongest control for flowering time. Plot altitude was retained as a complementary predictor ($r = 0.04$ with snowmelt), while peak-flowering day and both GDD values were excluded due to collinearity with snowmelt (peak-flowering day and GDD 2025: $r > \pm 0.95$; GDD 2024: $r = -0.79$). VIF values for the retained predictors were all below 2. Both predictors were scaled prior to inclusion. Collection date was excluded from all microclimate models due to collinearity with snowmelt ($VIF > 8$). Seed weight and ripeness score were retained as continuous covariates to partially account for the confounding between seed quality and plot origin established in the seed trait analysis.

The random effects structure was re-tested empirically for each response variable using AIC. For germination probability, the full structure of plot, mother-plant, and seed collection group was retained; plot contributed meaningful residual variance (0.546) despite the inclusion of plot-level fixed predictors, with AIC increasing by 5.1 when plot was removed. For germination timing, plot was dropped; its variance collapsed to near-zero (0.009) when snowmelt and altitude were included as fixed effects, indicating that these predictors absorbed the between-plot variation in timing, and AIC was lower without plot. Mother-plant and seed collection group were retained for germination timing, consistent with the AIC comparison showing those two grouping levels still contributed meaningfully. For survival, mother-plant alone was retained, consistent with all previous sections. For growth, both plot and mother-plant were retained, with AIC increasing by 24.6 and 71.9 respectively when each was removed; plot retained meaningful residual variance (0.104) despite the plot-level fixed predictors.

The same model families used previously for each response variable were retained. Treatment, scaled snowmelt day, and scaled altitude were included as fixed effects, with interaction terms between treatment and each microclimate predictor to test whether the warming response differed across environmental gradients. The treatment $\times$ age and treatment $\times$ age² interactions were also retained in growth models. Seed weight and ripeness score were included as covariates throughout. A Kaplan-Meier survival curve was additionally produced for each plot, ordered by snowmelt day, as a visual complement to the Cox model results.

Mother-Plant Level Variables

To examine whether individual mother-plant characteristics influenced the germination, survival, and growth responses of their offspring to simulated warming, mother-plant-level predictors were substituted for the microclimate predictors used in the previous section. Two predictors were used: cushion area, calculated as described previously, and individual peak-flowering day. Terms for mother-plant sex and sickness status were excluded from the models; preliminary testing confirmed non-significant effects of sex (OR = 1.26, $p = 0.474$ for germination; HR = 1.31, $p = 0.130$ for survival), and sick individual sample size was too small for reliable estimation ($n = 5$). A collinearity check confirmed that cushion area and flowering day were not strongly correlated with each other or with the retained seed trait covariates, with all VIF values below 2. Collection date was excluded as it is collinear with snowmelt day at the plot level ($VIF > 8$ in microclimate models) and therefore carries largely the same between-plot information already captured by the plot random effect and individual flowering day in these models.

The random effects structure was re-tested empirically for each response variable using AIC. For germination probability, the full structure of plot, mother-plant, and seed collection group was retained, with AIC increasing by 4.5, 4.1, and 7.4 respectively when each was removed. For germination timing, the full structure was also retained; although removing mother-plant marginally improved AIC by 0.1, mother-plant variance was non-zero and the full structure was

preferred for consistency. For survival, mother-plant alone was retained, consistent with all previous sections. For growth, both plot and mother-plant were retained, with AIC increasing by 24.5 and 68.9 respectively when each was removed.

The same model families used previously for each response variable were retained. Models included treatment $\times$ cushion area and treatment $\times$ flowering day interaction terms to test whether the warming response differed across the range of mother-plant characteristics. The treatment $\times$ age and treatment $\times$ age² interactions were also retained in growth models. Mother-plant was retained as a random effect alongside the mother-plant-level fixed predictors, as cushion area and flowering day are unlikely to capture all sources of individual-level variation.

As flowering day is strongly influenced by plot microclimate, the extent to which individual peak-flowering day captured genuine within-plot variation was assessed using an intraclass correlation coefficient (ICC). The ICC was 0.907, indicating that 90.7% of the variation in peak-flowering day was between plots rather than between individual mothers within plots. This means the treatment $\times$ flowering day interaction in the main model largely reflects plot-level rather than individual-level response. Flowering day was therefore additionally centred within each plot by subtracting the plot mean from each mother's value, and the treatment $\times$ flowering day interaction was re-tested using these within-plot centred values. For growth, within-plot flowering day was entered in raw days rather than scaled, so that the coefficient is directly interpretable as the effect per day of deviation from the plot mean; this was preferred over scaling given that a genuine individual-level effect was subsequently detected, making the coefficient directly interpretable in biologically meaningful units.

Model Validation and Robustness Checks

To validate the choice of snowmelt and altitude as the primary microclimate predictors, a principal component analysis (PCA) was conducted on all five plot-level microclimate variables (altitude, snowmelt day, peak-flowering day, GDD 2024, GDD 2025), scaled prior to analysis. PC scores were extracted and added to the dataset, and germination probability, germination timing, survival, and growth models were re-run using PC1 and PC2 as microclimate predictors in place of snowmelt and altitude. The same model families and random effects structures as the primary microclimate analyses were used.

Additionally, soil moisture was examined as a sensitivity analysis, after excluding values from Plot L, which had no moisture data available. The primary microclimate model for germination probability was re-run with soil moisture included as an additional covariate ($n = 9$ plots) using the same binomial GLMM structure as the primary model. This was done for germination probability only as this was the response variable with the strongest statistical result.

As a further check on the germination probability result, the primary microclimate model was re-fitted with treatment $\times$ seed weight and treatment $\times$ ripeness score interactions added, retaining the same random effects structure. Because both seed traits declined with snowmelt day, this tested whether the treatment $\times$ snowmelt interaction might instead reflect seed quality covarying with the gradient and modifying the warming response, rather than a genuine population-level difference.

Reaction Norm and Variance Partitioning

To assess whether between-population differences observed in the field at Latnjajaure reflect a genetic contribution or purely plastic responses to local environmental conditions, several complementary approaches were used. Crucially, within each treatment, all seeds experienced identical conditions, meaning that, after accounting for seed quality, any remaining between-plot variation in response represents pre-existing population-level differences independent of experimental conditions.

Reaction norm plots were produced for the four response variables at the plot level. For each response variable, model-predicted values under control and simulated warming were computed for each plot and plotted as a separate line per plot, each connecting that plot's predicted control and heated values, with treatment on the x-axis and predicted response on the y-axis. Each line was coloured by snowmelt day to facilitate visual assessment of how responses vary along the environmental gradient. For survival, observed experimental rates were used instead of model-predicted values, as the Cox mixed-effects model cannot produce absolute survival probabilities. For germination timing and growth, the standard prediction approach used for germination probability was not available, as the model type used (glmmTMB) does not support plot-specific predictions, meaning all plots would otherwise receive identical predicted values regardless of their actual behaviour in the data. Instead, each plot's individual deviation from the overall average was extracted from the model and incorporated into the predictions, giving each plot its own line that reflects its actual position in the data after accounting for seed quality and treatment.

Reaction norm plots for germination probability are shown on the probability scale; since absolute changes are constrained by baseline probability levels, they do not truly represent the relative warming response. The model interaction term, estimated on the log-odds scale where this constraint does not apply, therefore provides the more appropriate basis for comparing responses between populations.

To quantify the relative contribution of each biological level (seed traits, mother-plant, plot) to overall variation in each response variable, variance partitioning was conducted using the random effect variances from the main treatment models; this indicates where the variation in response may stem from. For germination probability and timing, all three random effects were retained, while for growth only plot and mother-plant were included, consistent with previous models. Full partitioning was not possible for survival as the Cox model provides only the mother-plant random effect variance; this is reported separately as a standard deviation. For binomial GLMMs, residual variance was approximated as $\pi^2/3$, the theoretical variance of the logistic distribution, which is the standard approach for variance partitioning on the latent logit scale. For Gamma GLMMs, residual variance was taken as σ^2 , the squared dispersion parameter returned by the model.

To formally test whether the relative germination response to warming declined with snowmelt day at the plot level, a linear regression of the observed germination rate ratio (heated/control) against plot snowmelt day was conducted across the nine plots for which a finite ratio could be calculated. Plot I was excluded as no seeds germinated in the control treatment, rendering the ratio undefined. This analysis complements the treatment $\times$ snowmelt interaction term from the main model by directly testing whether the gradient in relative response is detectable in the raw plot-level data.

Additionally, to examine whether the variation in germination probability between plots differed between treatments and reflected the snowmelt gradient, the primary microclimate germination probability model was re-fitted separately on the control and heated subsets, retaining the rest of the model structure, and the plot-level random effect variance was extracted from each; the snowmelt effect within each treatment was also extracted. A larger plot-level variance in the heated model relative to the control would indicate that populations diverge more in their germination responses under warming, consistent with differential population-level sensitivity to temperature. As Plot I had no germination in the control, it was identified as a potentially influential observation in the control subset; a sensitivity analysis excluding it confirmed that directional conclusions were unchanged, though the heated plot-level variance estimate was substantially reduced (0.468 to 0.199 when Plot I was excluded), indicating it contributes considerably to estimated between-population divergence under warming; all 10 plots were therefore retained.

Model Assumptions and Diagnostics

Model residuals for binomial and Gamma GLMMs were assessed using DHARMA simulated residuals. DHARMA uses a simulation-based approach to generate scaled residuals that are uniformly distributed under a correctly specified model, enabling standard visual and statistical diagnostic tests regardless of model family. Tests conducted included KS tests, dispersion tests, and outlier tests. Gamma GLMMs for germination timing and growth showed some residual quantile deviations consistently across models; these were considered acceptable given the biological clarity of the treatment effects and the repeated-measures structure of the growth data. Dispersion tests were non-significant across all growth models (p range: 0.120–0.200). Formal residual-based diagnostics are not available for mixed-effects Cox models; model adequacy was therefore evaluated through inspection of hazard ratio plausibility, coefficient stability across model specifications, and agreement between model-implied estimates and Kaplan-Meier survival curves. All random effect variances were inspected for near-zero estimates throughout.

Statistical Software

All data analysis was carried out in R version 4.4.1 (June 2024; R Core Team, 2024). Data were imported using readxl (Wickham & Bryan, 2023) and manipulated using dplyr (Wickham et al., 2023), tidyr (Wickham et al., 2024) and tibble (Müller & Wickham, 2023). Visualisations were produced using ggplot2 (Wickham, 2016), with multi-panel figures assembled using patchwork (Pedersen, 2025), and non-overlapping labels in biplots handled using ggrepel (Slowikowski, 2024). Binomial generalised linear mixed models (GLMMs) and linear mixed models were fitted using lme4 (Bates et al., 2015), and Gamma GLMMs were fitted using glmmTMB (Brooks et al., 2017). Model residuals were assessed using DHARMA (Hartig, 2024) and variance inflation factors were calculated using car (Fox & Weisberg, 2019). Survival objects and Kaplan-Meier estimates were constructed using survival (Therneau, 2026), with Kaplan-Meier curves visualised using survminer (Kassambara et al., 2026). Cox mixed-effects models were fitted using coxme (Therneau, 2024), and parametric Weibull and exponential survival models were fitted using flexsurv (Jackson, 2016). Principal component analyses and linear regressions were conducted using base R functions (prcomp and lm respectively).

Results

Of the 1569 seeds sown in each treatment, the germination rates for the control and heated treatments were 17.8% and 35.4% respectively. Of those that germinated, the control and heated treatments had a survival rate of 43.6% and 56.3% respectively (Table 1). Seedlings under heated treatment were consistently and substantially larger than control seedlings at all ages. Summary plots of these data can be found in Appendix 6. Prior to adding treatment, size increased strongly with age ($\text{exp} = 1.619$, $p < 2 \times 10^{-16}$) but decelerated at older ages (age^2 : $\text{exp} = 0.821$, $p < 2 \times 10^{-16}$), consistent with a growth plateau over the experimental period.

Table 1: Summary of experimental results

Treatment	Total seeds	Number germinated	Germination rate (%)	Number died	Survival rate (%)	Mean age at death (days)
Control	1569	280	17.8	158	43.6	54.8
Heated	1569	556	35.4	243	56.3	41.5

Question 1 – Seed Traits and Treatment Effect

Seed Traits

Ripeness score and collection date did not have any significant effects within the seed trait models. Additionally, germination timing and survival were not significantly affected by any seed traits. Seed weight was a significant predictor of germination probability (OR = 1.47, 95% CI: 1.17–1.86, $p = 0.001$) and seedling size ($\exp = 1.155$, 95% CI: 1.091–1.223, $p < 0.0001$).

Germination Probability

Experimental warming had a positive effect on germination probability compared to the control. The addition of treatment to the germination model substantially improved fit ($\Delta AIC = 146.3$, LRT $\chi^2 = 148.3$, $p < 2.2e-16$). Simulated warming approximately tripled the odds of germination (OR = 3.00, 95% CI: 2.50–3.59, $p < 2e-16$), after accounting for seed quality (Figure 3a). Plot and mother-plant accounted for considerable variation with variances of 0.525 and 0.556 respectively.

Germination Timing

Germination timing advanced under warming, with seeds under treatment germinating approximately 24% earlier than those in the control (Figure 3b) ($\exp = 0.764$, 95% CI: 0.690–0.846, $p = 2.33e-7$). Adding treatment significantly improved model fit ($\Delta AIC = 24.7$, LRT $p = 2.43e-7$).

Survival

Simulated warming overall led to reduced seedling mortality (HR = 0.724, 95% CI: 0.587–0.893, $p = 0.003$), with adding treatment significantly improving model fit (LRT $p = 0.003$). The Kaplan-Meier curves (Figure 4a) show broadly similar survival under both treatments during the first half of their lifespan, with a slight advantage for control seedlings, followed by heated seedlings having a pronounced survival advantage from approximately 60 days onwards. The hazard ratio therefore reflects an average effect across the full experimental period.

Mortality risk showed a statistically significant age-dependent pattern under control conditions, though the biological magnitude was modest. For control seedlings, the Weibull model fit substantially better than the exponential ($\Delta AIC = 45.9$), with a shape parameter of 1.692 (95% CI: 1.479–1.935, excludes 1), indicating increasing mortality risk with age (Figure 4b). However, the difference in survival curve shape (Figure 4a) was not visually pronounced, suggesting that while the accelerating hazard is statistically detectable, it does not represent a dramatic biological effect. For heated seedlings the two models fit essentially equally ($\Delta AIC = -1.9$), with a Weibull shape of 0.978 (95% CI: 0.874–1.095, spans 1), consistent with age-independent constant-rate mortality (Figure 4b). Taken together, these results suggest that the age-dependent component of mortality observed under control conditions was absent or greatly reduced under warming.

Growth

Experimental warming had a strong positive effect on seedling size, with heated seedlings approximately 84% larger than control seedlings at mean age ($\exp = 1.836$, 95% CI: 1.719–1.961, $p < 2 \times 10^{-16}$), after accounting for seed quality. Adding treatment to the model substantially improved the fit ($\Delta AIC = 315.1$, LRT $\chi^2 = 321.1$, $df = 3$, $p < 2.2 \times 10^{-16}$). The treatment $\times$ age² interaction was significant and negative ($\exp = 0.915$, 95% CI: 0.876–0.955, $p < 0.0001$), indicating that heated seedlings decelerated in growth rate more strongly with age, while the treatment $\times$ age interaction was non-significant ($p = 0.805$), indicating that the treatments differed in trajectory shape rather than initial growth rate (Figure 5).

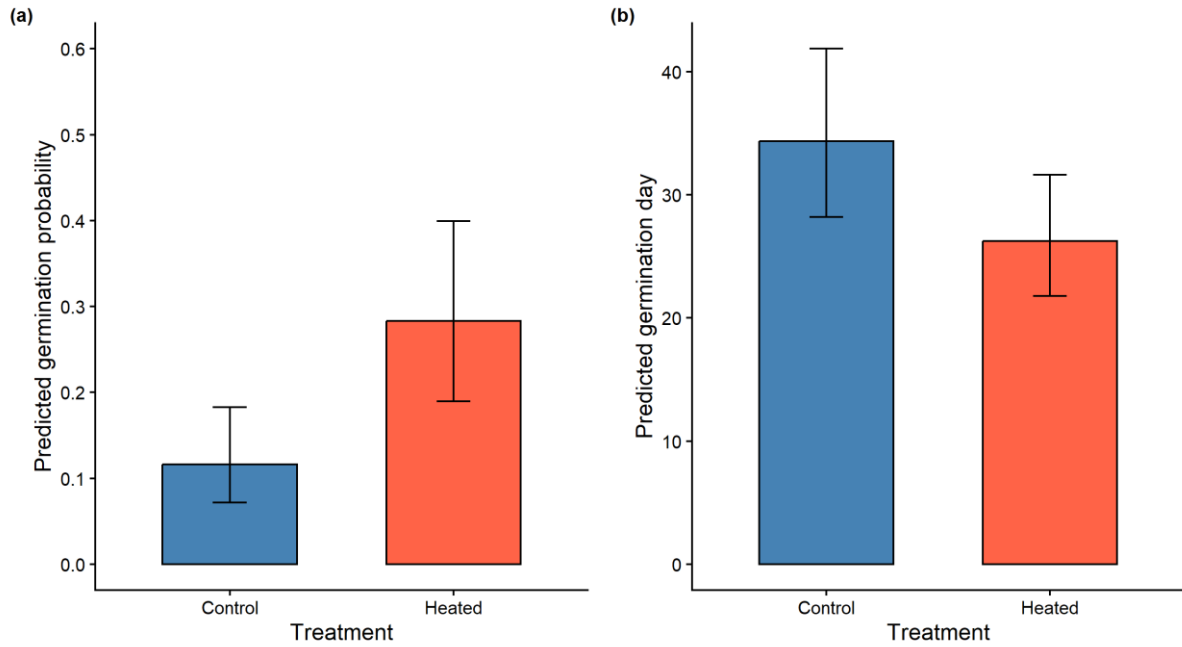


Figure 3: Predicted germination probability and timing of *Silene acaulis* seedlings under control and heated treatments, with error bars representing 95% confidence intervals. Predictions exclude random effects and hold seed trait covariates at their mean values. (a) Model-predicted germination probability by treatment. (b) Model-predicted germination day by treatment.

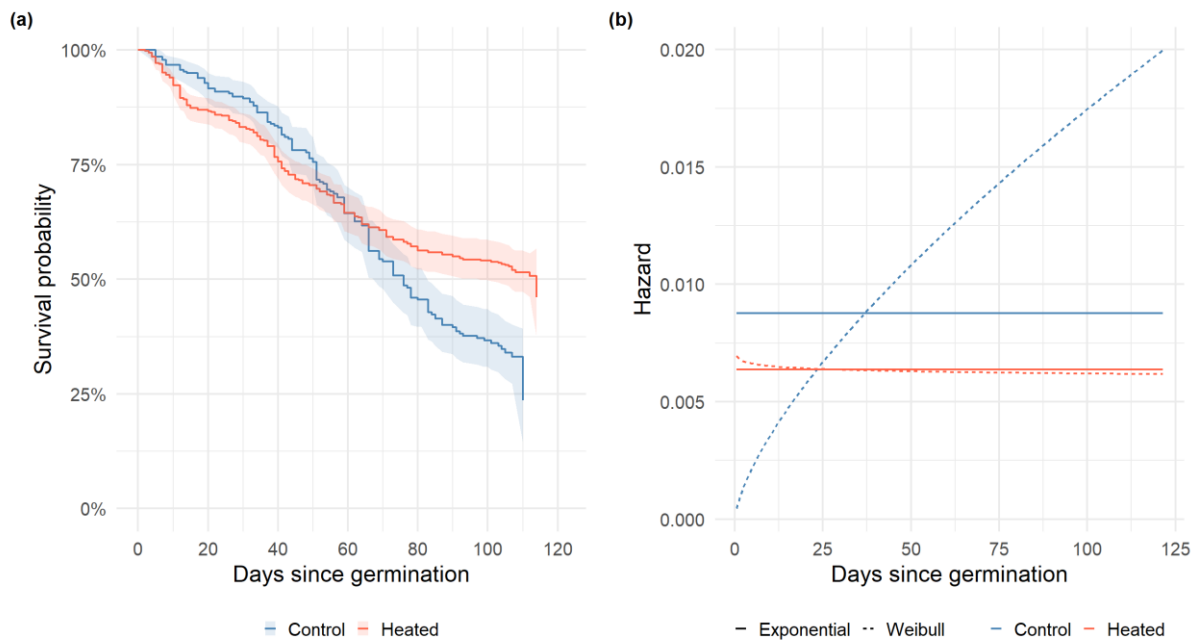


Figure 4: Survival analysis of *Silene acaulis* seedlings under control and heated treatments. (a) Kaplan-Meier survival curves showing observed survival probability over time, with shaded areas representing 95% confidence intervals, showing an initial slight survival advantage for control seedlings before an age of 60 days and a larger disadvantage after an age of 60 days. (b) Estimated hazard rates from exponential and Weibull parametric models fitted separately for each treatment, showing age-dependent mortality risk. Exponential models estimate a constant death rate, while Weibull models are able to show how death rate actually changes with time. Given that for heated seedlings, the Weibull line is almost flat, producing a similar curve to the exponential model, the rate of mortality for these seedlings is constant with time. For the Control, the Weibull curve is clearly different to the exponential, indicating that mortality in these seedlings is age-dependent.

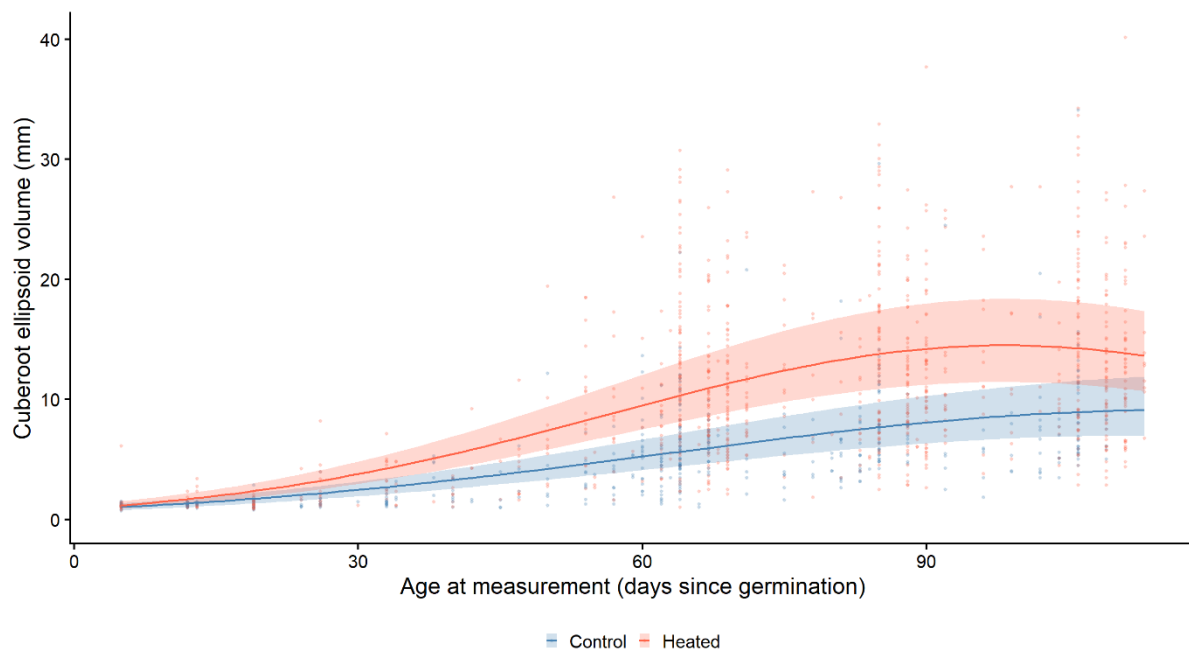


Figure 5: Growth trajectories of *Silene acaulis* seedlings under control and heated treatments. Lines show model-predicted cuberoot ellipsoid volume against age since germination, with shaded areas representing 95% confidence intervals; points show all individual size measurements, coloured by treatment. Predictions exclude random effects and hold seed trait covariates at their mean values. Heated seedlings were consistently larger than controls throughout the experimental period, with both treatments showing deceleration in growth rate with age.

Question 2 – Microclimate and Maternal Effects

Seed Traits

At the plot level, seed traits were strongly structured by snowmelt timing; both mean seed weight and mean ripeness score declined with later snowmelt ($r = -0.85$, $p = 0.002$ and $r = -0.86$, $p = 0.002$ respectively). Neither trait was related to altitude (weight $r = 0.02$, $p = 0.95$; ripeness $r = 0.12$, $p = 0.74$). This confirms that seed quality covaries with snowmelt but not altitude, which motivates retaining seed weight and ripeness as covariates throughout and underlies the robustness check reported below.

PCA – Predictor Choice Validation

The PCA reduced the five plot-level microclimate variables to two dominant axes (Figure 6). PC1 explained 72.6% of the variance with high positive loadings for snowmelt day (0.517) and peak flowering day (0.497) and high negative loadings for GDD 2025 (-0.519) and GDD 2024 (-0.457); PC1 represents a microclimate-harshness gradient from milder early-snowmelt plots to harsher late-snowmelt plots. PC2 explained 22.6% of variance and was dominated almost entirely by altitude with a very high positive loading (0.911), largely independent of PC1. Together, both PCs explained 95.2% of the total microclimate variance, validating the choice of snowmelt as the primary proxy with altitude as a complementary independent axis.

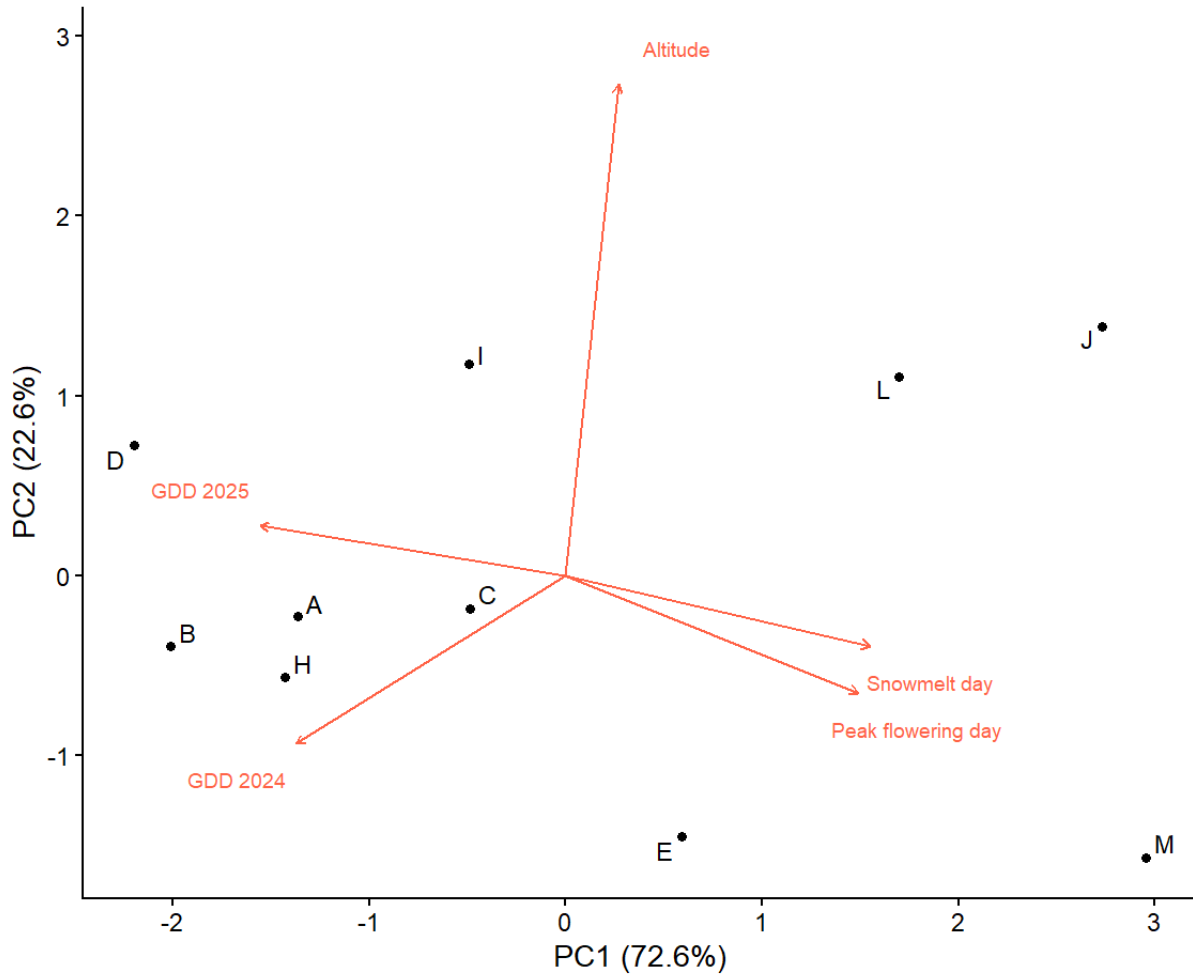


Figure 6: Principal component analysis (PCA) biplot of five plot-level microclimate variables (snowmelt day, peak flowering day, GDD 2024, GDD 2025, and altitude). Arrows show variable loadings on PC1 (72.6% of variance) and PC2 (22.6% of variance). PC1 represents a gradient from milder early-snowmelt plots to harsher late-snowmelt plots, driven by snowmelt day, peak flowering day, and growing degree days. PC2 is dominated by altitude and is largely independent of PC1. Plot labels indicate the position of each population along both axes.

Germination Probability

Warming promoted germination across all populations, but seeds from populations with harsher, later-snowmelt home microclimates responded less strongly to the treatment (Figure 7). The treatment $\times$ snowmelt interaction was significant and negative (OR = 0.621, 95% CI: 0.502–0.769, $p < 0.0001$), indicating a smaller warming benefit on germination probability in seeds from later-snowmelt plots. The treatment $\times$ altitude interaction was non-significant (OR = 1.003, $p = 0.977$), as was the altitude main effect, which trended negative (OR = 0.905, $p = 0.715$). Seed weight remained a significant positive predictor (OR = 1.497, $p = 0.001$).

In a sensitivity model that added soil moisture and excluded plot L (which lacked moisture data), soil moisture itself was non-significant (OR = 1.300, $p = 0.418$) and the treatment $\times$ snowmelt interaction remained significant (OR = 0.643, $p = 0.0001$), confirming the result was robust to both. This model produced a minor convergence warning ($\max|\text{grad}| = 0.006$), but as its key conclusion matched the primary model the result is considered reliable.

The interaction was further supported by the PCA sensitivity analysis, in which snowmelt and altitude were replaced by their principal components. The treatment $\times$ PC1 interaction was significant and negative (OR = 0.615, 95% CI: 0.497–0.761, $p < 0.0001$), directly mirroring the

snowmelt interaction, while the treatment $\times$ PC2 interaction was non-significant (OR = 1.104, p = 0.353), consistent with the non-significant altitude interaction.

The interaction also remained robust when allowing seed quality variables to interact with treatment in the model. When treatment $\times$ seed weight and treatment $\times$ ripeness interactions were added to the primary model, the treatment $\times$ snowmelt interaction was essentially unchanged (OR = 0.60, 95% CI $\approx$ 0.47–0.77, p < 0.0001), while neither the treatment $\times$ seed weight (OR = 1.21, p = 0.100) nor the treatment $\times$ ripeness (OR = 0.83, p = 0.089) interaction was significant. This indicates that the decline in warming benefit across the snowmelt gradient is not an artefact of seed quality covarying with snowmelt, on either baseline germinability or the magnitude of the warming response.

To test whether the relative warming benefit declined across the snowmelt gradient, the observed germination rate ratio (heated/control) was regressed against plot snowmelt day across the nine plots with a defined ratio (Plot I excluded, as it had zero control germinations) (Figure 8a). The regression was significant (β = -0.032 per day, R^2 = 0.69, p = 0.006), confirming that the warming benefit declined in seeds from later-snowmelt plots. Ratios ranged from approximately 2.0–3.9 in early-snowmelt populations to 1.0 in the latest-snowmelt population, indicating no net warming benefit there, though these are based on few germination events per treatment and should be interpreted cautiously. This provides independent plot-level support for the treatment $\times$ snowmelt interaction from the primary model.

To examine the snowmelt relationship within each treatment, the germination model was refitted separately on the control and heated subsets. Neither showed a significant effect of snowmelt within a single treatment (control: OR = 1.47, 95% CI: 0.91–2.37, p = 0.119; heated: OR = 0.80, 95% CI: 0.47–1.34, p = 0.394), though the directions were consistent with the interaction: a weak positive trend under control and a negative trend under warming (Figure 8b). The control trend was heavily influenced by Plot I, which had zero control germinations. This indicates that with only ten plots, power is insufficient to detect the snowmelt gradient within a single treatment, and that the gradient in relative warming response is only reliably detectable through the contrast between treatments. Substantial variation in raw germination rates was nonetheless observed among plots within each treatment (0% to 34% under control and 4% to 69% under warming), reflecting between-population differences in germination capacity that are not specifically structured by snowmelt but are consistent with the large plot-level variance reported in the variance partitioning below.

When investigating the effects of mother-plant traits, the treatment $\times$ flowering day interaction was significant and negative (OR = 0.674, 95% CI: 0.547–0.831, p = 0.0002), indicating that later-flowering mothers responded less strongly to the warming treatment. However, when flowering day was centred within each plot, the interaction became non-significant (OR = 1.187, p = 0.101), confirming that the effect was driven entirely by between-plot differences in phenology, mirroring the snowmelt interaction. The treatment $\times$ cushion area interaction was non-significant (OR = 1.092, p = 0.411), while seed weight remained a significant positive predictor (OR = 1.508, p = 0.001).

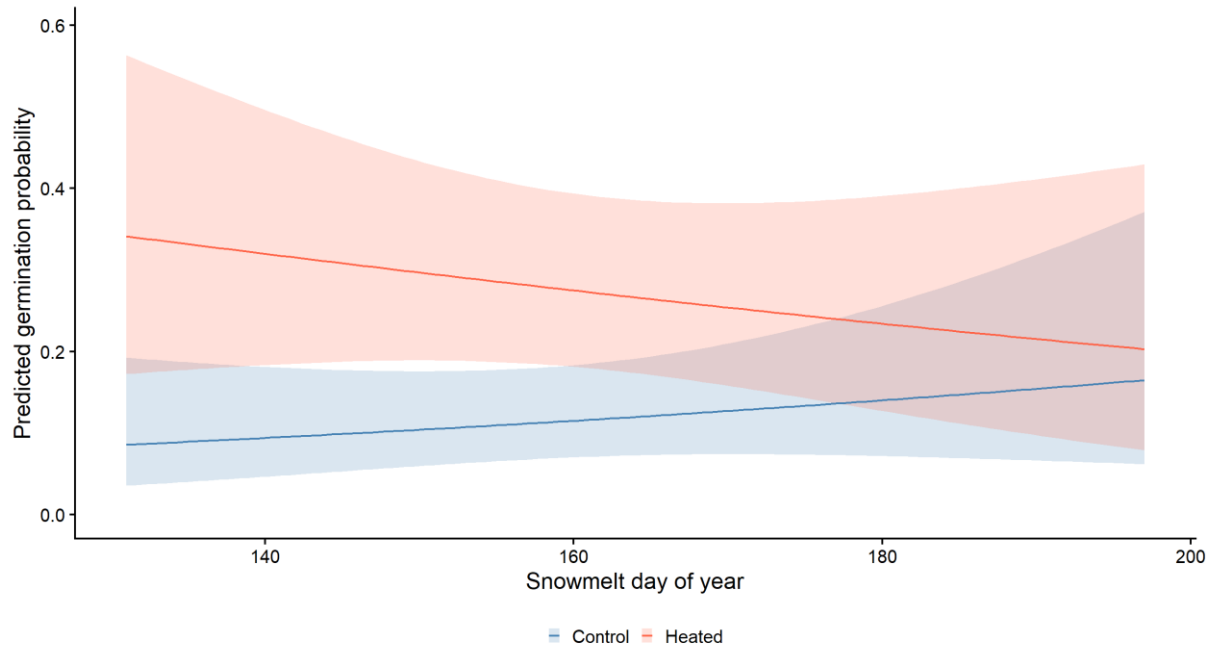


Figure 7: Model-predicted germination probability of *Silene acaulis* seedlings under control and heated treatments across the snowmelt gradient, from the primary microclimate model. The diverging lines reflect the significant treatment $\times$ snowmelt interaction, with the warming benefit declining towards later-snowmelt (harsher) plots. Shaded areas represent 95% confidence intervals. Predictions hold seed quality covariates and altitude at their mean values.

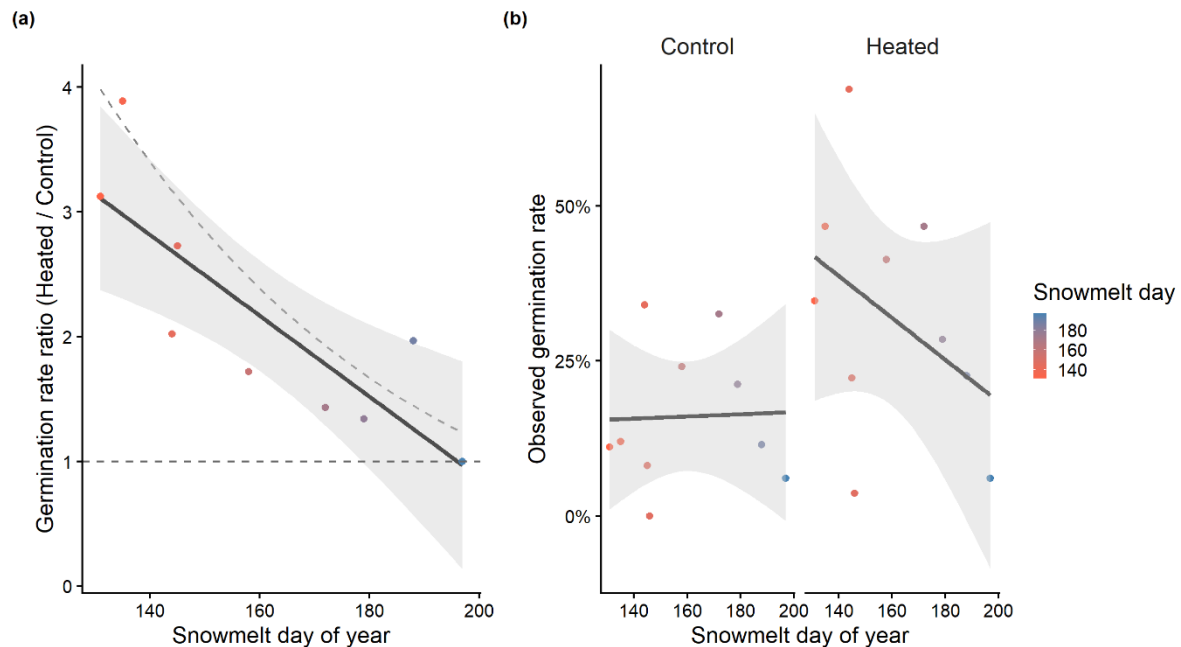


Figure 8: Observed germination rates of *Silene acaulis* seedlings across the snowmelt gradient. (a) Germination rate ratio (heated/control) plotted against plot snowmelt day, with a linear regression line and 95% confidence interval (solid line and shading) with the model-predicted ratio from the primary microclimate model overlaid (dashed curve), showing the expected decline in warming benefit with snowmelt day based on the estimated treatment $\times$ snowmelt interaction. The dashed horizontal line indicates a ratio of 1, representing no difference between treatments. Plot I is excluded due to zero germinations in the control treatment. (b) Raw observed germination rates plotted against snowmelt day separately for control and heated treatments, with OLS regression lines and 95% confidence intervals shown for visual reference only. Points are coloured by snowmelt day, with warmer colours indicating earlier snowmelt. All 10 plots are included.

Germination Timing

Germination timing advanced equally under warming treatment across all populations. Neither the treatment $\times$ snowmelt interaction ($\exp = 1.014$, $p = 0.831$) nor the treatment $\times$ altitude interaction ($\exp = 1.005$, $p = 0.922$) were significant. Both these results were consistent with those from the PCA models, with both the treatment $\times$ PC1 interaction ($\exp = 1.016$, $p = 0.802$), and the treatment $\times$ PC2 interaction ($\exp = 0.984$, $p = 0.780$) being non-significant. The snowmelt main effect was not significant ($\exp = 1.046$, $p = 0.606$); both treatments showed a weak positive trend in germination timing across the snowmelt gradient, but this cannot be confidently distinguished from random variation given the small number of plots. However, altitude had a significant positive main effect on germination timing ($\exp = 1.168$, 95% CI: 1.012–1.349, $p = 0.034$), with plants from higher-altitude plots germinating later regardless of treatment (Figure 9). The PCA model results were also consistent with this; PC2 had a significant positive main effect ($\exp = 1.166$, 95% CI: 1.001–1.357, $p = 0.048$), mirroring the altitude main effect. Ripeness score was also a significant predictor ($\exp = 0.867$, $p = 0.006$), with riper seeds germinating earlier (not significant in the seed trait model where collection date was also included, likely due to their moderate correlation).

Neither the treatment $\times$ cushion area interaction ($\exp = 1.058$, $p = 0.328$) nor the treatment $\times$ flowering day interaction ($\exp = 1.014$, $p = 0.811$) were significant for germination timing. The advancement of germination timing under warming was consistent across all mother-plant types. Ripeness score remained a significant predictor ($\exp = 0.872$, $p = 0.016$).

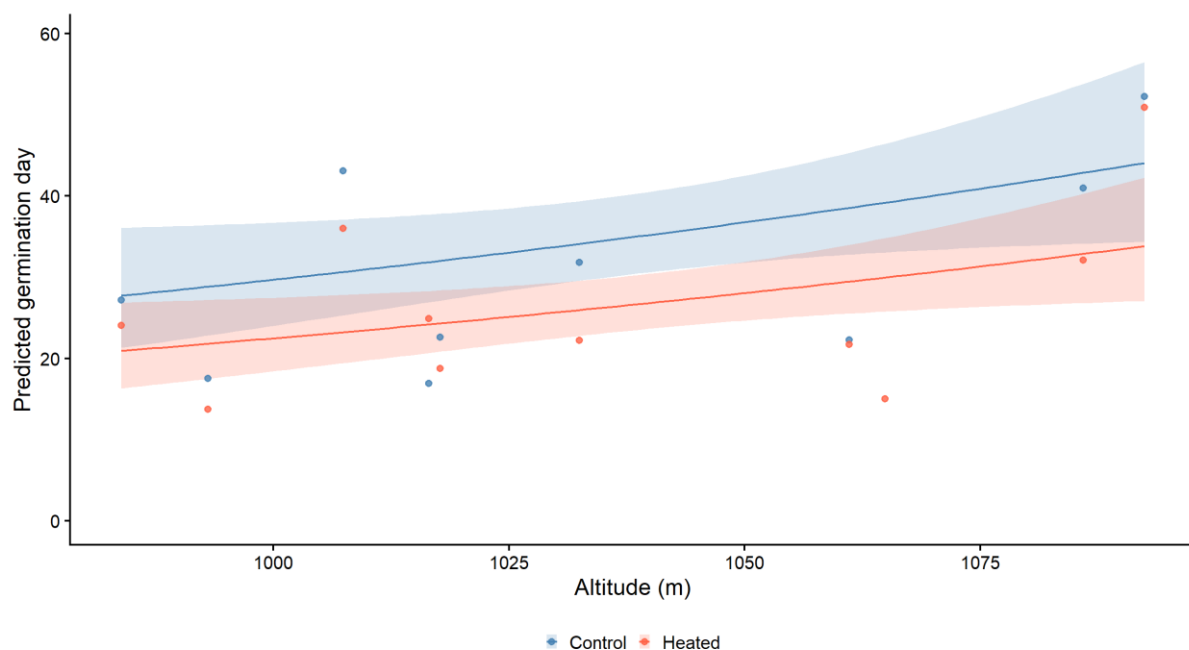


Figure 9: Predicted germination day of *Silene acaulis* seedlings under control and heated treatments across the altitude gradient, from the primary microclimate model. The parallel lines indicate a uniform advance in germination timing under warming with no treatment $\times$ altitude interaction, while the positive slope reflects a significant altitude main effect, with seeds from higher-altitude plots germinating later regardless of treatment. Lines show model predictions, holding seed quality covariates and snowmelt day at their mean values, and shaded areas represent 95% confidence intervals. Points show the observed mean germination day for each plot under each treatment (unadjusted), coloured by treatment.

Survival

The reduction in mortality risk under warming was broadly consistent across seeds from all populations (Figure 10). Neither the treatment $\times$ snowmelt interaction ($HR = 0.854$, $p = 0.226$) nor the treatment $\times$ altitude interaction ($HR = 0.956$, $p = 0.694$) were significant (Figure 11). Both interactions showed a slightly larger benefit for seeds from later-snowmelt or higher-altitude plots,

though the confidence intervals were wide and the trends were not statistically distinguishable from zero. The overall survival benefit of warming persisted across the full microclimate gradient (HR = 0.706, $p = 0.002$).

The reduction in mortality risk under warming was also consistent across all mother-plant types. Neither the treatment $\times$ cushion area interaction (HR = 1.054, $p = 0.654$) nor the treatment $\times$ flowering day interaction (HR = 0.864, $p = 0.229$) were significant. The survival benefit of warming was uniform regardless of mother-plant size or phenology (HR = 0.657, $p < 0.001$).

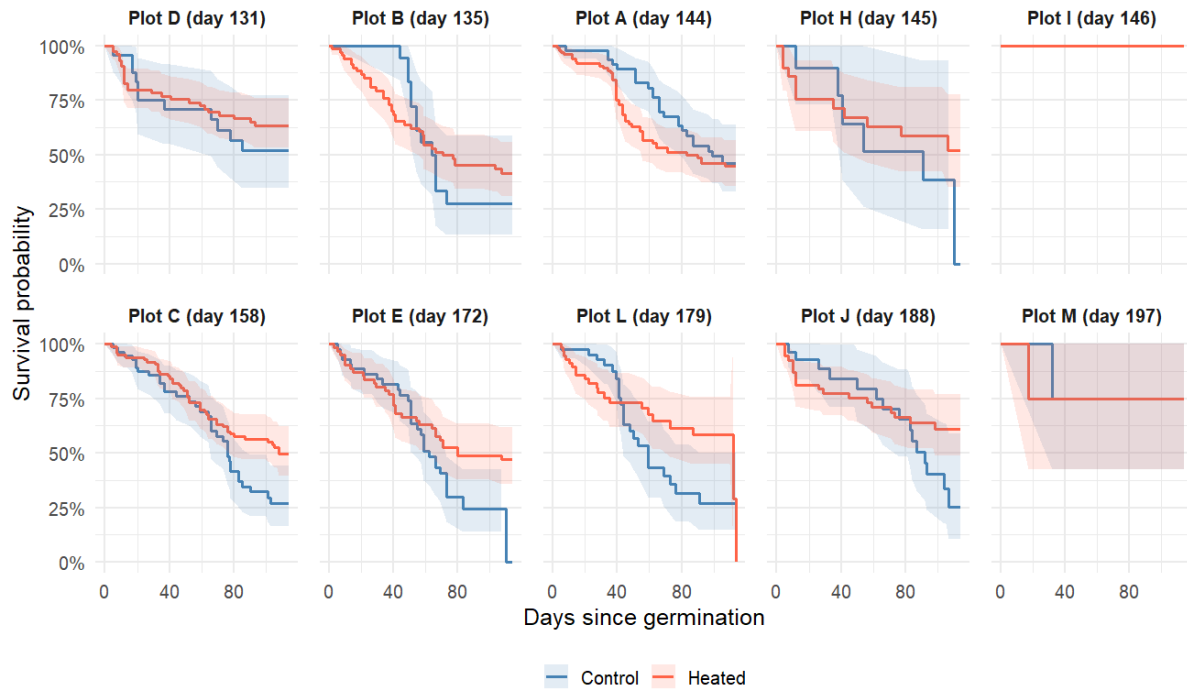


Figure 10: Kaplan-Meier survival curves for *Silene acaulis* seedlings under control and heated treatments for each population, ordered by snowmelt day. Shaded areas represent 95% confidence intervals. The survival advantage of warming is broadly consistent across populations, though the degree of crossover between treatments varies among plots. Plot I had very few germinations and should be interpreted cautiously. The number in parentheses indicates the snowmelt day of year for each population.

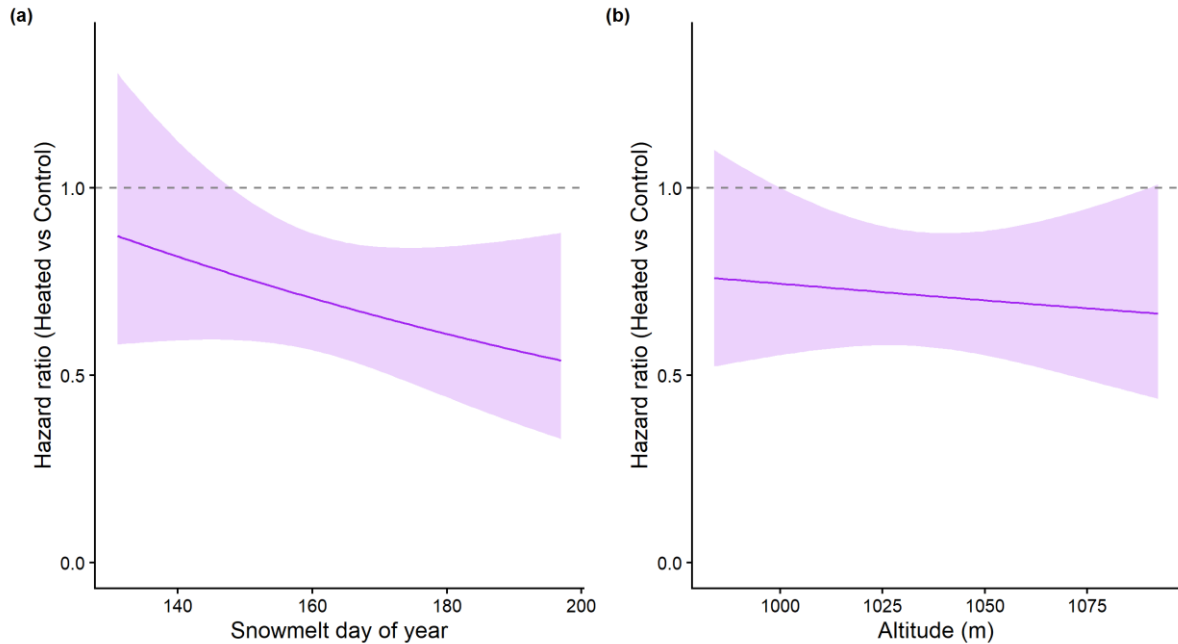


Figure 11: Predicted hazard ratio (heated relative to control) for *Silene acaulis* seedling mortality across snowmelt and altitude gradients. (a) Hazard ratio plotted against snowmelt day of year. (b) Hazard ratio plotted against altitude. The dashed horizontal line at 1 indicates equal mortality risk between treatments. Values below 1 indicate reduced mortality risk under warming. The broadly flat trends and wide confidence intervals confirm that the survival benefit of warming was approximately uniform across both microclimate gradients, with no significant treatment $\times$ microclimate interactions. Shaded areas represent 95% confidence intervals estimated via the delta method.

Growth

The size advantage of simulated warming was slightly greater in seeds from high altitude plots; the treatment $\times$ altitude interaction was significant ($\exp = 1.085$, 95% CI: 1.024–1.150, $p = 0.006$) (Figure 12). This however, although statistically significant, was small in magnitude and did not replicate in the PCA models; the treatment $\times$ PC2 interaction was non-significant ($\exp = 1.048$, $p = 0.096$), and thus this should be interpreted cautiously. The treatment $\times$ snowmelt interaction was not significant ($\exp = 1.030$, $p = 0.360$), nor was the snowmelt main effect ($\exp = 1.183$, $p = 0.135$). Heated seedlings remained substantially larger than those under control conditions ($\exp = 1.873$, $p < 2 \times 10^{-16}$), and the stronger deceleration of growth in the heated treatment was also retained (treatment $\times$ age² interaction: $\exp = 0.907$, $p < 0.0001$).

With regards to mother-plant characteristics, the treatment $\times$ flowering day interaction was significant in the main model ($\exp = 1.087$, 95% CI: 1.021–1.157, $p = 0.009$) (Figure 13a) but given that 90.7% of flowering day variation was between plots (ICC = 0.907), this largely reflects between-plot rather than individual-level differences. Neither the treatment $\times$ cushion area interaction ($\exp = 0.962$, $p = 0.206$) nor the cushion area main effect were significant.

When flowering day was centred within each plot and entered in raw days, the interaction remained significant ($\exp = 1.027$ per day, 95% CI: 1.008–1.046, $p = 0.004$) (Figure 13b); this indicates a genuine individual-level effect whereby the warming benefit was slightly larger for seedlings from later-flowering mothers within each plot. The negative main effect of within-plot flowering day ($\exp = 0.977$, $p = 0.044$) indicated that earlier-flowering mothers within a plot tended to produce slightly larger seedlings regardless of treatment. However, given the small within-plot variation in flowering day (median SD ≈ 2.8 days), the biological magnitude of both effects is modest.

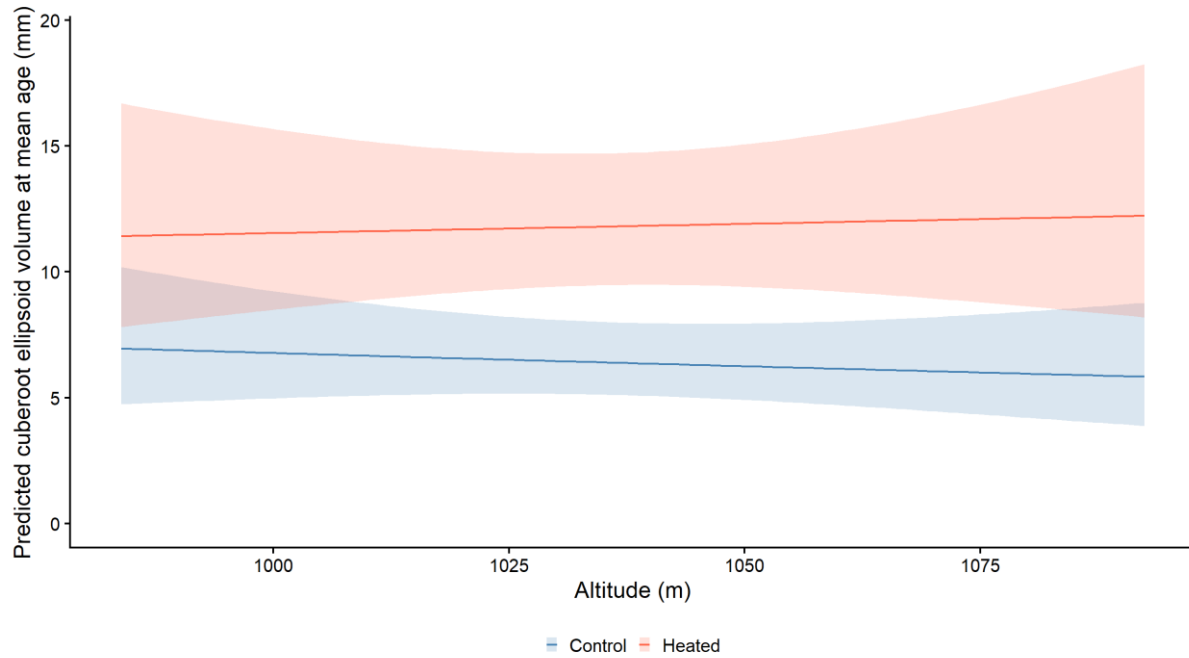


Figure 12: Predicted seedling size of *Silene acaulis* at mean age under control and heated treatments across the altitude gradient, from the primary microclimate model. Mean age is the average seedling age at measurement across all three measurement occasions; the lines therefore show predicted size for a seedling of that average age, holding the strong non-linear age effect constant, rather than size averaged over the whole growth period. The treatment $\times$ altitude interaction was significant but small in magnitude and did not replicate under the PCA sensitivity analysis, so it should be interpreted cautiously. Shaded areas represent 95% confidence intervals. Predictions hold seed quality covariates and snowmelt day at their mean values.

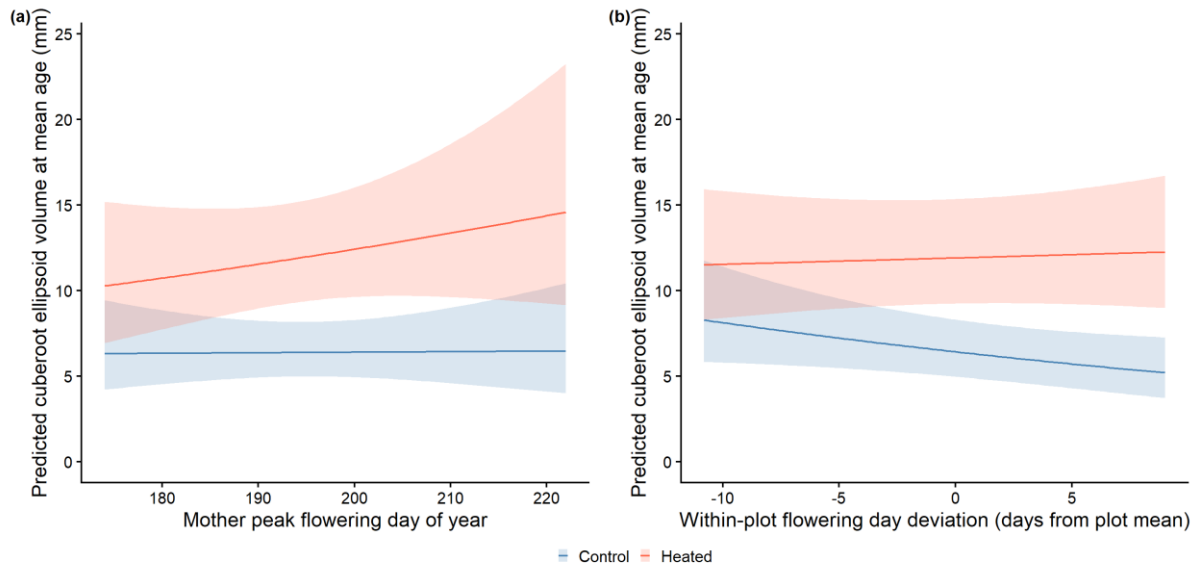


Figure 13: Predicted seedling size of *Silene acaulis* at mean age in relation to mother-plant flowering phenology under control and heated treatments. **(a)** Predictions from the main mother-plant model plotted against individual mother peak flowering day of year; because 90.7% of flowering-day variation is between plots ($ICC = 0.907$), this interaction largely reflects between-plot rather than individual-level differences. **(b)** Predictions from the within-plot centred model plotted against each mother-plant's deviation from its plot mean flowering day, isolating genuine individual-level maternal effects. The significant treatment $\times$ within-plot flowering day interaction indicates a modest warming benefit for seedlings from later-flowering mothers within a plot, though the biological magnitude is small given the narrow range of within-plot variation. As in Figure 12, mean age is the average seedling age at measurement, so the lines show predicted size at that representative age. Shaded areas represent 95% confidence intervals. Predictions hold seed quality covariates at their mean values.

Variance Partitioning

Variance partitioning revealed that the biological level at which variation is organised differs across response variables (Figure 14). These components were extracted from the treatment-level models, whose fixed effects were treatment, seed weight, seed ripeness and seed collection date (with seedling age additionally included for growth); the plot, mother-plant and seed collection group variances therefore represent variation remaining after these fixed effects are accounted for. Microclimate variables were not included in these models, so the plot-level variance reflects total between-plot differences including any association with snowmelt or altitude. For germination probability, plot and mother-plant each explained similar proportions of total variance (11.6% and 12.2% respectively), with seed collection group contributing 3.8% and residual variance dominating at 72.4%. For germination timing, mother-plant explained a slightly larger proportion (14.8%) than plot (6.1%), with seed collection group contributing 11.7% and residual 67.4%. For growth, the plot level dominated (37.0%), substantially exceeding the mother-plant contribution (9.7%), with residual variance at 53.3%. For survival, only the mother-plant random effect was available from the Cox model ($SD = 0.380$), indicating meaningful individual-level variation in survival risk beyond what seed quality and treatment explain.

Plot-level variance was substantially larger for growth (37.0%) than for germination probability (11.6%), indicating that population origin accounted for a greater proportion of variation in seedling size than in germination. The plot-level random effect variance from the within-treatment germination models was larger in the heated subset (0.468) than in the control subset (0.175), suggesting greater between-population divergence in germination under warming than under control conditions. Residual variance dominated all response variables, indicating that substantial variation remained unexplained at the individual seed or seedling level.

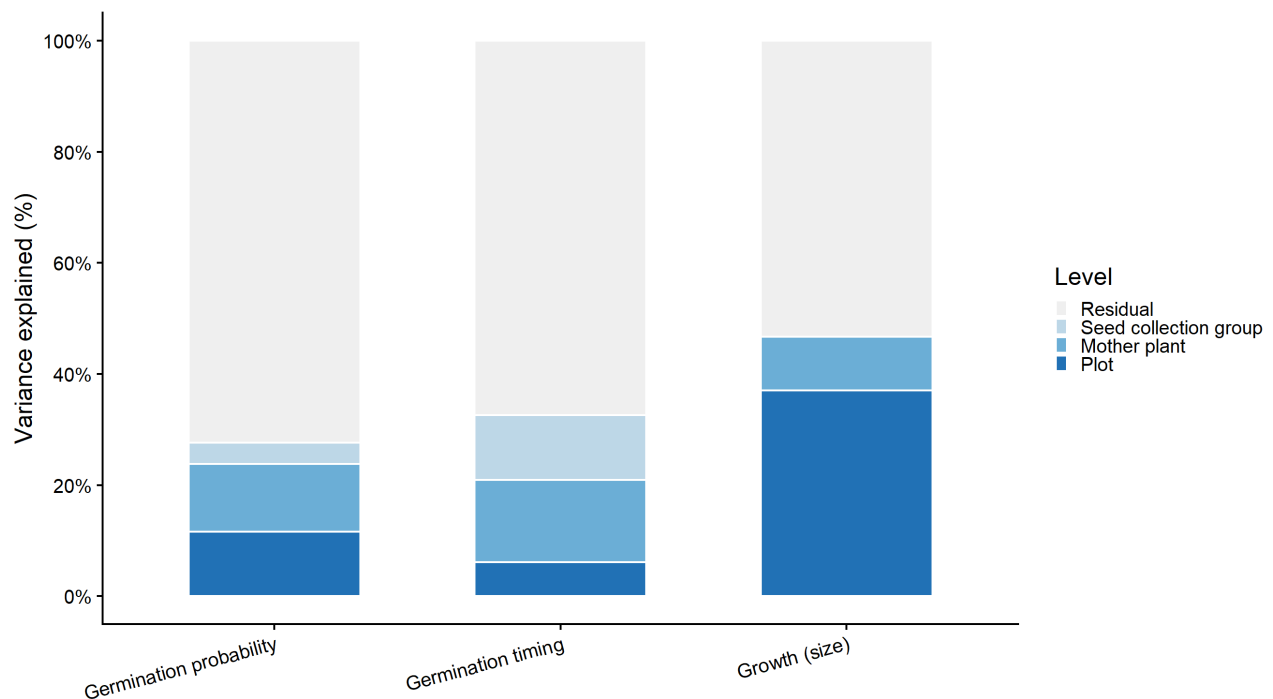


Figure 14: Variance partitioning of germination probability, germination timing, and seedling growth in *Silene acaulis*, based on random effect variances extracted from the main treatment models. Bars show the proportion of total variance attributable to each biological level: plot of origin, mother-plant, seed collection group, and residual individual-level variation. Survival is not shown as the Cox mixed-effects model provides only the mother-plant random effect variance, which is reported in the text. For germination probability, residual variance was approximated as $\pi^2/3$ following the standard approach for binomial GLMMs on the latent logit scale. For germination timing and growth, residual variance was taken as σ^2 from the Gamma GLMM dispersion estimate.

Reaction Norms

Plot-level reaction norms (Figure 15), typically used to visualise patterns of local adaptation, did not give any meaningful additional insight to the difference in warming response between plots from different snowmelt timings. However, what is apparent is the large between-population variation within each treatment. Since conditions were identical within each treatment, this divergence could indicate genetic variation between populations.

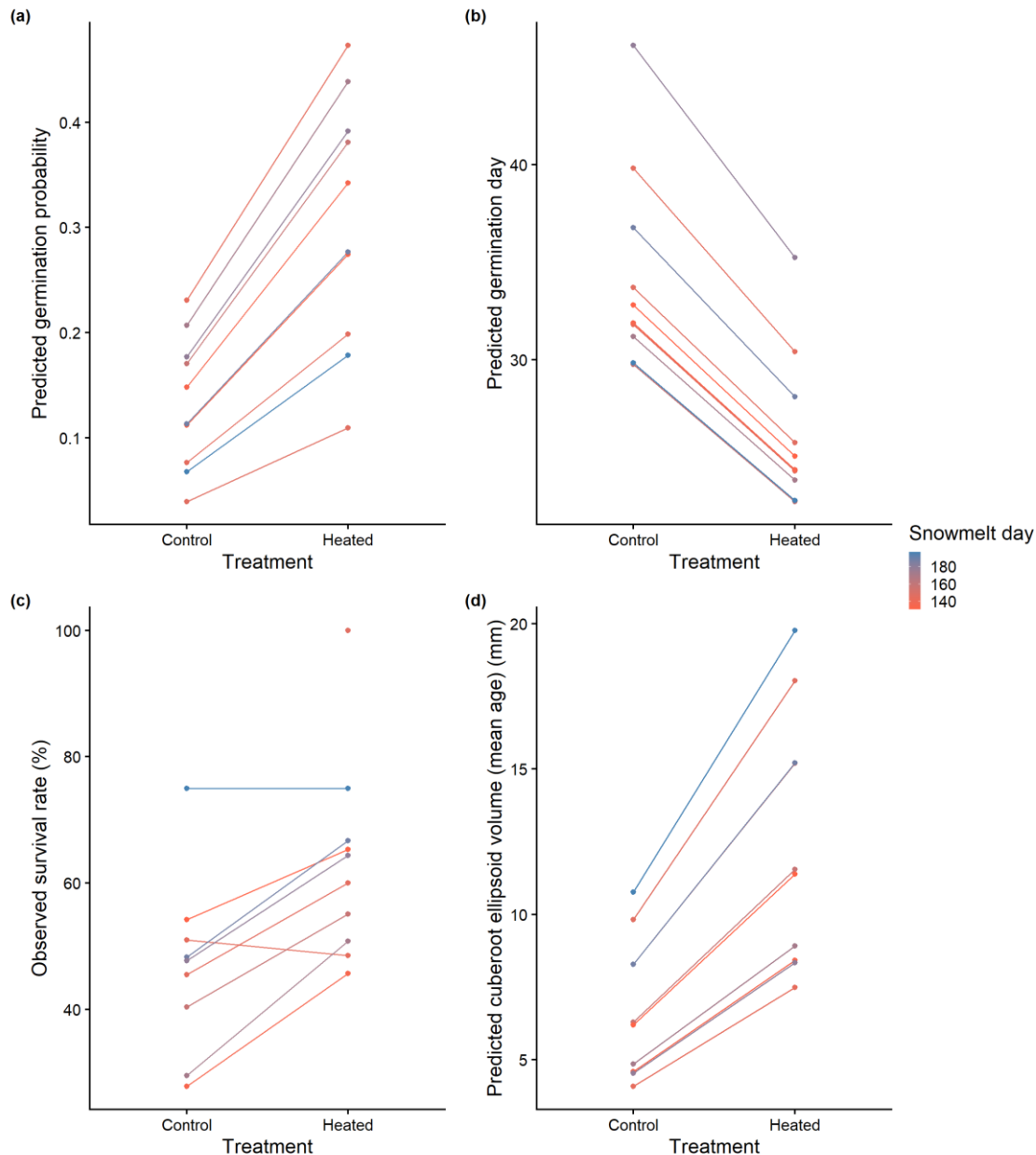


Figure 15: Plot-level reaction norms for *Silene acaulis* under control and heated treatments. (a) Predicted germination probability. (b) Predicted germination day. (c) Observed survival rate. (d) Predicted cuberoot ellipsoid volume at mean age. Each line represents one population, coloured by snowmelt day of year with warmer colours indicating earlier snowmelt. The between-population variation within each treatment reflects inherited differences in baseline values.

Summary

Seed weight was the only seed trait consistently associated with experimental outcomes, with heavier seeds showing higher germination probability and producing larger seedlings; ripeness score was a significant predictor of germination timing in the microclimate and mother-plant models, and collection date had no significant effects. Warming consistently promoted germination, accelerated germination timing, reduced seedling mortality, and increased seedling size across all populations, showing an overall positive effect of simulated warming on germination and early life in *Silene acaulis*. However, the magnitude of the germination response varied with population origin; seeds from harsher, later-snowmelt populations showed a smaller warming benefit, while germination timing, survival, and growth showed no significant variation across the snowmelt gradient. Plants from higher-altitude plots germinated later regardless of treatment, and the warming benefit on size was marginally greater at higher altitude, although this interaction was small and did not replicate in the PCA sensitivity analysis, and should therefore be interpreted cautiously. Plot-level origin explained substantially more variance in growth than in germination, indicating that population identity affects seedling size more strongly than it does the odds of germination.

Discussion

This study aimed to gain an insight into how *Silene acaulis* seeds from different populations across a microclimate gradient at Latnjajaure in Northern Sweden respond to simulated warming, and whether observed phenological differences between populations arise from inherent population differences such as genetic diversity or else are purely a response of phenotypic plasticity; this could help give a better understanding to how *S. acaulis* may respond to climate change. Warming was found to be broadly beneficial across all germination and early life factors measured; however, the response varied between seeds from different populations, and the degree of response was in some cases structured along the home-plot microclimate.

Question 1 – Effects of Warming on Early Life

The first part of the experiment aimed to observe the direct effects of warming on germination and early life. The hypothesised results were that warming would benefit germination rates and timing, and increase growth, but would lead to reduced survival rates due to increased environmental stress in the seedling stage. However, this hypothesis was only partially supported, as the experimental results showed that warming was beneficial for all early life factors including survival rates. Under warming, the odds of germination tripled, germination timing advanced by around a week, seedling sizes were greater than those under control conditions at all ages, and final survival rates were 13 percentage points higher than the control. Growth and mortality rates varied with time; this will be discussed further on.

The findings on the effect of warming on germination were to be expected, given that temperature is a strong germination cue, even in the Arctic (Billings & Mooney, 1968). The strength of temperature as driver of germination varies, with species having specific optimum temperature ranges in which germination is at its peak. Additionally, species have varying minimum and maximum temperatures, defining the entire thermal range germination may occur in. Temperature directly controls the speed of metabolic activity that triggers germination, with low temperatures resulting in slow or incomplete enzymatic processes, and high temperatures possibly leading to denaturation of the enzymes near the upper limit (Baskin & Baskin, 2000). When looking at thermal

requirements, temperature is typically calculated as an accumulation over several days, measured as growing degree days (GDD), which is a measure of accumulated warmth above a base temperature threshold over time. Germination typically requires that a species-specific sum be met; with higher temperatures under experimental conditions, GDD naturally accumulated faster, increasing germination rate and speed (Trudgill et al., 2000).

Milbau et al. (2009), conducted a similar study on the effects of temperature on Arctic species, including *Silene acaulis*. They found that a moderate warming of 2.5°C led to seeds germinating around 6 days earlier, mirroring the results from my experiment. Their warming treatment accelerated germination timing across species without significantly changing overall germination percentage, although for *S. acaulis* specifically an increase in germination was reported when warming was combined with reduced snow cover. The contrast with the much larger increase in germination probability observed here is likely attributable both to the larger temperature difference in my experiment (+4°C versus +2.5°C) and to differences in temperature regime, with the authors using a static day-night cycle, with increases every couple of months, representing changing growing season conditions.

The increased seedling size under warming was to be expected for similar reasons; the metabolic processes underlying cell division and elongation are likewise temperature-dependent. This is consistent with other studies; Alatalo & Little, (2014) found that warming resulted in faster growth, larger leaves, and longer stems in *S. acaulis*, and Baruah et al. (2017) demonstrated increased growth under warming in several other Arctic species.

Beyond absolute growth, the relative growth rate differed between the two treatments. Under warming conditions, the growth rate was initially faster than under control conditions but then began to plateau, with a slight decrease in size near the end, while the control seedlings had a mostly steady, albeit slower, growth rate, with only a slight indication of stabilisation. As the experiment ended before all seedlings had stopped growing or died, the exact reason for the decline under warming is difficult to resolve. A degree of deceleration is expected, as relative growth rate typically declines as seedlings increase in size, however it is hard to tell the extent of this effect. I suspect that this is very likely largely a result of heat stress, resulting in desiccation or dying of stems, which would reduce absolute growth given a decrease in living biomass, which in turn is reflected in the results given that dead or drying biomass was included in the size measurements. This affected many of the older, larger seedlings, at times observed to have significant portions of their biomass desiccated or dead; the extent of desiccation was observed to a much lower degree under control conditions. Vázquez-Ramírez & Venn (2025) found that warming had negative impacts on seedling establishment in alpine environments over a longer timeframe; this lends further weight to the heat stress argument, particularly when taking into account the relatively short timeframe of my experiment. However, data were not collected on seedling health or the extent of desiccation, so a definitive conclusion cannot be reached.

Contrary to initial prediction, survival rates turned out to be higher under warming than the control conditions. The initial assumption was based on the premise that heat stress from the elevated temperatures would increase mortality rates. Although this was not the case, as described for the growth rates, many seedlings did show signs of heat stress and drying under warming, as well as most seedling deaths appearing to be a result of drying (based on visual inspection of dead seedlings). This suggests that although warming was observed to be beneficial within the timeframe of the experiment, this may not necessarily be the case over longer periods of time; it is unclear whether these trends would persist, diminish, or reverse over a longer timeframe under the same conditions.

The reason for better survival under warming may have to do with the increase in seedling size; seedlings under control conditions grew at slower rates, ultimately resulting in smaller, weaker

seedlings, possibly making them more vulnerable to accumulated damage and stress. Larger seedlings can afford to lose more of their living biomass before succumbing to it. This may be tied to the age-dependence of mortality under control conditions; initially hazard rates were approximately even between treatments but diverged at around age 60 days, with control seedlings having a relatively large decrease in survival past that point.

While not including *S. acaulis*, another study by Milbau et al. (2017) on warming response of Arctic species, corresponded with the initial predictions, rather than matching the experimental findings. They found that heating, while increasing germination, also increased mortality, although it is suggested that this may not be a direct effect of temperature itself, but an interaction with other environmental variables. This study's findings likely diverged from mine due to the nature of the experimental set-up. Mine was carried out under controlled conditions, eliminating other potential stressors such as water availability or competition, while Milbau et al.'s experiment was carried out in the field, exposing seedlings to other unmeasured factors such as biotic interaction and climatic variability; these could have an unmeasured impact on survival. The authors also discuss how warming affects early life altogether, and suggest that the resultant early germination could reduce mortality, with the reasoning that "*seedlings grown under warmer conditions, thereby reaching higher biomass, are accordingly expected to have higher survival rates*". This reasoning is similar to my proposition that larger seedlings were able to tolerate larger levels of stress, leading to the observed results.

Question 2 – Population Differentiation and Local Adaptation

The second, and more novel, aim of this experiment was to assess whether there appeared to be a degree of population-specific genetic differentiation and site-specific microclimate adaptation in the *Silene acaulis* populations at Latnjajaure. The predicted outcome was that under experimental warming, seeds from early-snowmelt plots would outperform those from late-snowmelt plots. The assumption was that each population is best adapted to their own microclimate, with between-population differences in thermal optima. The experimental outcomes supported the hypothesis, but cannot be taken as conclusive evidence of local adaptation to microclimate conditions.

In the experimental set-up, all conditions were kept constant between treatments except temperature. Each chamber had the same number of seeds from each seed sample, and seed traits and the hierarchical data structure are controlled for in the models. Therefore, any variation in response between populations within a treatment is unlikely to be a plastic response to current conditions since all seeds within a treatment were grown in an identical environment; instead, variation most likely reflects inherent differences between the seed sources, with the difference in relative response between treatments pointing in the same direction. These differences could be genetic in origin, but as seeds were collected directly from mother-plants in the field, they could also reflect maternal environmental effects carried over from the parent plant rather than the seedling's own plastic response; this distinction is developed further on, after the discussion of the results.

Snowmelt timing was the main microclimate variable in question, given that this was correlated with population flowering phenology, the main observable difference between populations. Altitude was chosen as the secondary microclimate variable given that it was the only one from those collected that was not shown to have a strong correlation with snowmelt timing, and thus incorporating another aspect of the population microclimate. Although flowering phenology differences served as the inspiration for this study, flowering itself was not assessed, as the timeframe was too short to observe meaningful flowering. It also follows that the experiment cannot determine whether the field differences in flowering phenology are themselves plastic or genetic; growing all seeds in common conditions minimises any plastic response to the home microclimate, so the design reveals whether population differences persist independently of the

home environment rather than quantifying the plastic component of the original field differences. Instead, potential population differences were investigated through early-life factors (germination probability and timing, survival, and size), which fit better into the available timeframe and are easily observable. The initial prediction failed to specify whether the differences would be solely observable within the warming treatment, or in the relative degree of change between the two treatments. Out of the four experimental variables, only germination probability was significantly correlated with snowmelt timing, while germination timing and growth showed a modest yet statistically significant correlation with altitude. The lack of significant results may be related to the small sample size; with only 10 plots represented this may have limited the statistical power of my models.

The spread of plot-level results within each treatment did not appear to follow the snowmelt gradient to any significant degree. This is observable within the plotted reaction norms. What is apparent, is that in many instances there still seems to be a wide spread between populations. This could be understood as a potential indicator for population-level differentiation, but cannot be inferred as adaptation. The results from the variance partitioning further hint at potential plot-level differentiation. The size of seedlings was heavily influenced by plot provenance; this was not observed to any large degree for the other result variables, although all showed a degree of plot-level variance. The significance of growth here is more telling than germination effects; germination is strongly influenced by ambient conditions and metabolic activity (Baskin & Baskin, 2000), so within-treatment variation in germination may reflect environmental noise as much as any underlying signal. Because seed weight and ripeness are included in the growth models, the large plot-variance in seedling size is estimated after accounting for seed quality, making it a more informative indicator of underlying differentiation. Early seedling size is nonetheless partly determined by seed provisioning, so this variance is not entirely independent of the maternal environment.

The relationship between snowmelt and the warming response of germination provides the strongest indication of microclimate-specific differentiation. The relative response to warming was significantly structured along the snowmelt timing gradient, whereby seeds from populations within earlier-snowmelt plots showed a significantly stronger response to warming than those from later-snowmelt plots. Seed provisioning varied steeply across this gradient, with mean seed weight and ripeness both declining with later snowmelt, consistent with the shorter growing season for later-snowmelt populations constraining seed maturation. However, the interaction was not an artefact of provisioning; it remained large and highly significant when seed weight and ripeness were allowed to interact with treatment in the model, and neither interaction was significant. This indicates that the snowmelt structuring of the warming response is not driven by measured differences in seed quality, and points to genuine population-level variation in the germination response (Kawecki & Ebert, 2004), although this cannot be definitively attributed to genetic differences.

Beyond snowmelt, altitude was also found to have a significant, albeit modest, effect. Germination timing was correlated with altitude regardless of treatment, after controlling for seed traits; seeds from higher altitude plots consistently germinated later than those from lower elevations, consistent with altitude-structured differentiation in germination timing (Halbritter et al., 2018). The altitude effects are also less vulnerable to the seed provisioning effects observed for snowmelt timing. Seed weight and ripeness score did not show correlations with altitude, strengthening the claim that the results reflect genuine between-population differentiation that cannot be attributed to provisioning differences. A weak but statistically significant trend was also observed for growth, with higher altitude plots having a slightly larger growth benefit from warming, although this may not be biologically meaningful given how weak the trend was. Based on the PCA and multicollinearity

checks, altitude and snowmelt are not strongly correlated, indicating that the effects of altitude are independent from those of snowmelt, and likely cannot be attributed to one another, strengthening the case for treating altitude as a separate axis of differentiation.

Altogether, the data point to a degree of differentiation between the seeds of each population, with the strongest signal being the trend in germination response to warming with snowmelt timing. This is consistent with variation in germination cues, in both the required strength of thermal accumulation, as well as sensitivity to, and requirement for, other germination cues. Specifically, these results may suggest that seeds from earlier snowmelt plots have a higher germination temperature threshold than those from later snowmelt plots. This makes biological sense, as in the early weeks of the growing season the weather is still unpredictable and frost is not uncommon. This would potentially punish early germinating seeds; a higher temperature threshold for germination prevents this from happening by requiring a larger accumulation of heat, increasing the chances of germinating under ideal conditions (Fernández-Pascual et al., 2021). The relationship between altitude and germination timing likely follows a similar logic, as higher altitude sites are typically colder, have shorter growing seasons, and experience more frequent frost and freeze-thaw events (Körner, 2003), particularly in the early-season, conditions under which a more conservative, delayed germination would likewise be favoured.

Under control conditions, however, germination did not meaningfully increase for seeds from late-snowmelt plots once seed traits were accounted for, which suggests additional mechanisms beyond bet-hedging against frost. It may be the case that the experimental conditions did not reproduce all of the dormancy-breaking cues that would typically be experienced. The chambers ran a fixed repeating cycle, with no simulated seasonal progression, as well as all seeds receiving the same stratification technique, which may not have been sufficient to replicate the colder deep snowpack conditions in later-snowmelt areas. Seeds from later-melting plots may therefore require longer or differently structured stratification methods to release the full dormancy and optimise germination success (Bernareggi et al., 2016; Mondoni et al., 2012), opening up the suggestion that germination under the imposed experimental conditions may underrepresent the true field potential.

Mother-plant provenance seemed to have little effect overall, but a few patterns stood out. Within plots, mother-plant flowering time showed a degree of influence on growth, with early flowering mothers tending to produce larger seedlings. Seed weight was also a significant predictor of the results, but this is to be expected and cannot truly be distinguished from ripeness. The results of variance partitioning also showed a degree of variation attributed to the mother although this was not to any substantial degree. The small degree of influence attributed to mother-plants, especially compared to the degree associated with plot for growth, may indicate that the individual mothers within each plot are more similar to each other than they are to those from other plots; this further strengthens the idea that plots are distinctly differentiated, whether or not this is attributable to microclimate adaptation.

Whether this observed differentiation reflects underlying genetic variation or is a product of the maternal environment cannot be directly resolved, since seeds were collected in the field and a single generation cannot separate the two. However, there is some evidence suggesting that the observed results are not purely a result of maternal effects, and that it is possible that a genetic component may be at play here. Firstly, differences in seed provisioning were measured and controlled for, with seed weight and ripeness included in both models, and the result remained significant when the seed traits were allowed to interact with treatment in the model. Neither interaction was significant, for the most part ruling out provisioning effects on both the baseline results and the response to warming. Secondly, the main correlation with snowmelt is in the response to warming rather than in the baseline germination results, with no snowmelt trend observed within the control. Maternal provisioning effects would more naturally shift baseline

germination probability rather than the shape of the temperature response, and the provisioning aspect for this was specifically tested for and not found. Third, genetic differentiation along microclimate and elevation gradients is documented in alpine plants (Halbritter et al., 2018; Kawecki & Ebert, 2004), and germination-specific local adaptation has been suggested in the congener *Silene elisabethae* (Mondoni et al., 2009), so a genetic basis is plausible when taking into account previous studies. However, a purely maternal explanation cannot be excluded, as the maternal environment can influence seed dormancy and germination requirements in ways not captured through the assessed seed traits (Bernareggi et al., 2016).

A study by Gehring and Delph (1999) serves as the closest available comparison, having examined fine-scale genetic structure in *S. acaulis* on Pennsylvania Mountain in central Colorado. The authors propose that gene flow operates on two contrasting spatial scales: limited seed dispersal produces patches that act as family groups, internally related but differentiated from one another, at a scale comparable to the plots used here, while long-distance pollen dispersal homogenises larger-scale differentiation over a distance of a few kilometres. This offers a mechanism for the differentiation observed in the present study; if seed dispersal is restricted, the plots may behave as semi-distinct family groups, consistent with the suggestion that mothers within a plot are more similar to each other than to those from different plots. They observed that even patches situated a few metres away from each other could genetically differ, supporting the idea that the between-plot variation in my study could potentially arise from fine-scale genetic structure; although, this between-patch differentiation was pronounced mainly in ecologically marginal, low density populations, and was attributed partly to genetic drift. This raises the possibility that some of the observed differentiation that was not structured along microclimate gradients is neutral rather than adaptive. The authors also documented allele frequencies that followed an altitudinal gradient, which they attributed to natural selection rather than drift, showing that selection can maintain genetic clines along an environmental gradient even where gene flow is high. Whether this differentiation found in my study is ultimately genetic or maternal remains open. The data are compatible with both the selection-driven and drift-driven patterns documented in the species, and resolving its basis would require a further generation grown under common conditions.

Environmental Implications

Although the results seem to show that climate change could be broadly beneficial for *S. acaulis* recruitment, it is important to view this study in its own context, a controlled experiment isolating the effect of heating over a very short timeframe relative to typical *Silene acaulis* lifetimes. Although warming was overall beneficial in the present study, several seedlings under heated treatment were observed to be under significant heat stress. The observed effects of heating on *Silene acaulis* in the long-term are nuanced, and depend on the degree of warming and timescale. Alatalo & Little (2014) found that experimental warming in the short and medium term was broadly positive for *S. acaulis*, increasing stem elongation and leaf length, but cover subsequently declined in the longer terms when paired with increased nutrient availability. Rai et al. (2025) found that in mature *S. acaulis* plants, extreme heat events led to discolouration and sometimes dieback, an effect exacerbated by the cushion structure's tendency to trap heat. Bonanomi et al. (2023), also reported adverse effects of extreme heat events on mature plants, recording widespread dieback in the *S. acaulis* populations in the Apennines after the 2022 summer heatwave. Together, these findings suggest that the short-term benefits of warming may not persist over longer timescales, with long-term heating and extreme heat events posing significant threats to established populations.

Beyond direct heat stress, climate change is expected to drive a range of interconnected environmental changes in Arctic and alpine ecosystems, including altered precipitation regimes, increased nutrient availability from permafrost thaw and accelerated decomposition, and vegetation shifts such as shrubification and the northward migration of boreal species (Myers-Smith et al.,

2011; Schuur et al., 2015; Baruah et al., 2017). Villellas et al. (2016) observed that peripheral *S. acaulis* populations, near the edge of their typical habitats, showed reduced recruitment and lower population growth rates under ecologically marginal conditions of increased temperature and competition, conditions which are likely to become more widespread as warming progresses. Furthermore, climate change will likely result in longer and earlier growing seasons, with *Silene acaulis* phenology changing in response; this could lead to a temporal mismatch with pollinators, which if severe enough, could negatively impact seed production, further reducing recruitment (Pavolotskaia, 2024). Given its role as a foundation species, declines in *S. acaulis* populations would likely have cascading effects on the communities it supports (Molenda et al., 2012; Reid & Lortie, 2012).

The population-level differentiation suggested by this study may have nuanced implications for *Silene acaulis* under climate change. On one hand, if populations are differentiated, some may be better suited to a warming climate than others, potentially acting as refugia and sources of recruitment for areas where local populations are less well adapted. On the other hand, if populations are too narrowly adapted to their specific microclimate, this specificity could limit the ability to repopulate extirpated populations or colonise new areas to compensate for population losses. DeMarche et al. (2018) demonstrated this tension directly in *S. acaulis*, showing that both life-history plasticity and local adaptation shape range-wide responses to warming, such that strong local adaptation could drive declines in populations across the range rather than only at the warm range edge; by extension, locally adapted, cold-climate populations may struggle once warming exceeds their specific thermal tolerance. Compounding this, the slow generation turnover of *S. acaulis* (Morris & Doak, 1998; Cotto et al., 2017) limits the rate at which populations can evolve in response to rapidly changing conditions, making the existing degree of phenotypic plasticity a crucial buffer (Lande, 2009; Nicotra et al., 2010). Although the degree of gene-flow between populations at Latnjajaure was not established, Gehring and Delph (1999) demonstrated that gene flow can be high in *S. acaulis*; while this can homogenise populations and limit the retention of narrow local adaptation, it could also supply alleles better suited to changing conditions. Whether the degree of phenotypic plasticity present in *Silene acaulis* populations is sufficient to counter these potential effects remains unknown; multi-treatment warming experiments across populations spanning the full microclimate gradient would be needed to resolve this.

Limitations and Further Questions

Although the evidence points in the direction that populations differ, whether this differentiation is genetic or reflects maternal environmental effects remains unresolved, as discussed above. Even if the differences are genetic, the extent to which they represent adaptive rather than neutral divergence cannot be determined from this study alone. Furthermore, the observed field phenotypic variation is restricted primarily to flowering phenology, and it remains an assumption that the factors underlying these differences are the same as those influencing the germination and early survival responses measured here.

These results also reflect a single species from a single site and cannot be taken as representative for all Arctic species or areas, although they do shed light on the possible extent of fine-scale variation within Arctic populations. Additionally, seeds were collected from plants with unknown pollen provenance, meaning a portion of the observed variance may derive from genetic contributions of external populations. Given that additional *S. acaulis* populations exist beyond those sampled, it is likely that the microclimate gradient at Latnjajaure forms part of a broader ecotype gradient. As discussed above, with the potentially high gene flow characteristic of this species, nearby plots are more likely to be genetically blended than kept distinct, so the differentiation detected here probably understates rather than exaggerates the true degree of population difference on a larger scale. Seeds were also collected in a single year, and interannual

variation in seed quality and maternal environment may influence germination and early growth in ways that were not captured here.

It is also important to note a specific caveat in the experiment; only two chambers were used, one for treatment and one as the control. So theoretically, the effects attributed to the difference in temperature cannot be completely distinguished from any potential uncontrolled effect from the differences between the growth chambers themselves. Although further replicates were not possible due to constraints in lab space, extra precautions were taken to ensure as fair of a comparison as possible. The conditions in the chambers are constantly measured and were monitored frequently for any discrepancies. Additionally, before the experiment began, the chambers were monitored for a week using a separate set of data loggers. So with this in mind, there is a high degree of confidence that any differences between treatments are truly a result of temperature differences.

Further studies on this topic would benefit from multi-year data collection under controlled conditions to examine effects on flowering phenology directly, from sampling seeds from multiple years and a wider range of populations across the Arctic, and ideally from raising a generation under common conditions before testing, which would allow genetic differentiation to be distinguished from maternal effects. Expanding the number of warming treatments to identify population-specific thermal optima would also help resolve the degree of site-specific adaptation suggested by this study. Incorporating additional environmental variables may also help account for the large proportion of unexplained variance observed.

Conclusions

In conclusion, although warming was broadly beneficial to germination and early life of *Silene acaulis*, the degree of response varied between populations and was in some cases structured along the parent-plot microclimate gradient. These variations likely indicate that observed phenological differences in the field are, at least in part, attributable to genuine differences between populations, with evidence pointing towards a degree of microclimate-specific differentiation that is consistent with a genetic contribution, although whether it is genetic or reflects maternal effects cannot be fully resolved here. While these findings are limited to early life stages under controlled conditions, they provide a new insight into the fine-scale intraspecific variation in climate responses, and highlight the importance of considering intraspecific variation when predicting how Arctic species will respond to climate change, particularly for foundation species such as *S. acaulis*, whose population health has cascading consequences for the broader communities they support.

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Appendix 1 – Popular Science Summary

Understanding the impacts of climate change on the Arctic plant species, the Moss Champion

The effects of climate change are becoming more apparent around us, and nowhere are these changes happening as fast as they are in the Arctic which has warmed four times faster than the rest of the Earth. In my study, I wanted to understand how the plants that inhabit this threatened landscape could adapt to climate change.

One of the most iconic Arctic species is *Silene acaulis*, commonly known as the Moss Champion. This attractive plant grows in dense cushion-like forms, allowing it to survive the long, harsh, Arctic winter underneath the snow. It has small pink flowers that appear once the snow covering them melts, producing hundreds of seeds. Since the growing season in the Arctic is restricted to summer, it must form seeds quickly, which spend the winter buried under the snow, sprouting once conditions become favourable again. The success of germination and survival is a crucial aspect for the long-term survival of populations of *S. acaulis*. It also grows in a wide range of conditions, which vary even within the same site. My aim was to investigate how it may respond to climate change, and whether seeds from plants that grew in different conditions might react differently. This could help understand what the future of this species might look like.



Latnjajaure site, Northern Sweden

The way I came up with the answers for these uncertainties was by growing Moss Champion seedlings and observing any patterns. I first went to Latnjajaure, within the Swedish Arctic, where I collected seeds from ten populations growing at differing altitudes and snowmelt times. The seeds were then sown in two climate-controlled growth chambers. One of these chambers was set to represent the conditions found in Latnjajaure, while the other was set 4°C warmer to represent future conditions under climate change. They were monitored regularly and information on their germination, survival, and size was collected. These were then compared between the two treatments, as well as looking at how the conditions of their parent populations affected the results.



Silene acaulis, Moss Champion

What I found was that warming was actually beneficial; however, this does not necessarily mean that climate change itself is beneficial for this species. In my experiment warming was tested alone, but it has been found that when combined with other factors associated with climate change, warming has a negative impact in the long run. Additionally, I observed differences in germination between populations from different home conditions. Seeds from populations that experience earlier snowmelt showed a stronger germination response to warming, while seeds from higher elevations showed a delay in their germination timing.

These differences are thought to be of benefit to the particular environment they are from, preventing them from growing too early or under conditions that would not be favourable. These may be due to different genetics between populations, but may also be from the way the mother-plants reacted with the environment they grew in. Either way, this gives us some insight into how the Moss Champion may react to climate change, and whether some populations may be better adapted to resist a changing climate than others.



Moss Champion seedlings in the growth chamber



Moss Champion seedlings flowering

Appendix 2 – Seeds Used

seed collection id	seeds per treatment
A1_N	6
A1_M	6
A2_N	3
A2_M	3
A3_N	15
A3_M	15
A5_N	18
A24_N	24
A24_M	24
A26_N	30
B8_N	15
B8_M	15
B13_N	18
B13_M	18
B19_N	18
B22_N	18
B22_M	18
B25_N	30
C4_N	30
C4_M	30
C6_N	30
C6_M	30
C11_N	21
C12_N	30
C12_M	30
C21_N	18
C21_M	18
D3_N	24
D3_M	24
D4_N	18
D4_M	18
D6_N	24
D17_N	30
D17_M	30
D18_N	18
D19_N	30
E3_N	18
E6_N	15
E8_N	9
E10_N	9
E11_N	6

E17_N	9
E18_N	9
E23_N	30
E24_N	30
H7_N	12
H7_M	12
H10_N	12
H10_M	12
H11_N	15
H11_M	15
H16_N	24
H16_M	24
H20_N	9
I1_N	6
I15_N	6
I15_M	6
I19_N	3
I21_N	6
J2_N	15
J3_N	30
J4_N	18
J6_N	30
J10_N	30
J12_N	9
J16_N	30
J18_N	30
J20_N	30
J23_N	30
L1_N	12
L5_N	15
L9_N	24
L10_N	12
L15_N	12
L20_N	15
L22_N	27
L23_N	30
L24_N	30
L25_N	30
M4_N	12
M6_N	12
M15_N	12
M21_N	30

plot	total seeds per treatment	number of seed collection groups	number of individual mother-plants
A	144	10	6
B	150	8	5
C	237	9	5
D	216	9	6
E	135	9	9
H	135	9	5
I	27	5	4
J	252	10	10
L	207	10	10
M	66	4	4

Total seeds used for both treatments	3138
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Appendix 3 – Growth Chamber Conditions

hour	Control Room							Heated Room							Both rooms		
	Temperature (°C)							Temperature (°C)							Light Intensity	Humidity	CO ²
	M	T	W	T	F	S	S	M	T	W	T	F	S	S			
0	6	6	7	7	10	10	7	10	10	11	11	14	14	11	10	70	420
1	6	6	7	7	9	9	7	10	10	11	11	13	13	11	30	70	420
2	6	6	7	7	9	9	7	10	10	11	11	13	13	11	40	70	420
3	6	6	7	7	9	9	7	10	10	11	11	13	13	11	50	70	420
4	6	6	7	7	9	9	7	10	10	11	11	13	13	11	50	70	420
5	6	6	7	7	9	9	7	10	10	11	11	13	13	11	60	70	420
6	6	6	7	7	10	10	7	10	10	11	11	14	14	11	65	70	420
7	6	6	8	8	10	10	8	10	10	12	12	14	14	12	65	70	420
8	6	6	8	8	11	11	8	10	10	12	12	15	15	12	65	70	420
9	6	6	9	9	12	12	9	10	10	13	13	16	16	13	65	70	420
10	6	6	10	10	12	12	10	10	10	14	14	16	16	14	65	60	420
11	6	6	10	10	13	13	10	10	10	14	14	17	17	14	65	60	420
12	7	7	10	10	13	13	10	11	11	14	14	17	17	14	70	60	420
13	7	7	10	10	13	13	10	11	11	14	14	17	17	14	70	60	420
14	7	7	10	10	14	14	10	11	11	14	14	18	18	14	70	60	420
15	7	7	10	10	14	14	10	11	11	14	14	18	18	14	70	60	420
16	7	7	10	10	13	13	10	11	11	14	14	17	17	14	65	60	420
17	7	7	10	10	13	13	10	11	11	14	14	17	17	14	65	60	420
18	7	7	10	10	13	13	10	11	11	14	14	17	17	14	65	70	420
19	6	6	9	9	12	12	9	10	10	13	13	16	16	13	60	70	420
20	6	6	9	9	12	12	9	10	10	13	13	16	16	13	50	70	420
21	6	6	9	9	11	11	9	10	10	13	13	15	15	13	40	70	420
22	6	6	8	8	11	11	8	10	10	12	12	15	15	12	30	70	420
23	6	6	8	8	10	10	8	10	10	12	12	14	14	12	20	70	420

Appendix 4 – Plot Environmental Variables

ID	A	B	C	D	E	H	I	J	L	M
Latitude	68.36193	68.35684	68.36352	68.35497	68.35354	68.3585	68.35802	68.35303	68.35126	68.35937
Longitude	18.4951	18.49895	18.49408	18.50426	18.49613	18.49675	18.50023	18.50778	18.50857	18.49553
Altitude	1017.7	1016.5	1032.5	1061.1	983.9	1007.4	1064.9	1085.9	1092.4	993.1
Snowmelt day 2025	144	135	158	131	172	145	146	188	179	197
Peak flowering day 2025	182	185	194	179	200	184	184	206	207	221
GDD 2025	0492.8	0561.4	0462.2	0541.1	0350.7	0503.0	0459.6	0261.3	0299.4	0186.8
GDD 2024	1020.1	1067.0	1024.2	1078.3	0988.6	1036.2	0933.6	0824.5	0947.8	0926.2
Soil moisture 2025 (arbitrary units)	1798.0	2695.6	1796.8	1014.8	2000.1	2021.9	1648.3	2581.8	N/A	1638.2

Appendix 5 – Models

Germination probability, seed trait baseline						
Model syntax	glmer(formula = germinated_bin ~ weight_scaled + ripeness_scaled + doy_scaled + (1 plot_id) + (1 full_mother_plant_id) + (1 seed_id), data = data, family = binomial)					
R package	lme4					
Model output		Estimate	Std.Error	z	value	Pr(> z)
	(Intercept)	-1.3941	0.2563	-5.439	5.35e-08	***
	weight_scaled	0.3868	0.1181	3.277	0.00105	**
	ripeness_scaled	0.0785	0.2456	0.320		0.749
	doy_scaled	-0.0501	0.2311	-0.217		0.828
	Random effect				Variance	Std.Dev
	seed_id				0.1472	0.3837
	full_mother_plant_id			0.5007		0.7076
	plot_id				0.4702	0.6857
	N = 3138 observations; groups: seed_id = 83, full_mother_plant_id = 64, plot_id = 10					
Interpretation	Heavier seeds increased the odds of germination.					

Germination timing, seed trait baseline						
Model syntax	glmmTMB(formula = germination_day ~ weight_scaled + ripeness_scaled + doy_scaled + (1 plot_id) + (1 full_mother_plant_id) + (1 seed_id), data = data_germ, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)					
R package	glmmTMB					
Model output		Estimate	Std.Error	z	value	Pr(> z)
	(Intercept)		3.3530	0.0951	35.264	<2e-16 ***
	weight_scaled	-0.0142		0.0672	-0.211	0.833
	ripeness_scaled	-0.1881		0.1189	-1.582	0.114
	doy_scaled	0.0591		0.1124	0.526	0.599
	Random effect				Variance	Std.Dev
	plot_id				0.0438	0.2092
	full_mother_plant_id			0.0818		0.2861
	seed_id				0.0599	0.2447
	N = 836 observations; groups: plot_id = 10, full_mother_plant_id = 56, seed_id = 74					
Interpretation	No predictors reached significance (p < 0.05).					

Survival, seed trait baseline					
Model syntax	coxme(formula = Surv(life_duration, died_bin) ~ weight_scaled + ripeness_scaled + doy_scaled + (1 full_mother_plant_id), data = data_germ)				
R package	coxme				
Model output	Estimate	Std.Error	z	value	Pr(> z)
	weight_scaled	-0.0232	0.0864	-0.269	0.788
	ripeness_scaled	0.0041	0.1113	0.037	0.971
	doy_scaled	-0.0385	0.0985	-0.391	0.696
	Random effect			Variance	Std.Dev
	full_mother_plant_id		0.1415		0.3762
	N = 836 observations; groups: full_mother_plant_id = 56				
Interpretation	No predictors reached significance (p < 0.05).				

Growth, seed trait baseline																																																																							
Model syntax	glmmTMB(formula = cuberoot_size ~ age_scaled + age_scaled_sq + weight_scaled + ripeness_scaled + doy_scaled + (1 plot_id) + (1 full_mother_plant_id), data = growth_long, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)																																																																						
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Interpretation	Older age and heavier seeds increased seedling size; growth decelerated at older ages.																																																																						

Germination probability, treatment																																																																							
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Germination timing, treatment			
	Random effect	Variance	Std.Dev
	plot_id	0.0383	0.1957
	full_mother_plant_id	0.0927	0.3045
	seed_id	0.0730	0.2701
	N = 836 observations; groups: plot_id = 10, full_mother_plant_id = 56, seed_id = 74		
Interpretation	Warming advanced germination.		

Survival, treatment					
Model syntax	coxme(formula = Surv(life_duration, died_bin) ~ treatment + weight_scaled + ripeness_scaled + doy_scaled + (1 full_mother_plant_id), data = data_germ)				
R package	coxme				
Model output	Estimate	Std.Error	z	value	Pr(> z)
	treatmentH	-0.3226	0.1068	-3.019	0.00253 **
	weight_scaled	-0.0156	0.0869	-0.179	0.858
	ripeness_scaled	0.0106	0.1120	0.095	0.925
	doy_scaled	-0.0619	0.0993	-0.623	0.533
	Random effect			Variance	Std.Dev
	full_mother_plant_id		0.1446		0.3803
	N = 836 observations; groups: full_mother_plant_id = 56				
Interpretation	Warming improved survival.				

Growth, treatment						
Model syntax	glmmTMB(formula = cuberoot_size ~ treatment * age_scaled + treatment * age_scaled_sq + weight_scaled + ripeness_scaled + doy_scaled + (1 plot_id) + (1 full_mother_plant_id), data = growth_long, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)					
R package	glmmTMB					
Model output		Estimate	Std. Error	z	value	Pr(> z)
	(Intercept)		1.8617	0.1222	15.230	<2e-16 ***
	treatmentH		0.6076	0.0336	18.057	<2e-16 ***
	age_scaled		0.4415	0.0282	15.682	<2e-16 ***
	age_scaled_sq		-0.1398	0.0187	-7.484	7.21e-14 ***
	weight_scaled		0.1245	0.0287	4.331	1.49e-05 ***
	ripeness_scaled		-0.0461	0.1004	-0.459	0.646
	doy_scaled		0.0766	0.0931	0.823	0.41
	treatmentH:age_scaled		-0.0079	0.0319	-0.247	0.805
	treatmentH:age_scaled_sq		-0.0891	0.0219	-4.065	4.81e-05 ***
	Random effect				Variance	Std.Dev
	plot_id				0.1237	0.3518
full_mother_plant_id			0.0323		0.1798	
	N = 1345 observations; groups: plot_id = 10, full_mother_plant_id = 56					
Interpretation	Warming, older age, and heavier seeds increased seedling size; growth decelerated at older ages; the warming effect depended on age.					

Germination probability, microclimate	
Model syntax	glmer(formula = germinated_bin ~ treatment * snowmelt_scaled + treatment * altitude_scaled + weight_scaled + ripeness_scaled + (1 plot_id) + (1 full_mother_plant_id) + (1 seed_id), data = data, family = binomial)

Germination probability, microclimate						
R package	lme4					
Model output		Estimate	Std.Error	z	value	Pr(> z)
	(Intercept)	-2.0412	0.2845	-7.174	7.31e-13	***
	treatmentH	1.0717	0.0931	11.516	<2e-16	***
	snowmelt_scaled	0.2435	0.2846	0.856	0.392	
	altitude_scaled	-0.1001	0.2741	-0.365	0.715	
	weight_scaled	0.4037	0.1263	3.196	0.0014	**
	ripeness_scaled	0.0355	0.0943	0.376	0.707	
	treatmentH:snowmelt_scaled	-0.4761	0.1091	-4.366	1.27e-05	***
	treatmentH:altitude_scaled	0.0029	0.1023	0.028	0.977	
	Random effect			Variance		Std.Dev
	seed_id			0.1874		0.4329
	full_mother_plant_id		0.5359			0.7320
	plot_id			0.5459		0.7389
	N = 3138 observations; groups: seed_id = 83, full_mother_plant_id = 64, plot_id = 10					
Interpretation	Warming and heavier seeds increased the odds of germination; the warming effect depended on later snowmelt.					

Germination timing, microclimate																																																																																			
Model syntax	glmmTMB(formula = germination_day ~ treatment * snowmelt_scaled + treatment * altitude_scaled + weight_scaled + ripeness_scaled + (1 full_mother_plant_id) + (1 seed_id), data = data_germ, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)																																																																																		
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treatmentH:altitude_scaled	0.0054	0.0555	0.098		0.922																																																																														
Random effect				Variance	Std.Dev																																																																														
full_mother_plant_id		0.1104			0.3323																																																																														
seed_id				0.0650	0.2550																																																																														
N = 836 observations; groups: full_mother_plant_id = 56, seed_id = 74																																																																																			
Interpretation	Warming and riper seeds advanced germination; higher altitude delayed germination.																																																																																		

Survival, microclimate						
Model syntax	coxme(formula = Surv(life_duration, died_bin) ~ treatment * snowmelt_scaled + treatment * altitude_scaled + weight_scaled + ripeness_scaled + (1 full_mother_plant_id), data = data_germ)					
R package	coxme					
Model output		Estimate	Std.Error	z	value	Pr(> z)
	treatmentH	-0.3481	0.1118	-3.114	0.00185	**
	snowmelt_scaled	0.0484	0.1280	0.378	0.706	
	altitude_scaled	0.0135	0.1057	0.128	0.898	
	weight_scaled	-0.0152	0.0887	-0.172	0.864	
	ripeness_scaled	-0.0488	0.0711	-0.685	0.493	
	treatmentH:snowmelt_scaled	-0.1573	0.1299	-1.211	0.226	
	treatmentH:altitude_scaled	-0.0449	0.1141	-0.394	0.694	

Survival, microclimate			
	Random effect	Variance	Std.Dev
	full_mother_plant_id	0.1413	0.3760
	N = 836 observations; groups: full_mother_plant_id = 56		
Interpretation	Warming improved survival.		

Growth, microclimate																																																																																																											
Model syntax	glmmTMB(formula = cuberoot_size ~ treatment * age_scaled + treatment * age_scaled_sq + treatment * snowmelt_scaled + treatment * altitude_scaled + weight_scaled + ripeness_scaled + (1 plot_id) + (1 full_mother_plant_id), data = growth_long, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)																																																																																																										
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Interpretation	Warming, older age, and heavier seeds increased seedling size; growth decelerated at older ages; the warming effect depended on age; the warming effect depended on higher altitude.																																																																																																										

Germination probability, mother-plant																																																																																									
Model syntax	glmer(formula = germinated_bin ~ treatment * cushion_area_scaled + treatment * flower_doy_scaled + weight_scaled + ripeness_scaled + (1 plot_id) + (1 full_mother_plant_id) + (1 seed_id), data = data, family = binomial)																																																																																								
R package	lme4																																																																																								
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Germination probability, mother-plant	
Interpretation	Warming and heavier seeds increased the odds of germination; the warming effect depended on later flowering.

Germination timing, mother-plant																																																																																									
Model syntax	glmmTMB(formula = germination_day ~ treatment * cushion_area_scaled + treatment * flower_doy_scaled + weight_scaled + ripeness_scaled + (1 plot_id) + (1 full_mother_plant_id) + (1 seed_id), data = data_germ, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)																																																																																								
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Growth, mother-plant	
Model syntax	glmmTMB(formula = cuberoot_size ~ treatment * age_scaled + treatment * age_scaled sq + treatment * cushion_area_scaled + treatment * flower_doy_scaled + weight_scaled + ripeness_scaled + (1 plot_id) + (1 full_mother_plant_id), data = growth_long, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)
R package	glmmTMB

Growth, mother-plant						
Model output		Estimate	Std. Error	z	value	Pr(> z)
	(Intercept)	1.8512	0.1263	14.652		<2e-16 ***
	treatmentH	0.6218	0.0347	17.894		<2e-16 ***
	age_scaled	0.4326	0.0298	14.494		<2e-16 ***
	age_scaled_sq	-0.1328	0.0193	-6.893		5.45e-12 ***
	cushion_area_scaled	0.0219	0.0395	0.555		0.579
	flower_doy_scaled	0.0061	0.0944	0.064		0.949
	weight_scaled	0.1251	0.0300	4.178		2.95e-05 ***
	ripeness_scaled	0.0345	0.0189	1.823		0.0683 .
	treatmentH:age_scaled	0.0004	0.0336	0.011		0.991
	treatmentH:age_scaled_sq	-0.0940	0.0226	-4.162		3.15e-05 ***
	treatmentH:cushion_area_scaled	-0.0384	0.0304	-1.265		0.206
	treatmentH:flower_doy_scaled	0.0834	0.0320	2.603		0.00925 **
	Random effect				Variance	Std.Dev
	plot_id				0.1313	0.3624
full_mother_plant_id		0.0375			0.1937	
N = 1287 observations; groups: plot_id = 10, full_mother_plant_id = 54						
Interpretation	Warming, older age, and heavier seeds increased seedling size; growth decelerated at older ages; the warming effect depended on age; the warming effect depended on later flowering.					

Germination probability, PCA sensitivity						
Model syntax	glmer(formula = germinated_bin ~ treatment * PC1_scaled + treatment * PC2_scaled + weight_scaled + ripeness_scaled + (1 plot_id) + (1 full_mother_plant_id) + (1 seed_id), data = data, family = binomial)					
R package	lme4					
Model output		Estimate	Std.Error	z	value	Pr(> z)
	(Intercept)	-2.0369	0.2802	-7.270	3.59e-13	***
	treatmentH	1.0654	0.0930	11.453	<2e-16	***
	PC1_scaled	0.1617	0.2866	0.564	0.573	
	PC2_scaled	-0.1804	0.2593	-0.696	0.486	
	weight_scaled	0.3983	0.1260	3.162	0.00157	**
	ripeness_scaled	0.0345	0.0940	0.368	0.713	
	treatmentH:PC1_scaled	-0.4868	0.1089	-4.471	7.79e-06	***
	treatmentH:PC2_scaled	0.0990	0.1065	0.929	0.353	
	Random effect				Variance	Std.Dev
	seed_id				0.1856	0.4309
	full_mother_plant_id		0.5340			0.7308
	plot_id				0.5254	0.7249
	N = 3138 observations; groups: seed_id = 83, full_mother_plant_id = 64, plot_id = 10					
Interpretation	Warming and heavier seeds increased the odds of germination; the warming effect depended on PC1.					

Germination timing, PCA sensitivity						
Model syntax	glmmTMB(formula = germination_day ~ treatment * PC1_scaled + treatment * PC2_scaled + weight_scaled + ripeness_scaled + (1 full_mother_plant_id) + (1 seed_id), data = data_germ, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)					
R package	glmmTMB					
Model output		Estimate	Std.Error	z	value	Pr(> z)
	(Intercept)		3.5767	0.0718	49.828	<2e-16 ***
	treatmentH		-0.2762	0.0529	-5.225	1.74e-07 ***
	PC1_scaled		0.0614	0.0888	0.691	0.489

Germination timing, PCA sensitivity					
	PC2_scaled	0.1532	0.0775	1.976	0.0481 *
	weight_scaled	-0.0052	0.0710	-0.073	0.942
	ripeness_scaled	-0.1452	0.0530	-2.738	0.00618 **
	treatmentH:PC1_scaled	0.0161	0.0641	0.251	0.802
	treatmentH:PC2_scaled	-0.0162	0.0580	-0.279	0.78
	Random effect			Variance	Std.Dev
	full_mother_plant_id		0.1105		0.3324
	seed_id			0.0678	0.2603
	N = 836 observations; groups: full_mother_plant_id = 56, seed_id = 74				
Interpretation	Warming and riper seeds advanced germination; PC2 delayed germination.				

Survival, PCA sensitivity					
Model syntax	coxme(formula = Surv(life_duration, died_bin) ~ treatment * PC1_scaled + treatment * PC2_scaled + weight_scaled + ripeness_scaled + (1 full_mother_plant_id), data = data_germ)				
R package	coxme				
Model output		Estimate	Std.Error	z value	Pr(> z)
	treatmentH	-0.3426	0.1120	-3.060	0.00221 **
	PC1_scaled	0.0458	0.1287	0.356	0.722
	PC2_scaled	-0.0172	0.1094	-0.157	0.875
	weight_scaled	-0.0172	0.0885	-0.195	0.846
	ripeness_scaled	-0.0486	0.0710	-0.684	0.494
	treatmentH:PC1_scaled	-0.1628	0.1323	-1.230	0.219
	treatmentH:PC2_scaled	0.0063	0.1171	0.054	0.957
	Random effect			Variance	Std.Dev
	full_mother_plant_id		0.1415		0.3761
	N = 836 observations; groups: full_mother_plant_id = 56				
Interpretation	Warming improved survival.				

Growth, PCA sensitivity					
Model syntax	glmmTMB(formula = cuberoot_size ~ treatment * age_scaled + treatment * age_scaled_sq + treatment * PC1_scaled + treatment * PC2_scaled + weight_scaled + ripeness_scaled + (1 plot_id) + (1 full_mother_plant_id), data = growth_long, family = Gamma(link = "log"), ziformula = ~0, dispformula = ~1)				
R package	glmmTMB				
Model output		Estimate	Std.Error	z value	Pr(> z)
	(Intercept)	1.8230	0.1126	16.184	<2e-16 ***
	treatmentH	0.6128	0.0336	18.221	<2e-16 ***
	age_scaled	0.4324	0.0284	15.202	<2e-16 ***
	age_scaled_sq	-0.1361	0.0187	-7.271	3.56e-13 ***
	PC1_scaled	0.1697	0.1018	1.667	0.0955 .
	PC2_scaled	-0.0438	0.0961	-0.456	0.649
	weight_scaled	0.1313	0.0294	4.469	7.87e-06 ***
	ripeness_scaled	0.0330	0.0187	1.762	0.0781 .
	treatmentH:age_scaled	0.0043	0.0322	0.133	0.894
	treatmentH:age_scaled_sq	-0.0947	0.0220	-4.305	1.67e-05 ***
	treatmentH:PC1_scaled	0.0347	0.0294	1.183	0.237
	treatmentH:PC2_scaled	0.0470	0.0282	1.663	0.0963 .
	Random effect			Variance	Std.Dev
	plot_id			0.0985	0.3139
	full_mother_plant_id		0.0355		0.1883
	N = 1345 observations; groups: plot_id = 10, full_mother_plant_id = 56				

Growth, PCA sensitivity	
Interpretation	Warming, older age, and heavier seeds increased seedling size; growth decelerated at older ages; the warming effect depended on age.

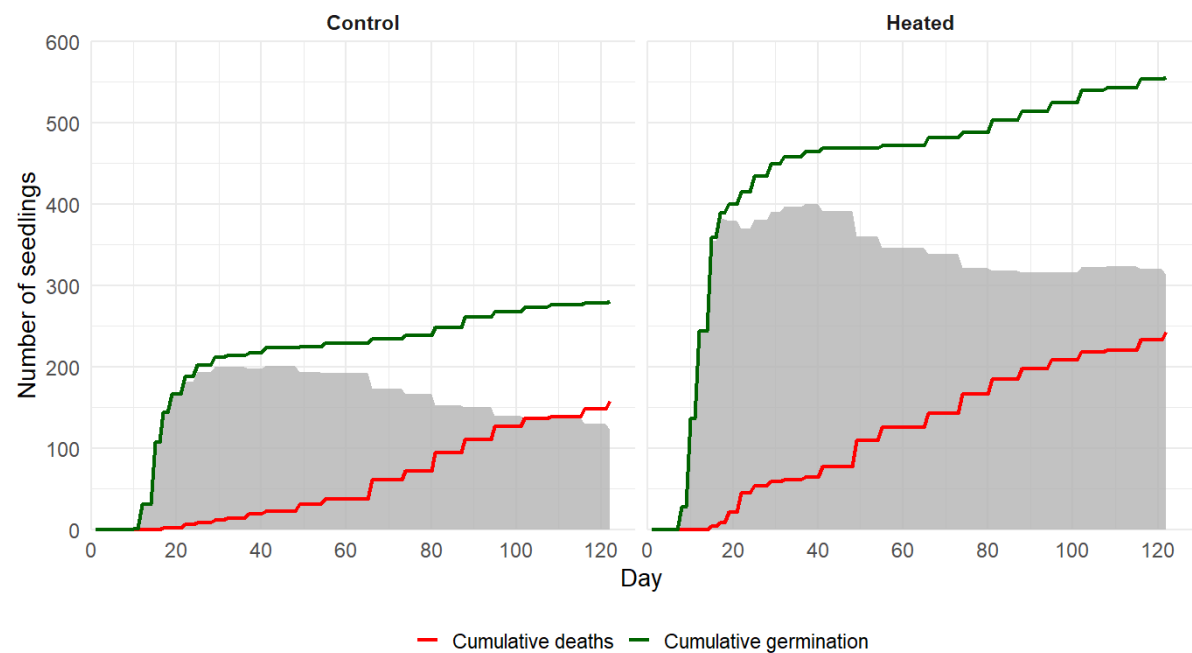
Germination probability, soil-moisture sensitivity																																																																																																
Model syntax	glmer(formula = germinated_bin ~ treatment * snowmelt_scaled + treatment * altitude_scaled + soil_moisture_scaled + weight_scaled + ripeness_scaled + (1 plot_id) + (1 full_mother_plant_id) + (1 seed_id), data = data_no_L, family = binomial)																																																																																															
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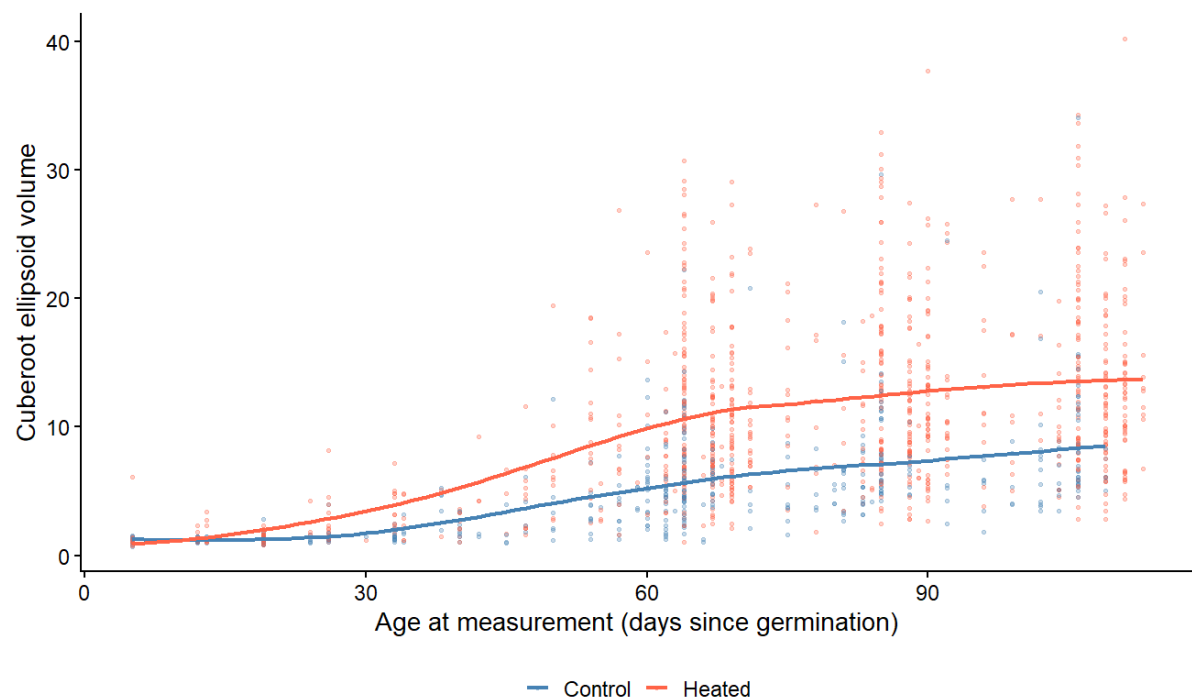
Growth, within-plot flowering	
Model syntax	glmmTMB(formula = cuberoot_size ~ treatment * age_scaled + treatment * age_scaled sq + treatment * flower_doy_within_raw + weight_scaled +

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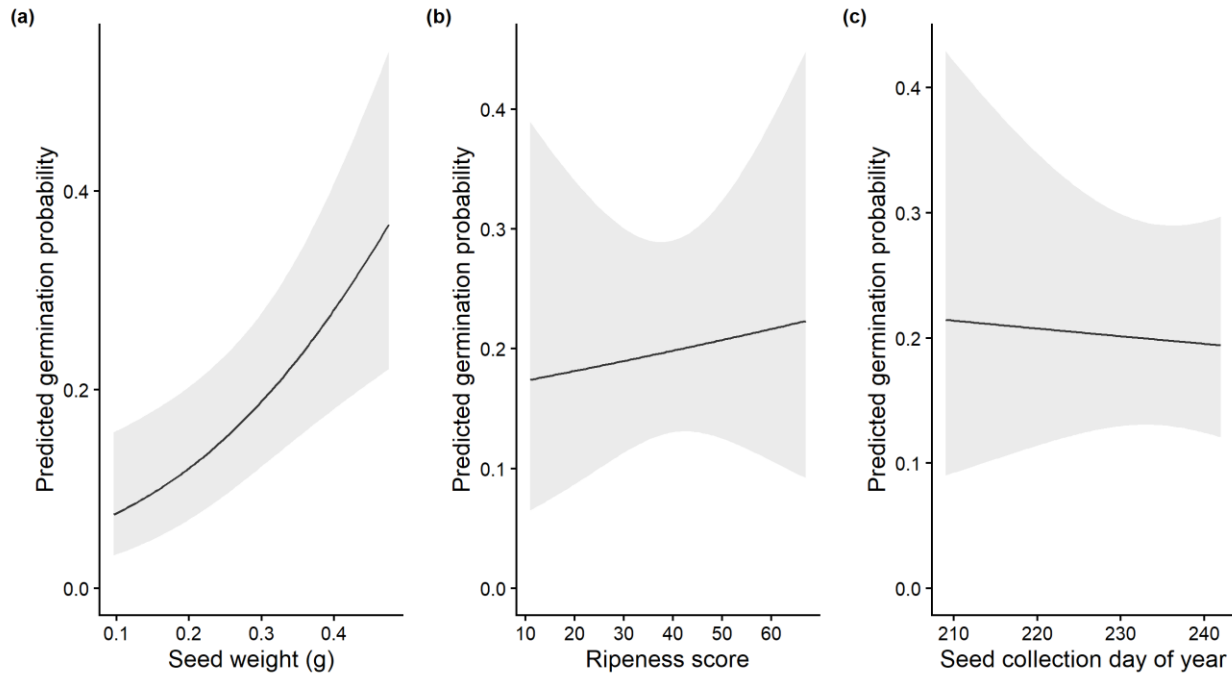
Appendix 6 – Extra Results Figures



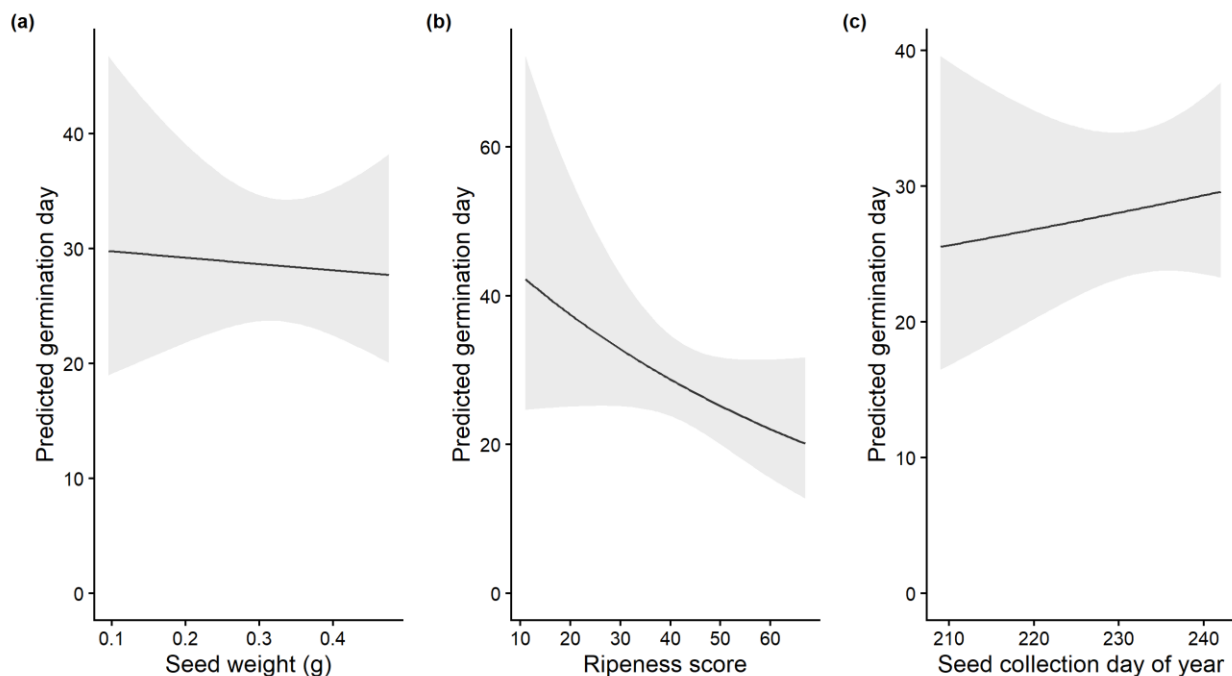
Time series for total live seedlings, overlaid by cumulative germination and death, split by treatment, using raw data. This shows the overall larger germination success under warming, as well as the delay in germination under control conditions. Germination timing can be observed to be mostly concentrated around the first weeks, dropping sharply after peaking.



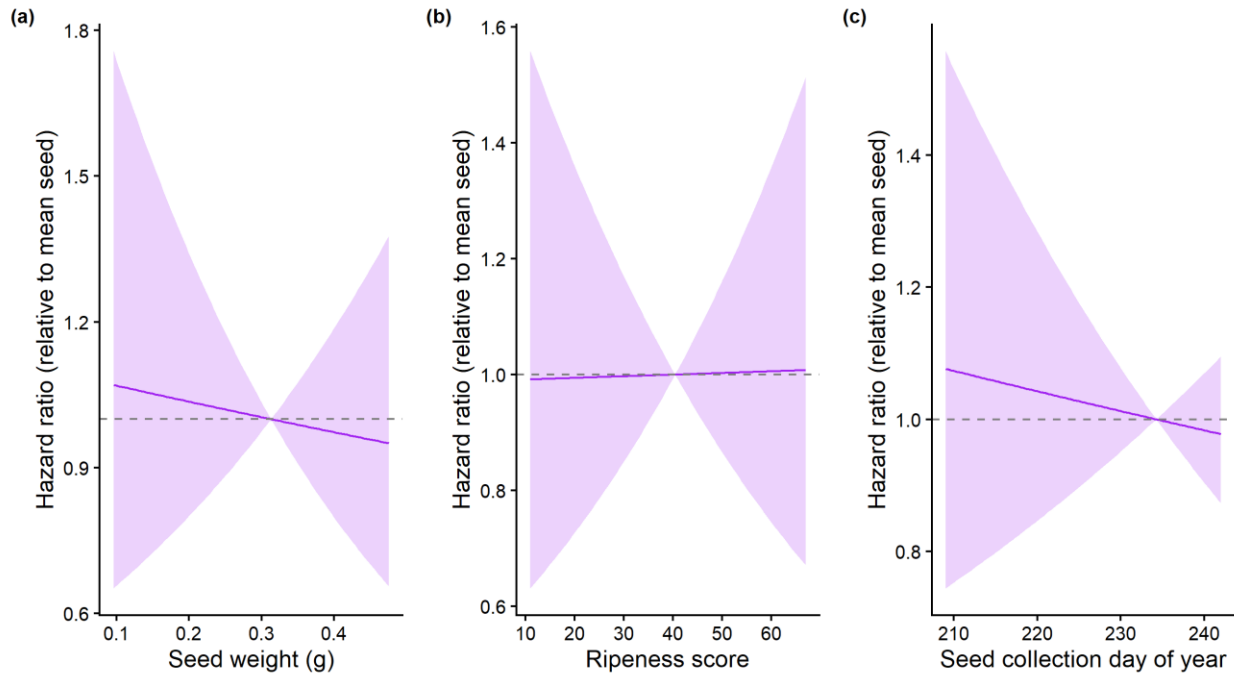
Scatter plot of seedling size against seedling age, split by treatment, using raw data. This shows the warming benefit on size across all ages.



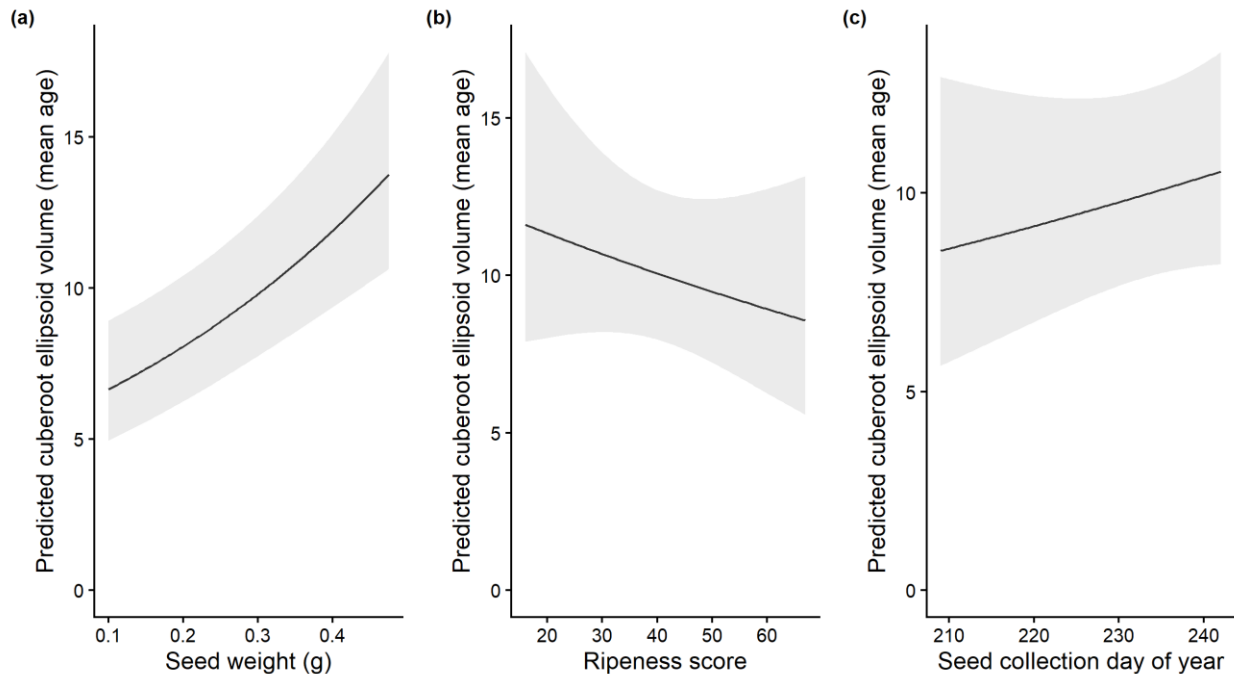
Model-predicted germination probability of *Silene acaulis* seeds in relation to seed traits, from the seed-trait GLMM (treatment not included). (a) Germination probability increased significantly with seed weight ($OR = 1.47$, 95% CI: 1.17–1.86, $p = 0.001$), but was not significantly related to (b) ripeness score ($OR = 1.08$, 95% CI: 0.67–1.75, $p = 0.75$) or (c) seed collection day ($OR = 0.95$, 95% CI: 0.60–1.50, $p = 0.83$). Odds ratios are per 1 SD increase in each standardized trait. Lines are fixed-effect predictions with the other two seed traits held at their means; shaded areas are 95% confidence intervals.



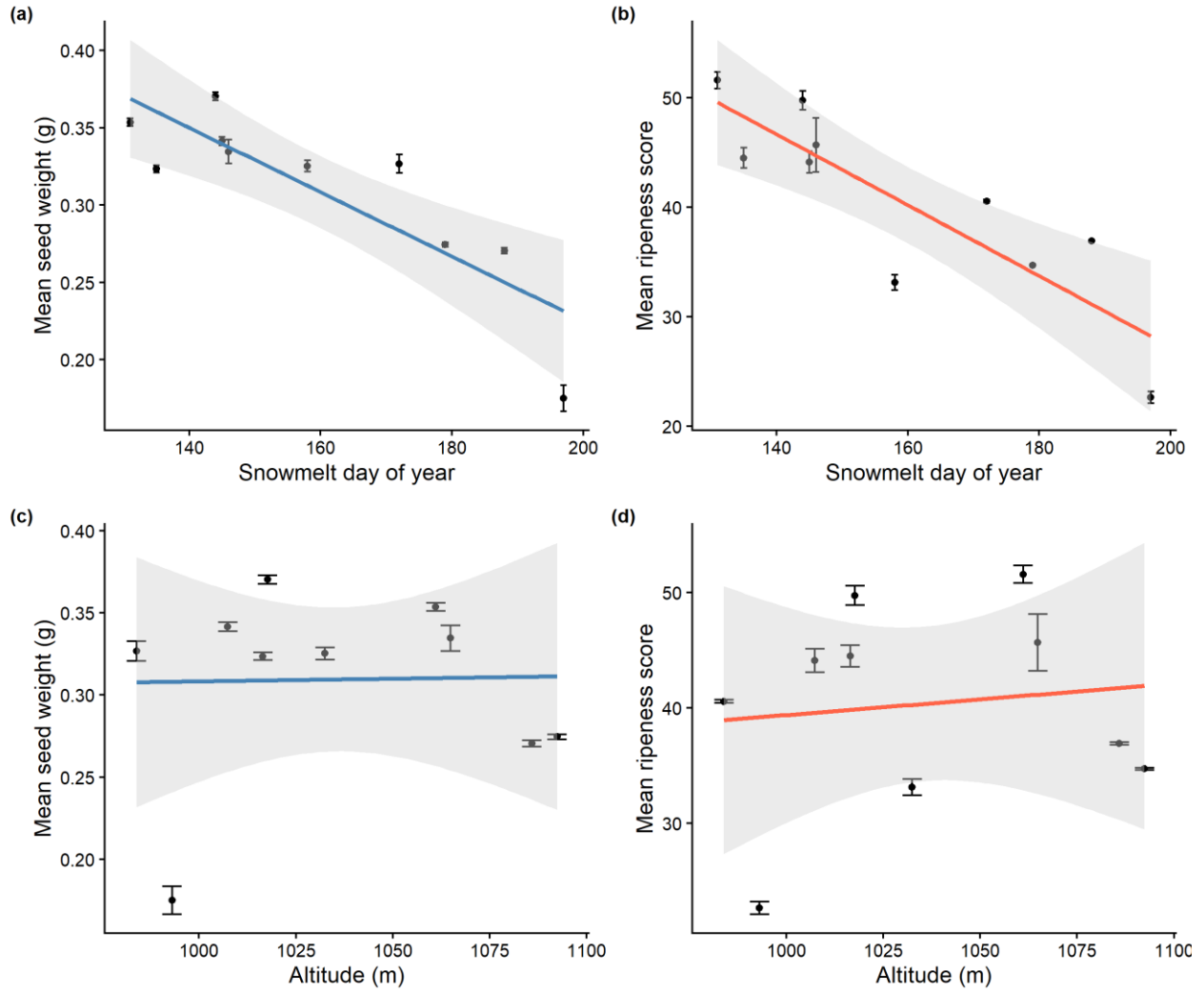
Model-predicted germination timing of *Silene acaulis* seeds in relation to seed traits, from the seed-trait Gamma GLMM (treatment not included). Germination timing was not significantly related to any seed trait. (a) Seed weight ($exp = 0.99$, 95% CI: 0.86–1.12, $p = 0.83$). (b) Ripeness score ($exp = 0.83$, 95% CI: 0.66–1.05, $p = 0.11$). (c) Seed collection day ($exp = 1.06$, 95% CI: 0.85–1.32, $p = 0.60$). Values (exp) are exponentiated coefficients — the multiplicative change in predicted germination day per 1 SD increase in each standardized trait. Lines are fixed-effect predictions with the other two seed traits held at their means; shaded areas are 95% confidence intervals.



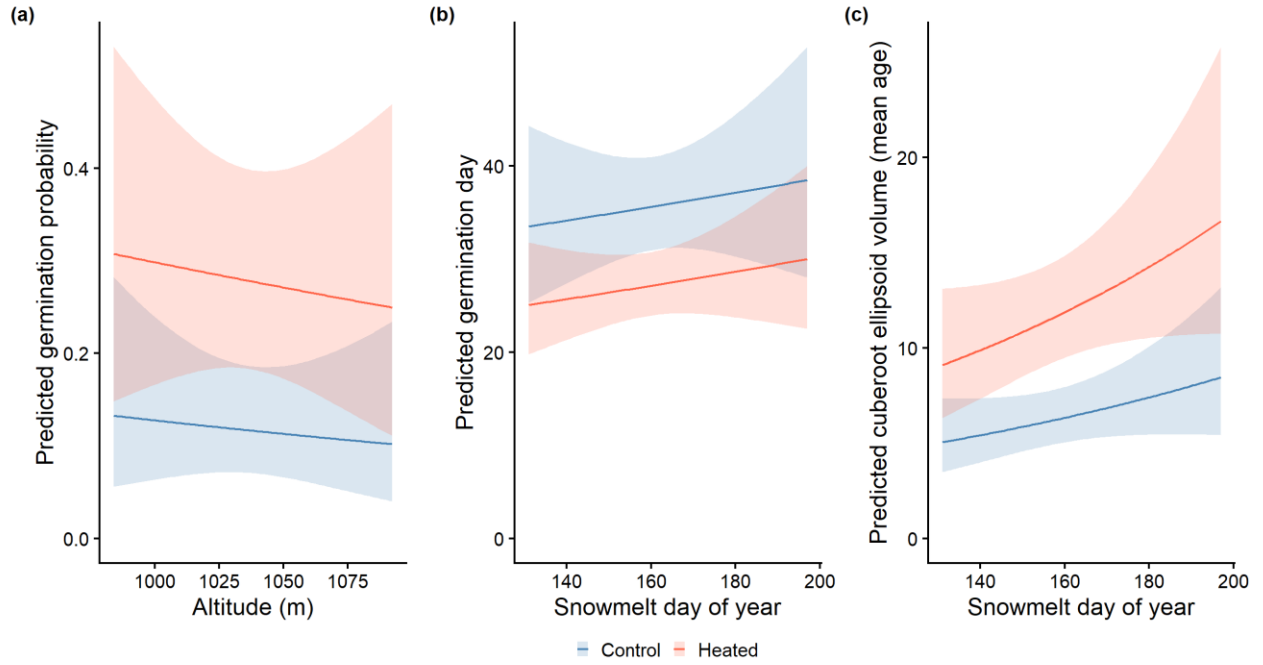
Model-predicted hazard ratio for *Silene acaulis* seedling mortality in relation to seed traits, from the seed-trait Cox mixed-effects model (treatment not included). Mortality risk was not significantly related to any seed trait. The dashed line at 1 marks the reference hazard — a seedling with mean seed-trait values — with values above 1 indicating higher mortality risk and below 1 lower. **(a)** Seed weight ($HR = 0.98$, 95% CI: 0.82–1.16, $p = 0.78$). **(b)** Ripeness score ($HR = 1.00$, 95% CI: 0.81–1.25, $p = 0.97$). **(c)** Seed collection day ($HR = 0.96$, 95% CI: 0.80–1.17, $p = 0.70$). Hazard ratios are per 1 SD increase in each standardized trait. Lines are fixed-effect predictions with the other two seed traits held at their means; shaded areas are 95% confidence intervals.



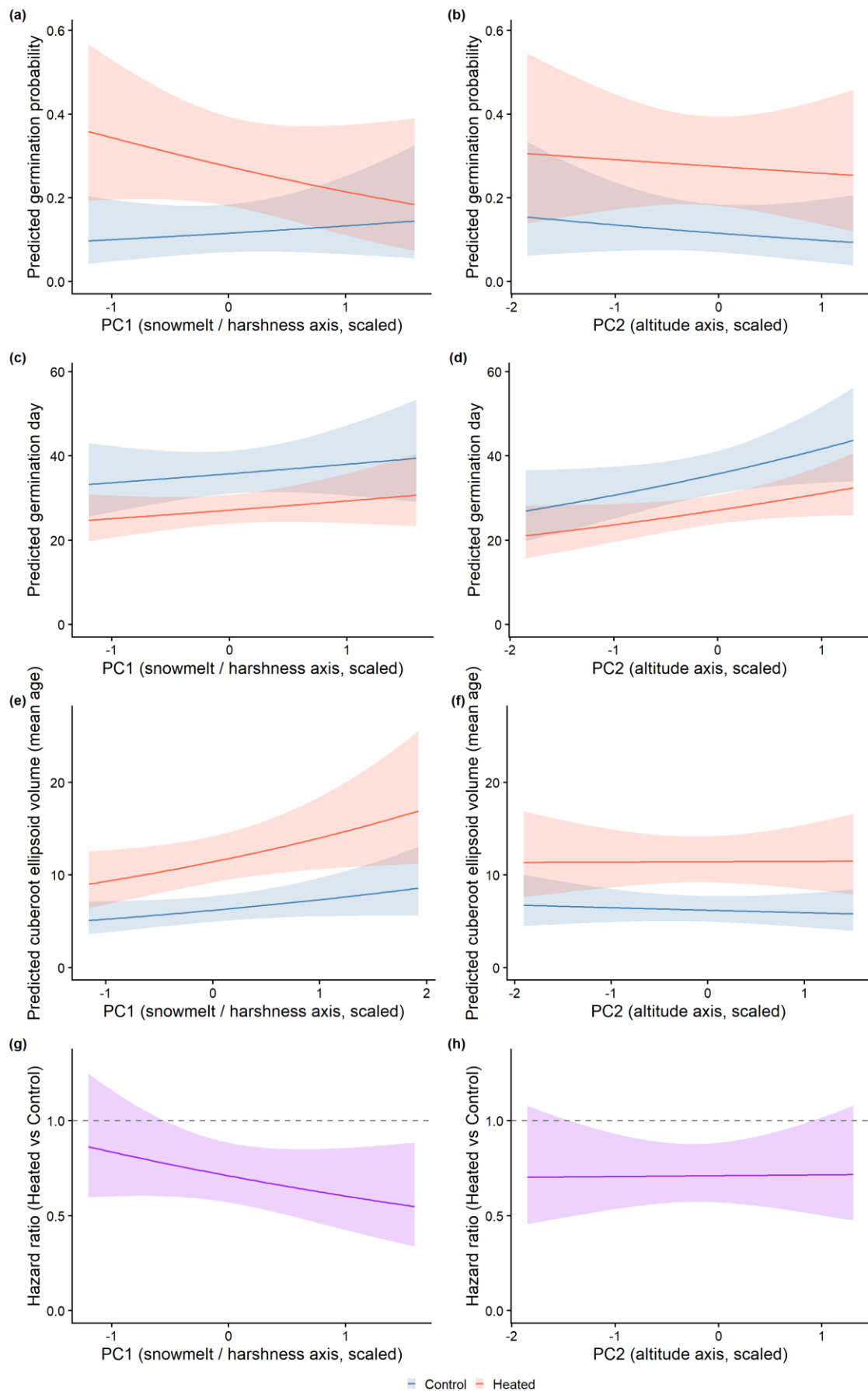
Model-predicted size (cuberoot ellipsoid volume at the mean measurement age) of *Silene acaulis* seedlings in relation to seed traits, from the seed-trait Gamma GLMM (treatment not included). **(a)** Seedling size increased significantly with seed weight ($\exp = 1.155$, 95% CI: 1.091–1.223, $p < 0.0001$), but was not significantly related to **(b)** ripeness score ($\exp = 0.92$, 95% CI: 0.76–1.11, $p = 0.37$) or **(c)** seed collection day ($\exp = 1.09$, 95% CI: 0.91–1.29, $p = 0.34$). Values ($\exp$) are exponentiated coefficients — the multiplicative change in predicted volume per 1 SD increase in each standardized trait. Lines are fixed-effect predictions with the other two seed traits held at their means; shaded areas are 95% confidence intervals.



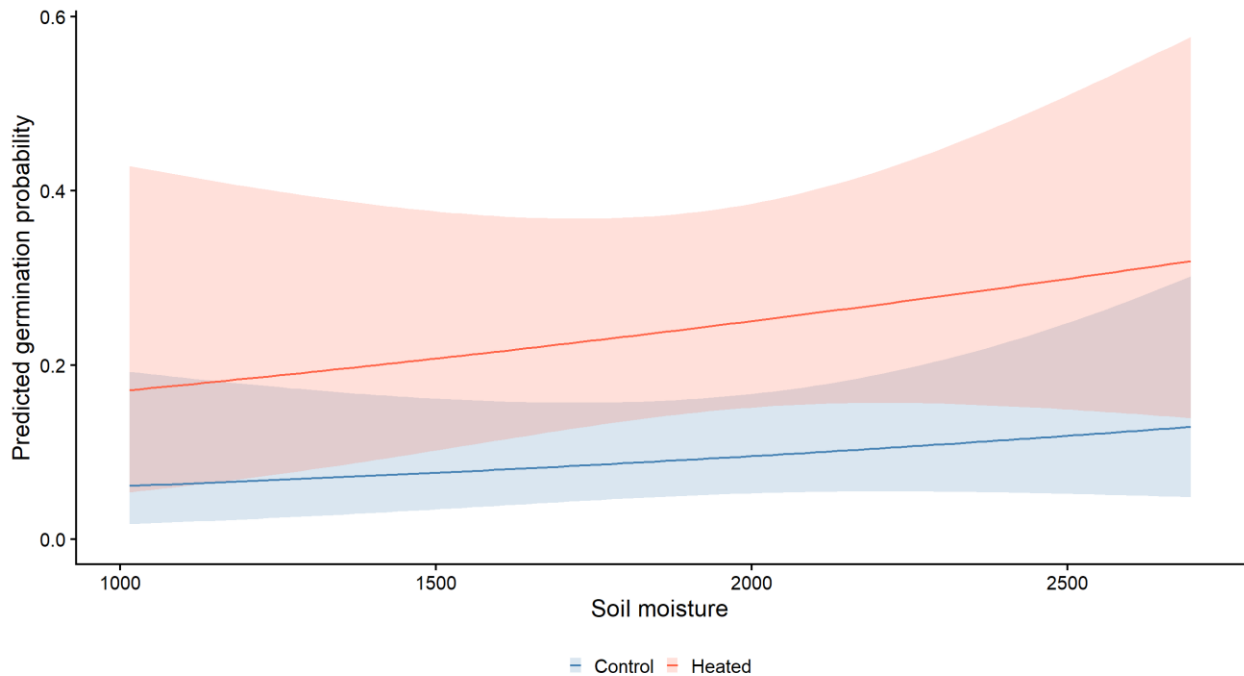
Plot-level mean seed weight and ripeness in relation to two microclimate axes across the ten study plots. Each point is a plot mean $\pm$ SE; lines are linear fits. Mean seed weight (a) and ripeness (b) both decreased significantly with later snowmelt (weight: Pearson $r = -0.85$, $p = 0.002$; ripeness: $r = -0.86$, $p = 0.002$), whereas neither was related to altitude ((c) weight: $r = 0.02$, $p = 0.95$; (d) ripeness: $r = 0.12$, $p = 0.74$).



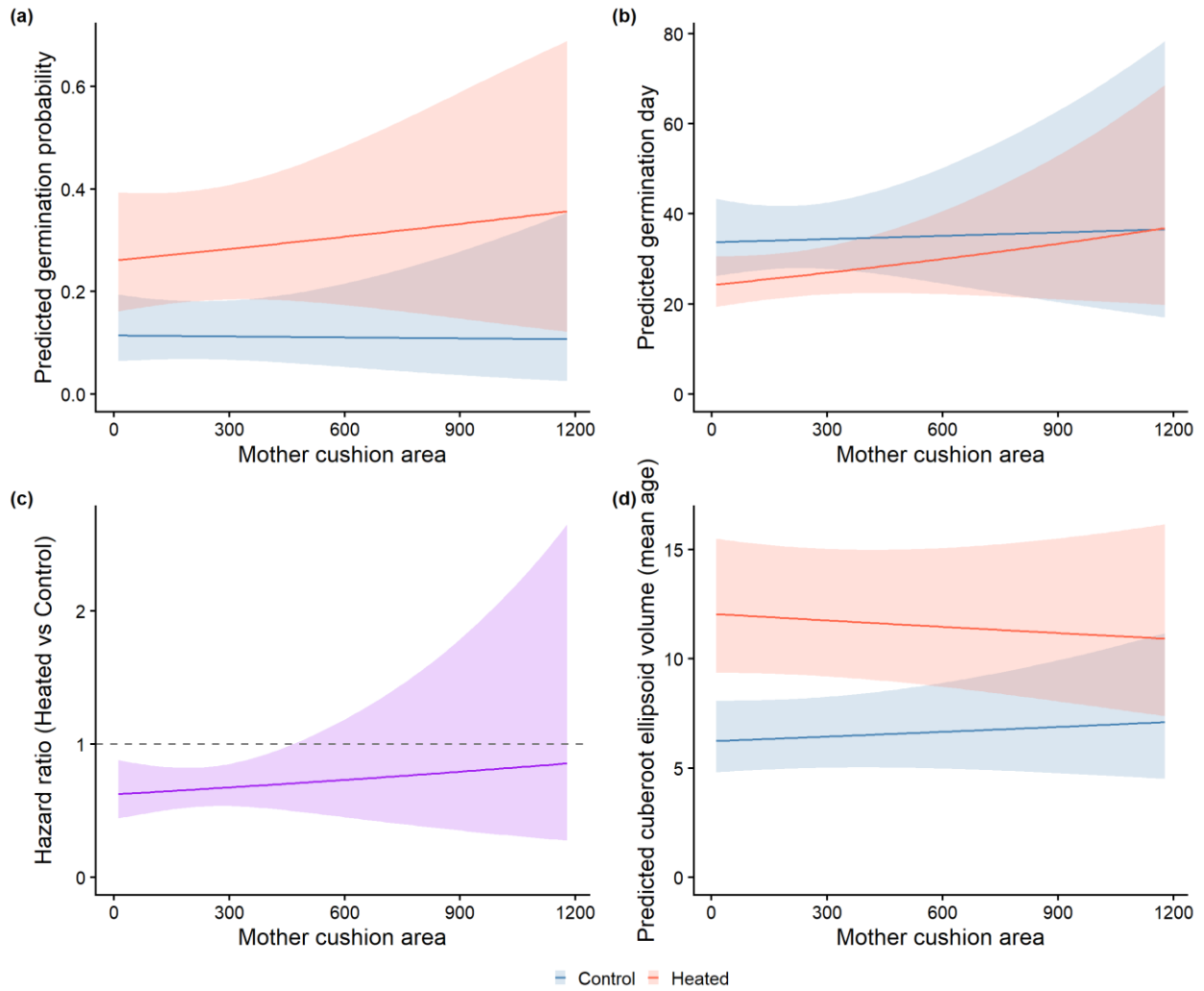
Model-predicted responses of *Silene acaulis* across the microclimate axis that did not have a significant effect for each variable, complementing the significant axis shown in the main results (snowmelt for germination probability; altitude for germination timing and seedling size). **(a)** Germination probability was not significantly related to altitude ($OR = 0.90$, 95% CI: 0.53–1.55, $p = 0.72$), and the warming effect did not vary with altitude (treatment $\times$ altitude $OR = 1.00$, 95% CI: 0.82–1.23, $p = 0.98$). **(b)** Germination timing was not significantly related to snowmelt ($exp = 1.05$, 95% CI: 0.88–1.24, $p = 0.61$), with no treatment $\times$ snowmelt interaction ($exp = 1.01$, 95% CI: 0.90–1.15, $p = 0.83$). **(c)** Seedling size (cuberoot ellipsoid volume at the mean measurement age) was not significantly related to snowmelt ($exp = 1.18$, 95% CI: 0.95–1.48, $p = 0.14$), with no treatment $\times$ snowmelt interaction ($exp = 1.03$, 95% CI: 0.97–1.10, $p = 0.36$). All effects are per 1 SD of the plotted gradient. Lines are fixed-effect predictions for the control and heated treatments with all other covariates held at their means; shaded areas are 95% confidence intervals.



PCA sensitivity analysis: model-predicted (a, b) germination probability, (c, d) germination timing, (e, f) seedling size, and (g, h) seedling mortality (heated vs control hazard ratio) of *Silene acaulis* against PC1 (snowmelt/harshness axis, 72.6% of variance) and PC2 (altitude axis, 22.6%), replacing the raw microclimate variables. The PCA models broadly reproduced the main results: the warming effect on germination probability varied with PC1 (the snowmelt axis), germination timing increased with PC2 (the altitude axis), and warming reduced mortality overall and consistently across both axes. The one exception was seedling size, whose significant treatment $\times$ altitude interaction in the raw model weakened to a non-significant trend on PC2. Germination probability, timing and size are shown for each treatment; the dashed line in (g, h) marks a hazard ratio of 1. PC axes are on the standardized scale; shaded areas are 95% confidence intervals



Model-predicted germination probability of *Silene acaulis* seeds against soil moisture, by treatment, from the sensitivity model that adds soil moisture and excludes Plot L (missing soil moisture data). Germination probability was not significantly related to soil moisture ($OR = 1.30$ per SD, 95% CI: 0.69–2.45, $p = 0.42$), and the main treatment $\times$ snowmelt effect was essentially unchanged in this reduced model ($OR = 0.64$, 95% CI: 0.52–0.80, $p < 0.001$), indicating the warming–snowmelt result is not driven by soil moisture. Lines are fixed-effect predictions for the control and heated treatments with all other covariates held at their means; shaded areas are 95% confidence intervals



Model-predicted (a) germination probability, (b) germination timing, (c) seedling mortality (heated vs control hazard ratio), and (d) seedling size of *Silene acaulis* against mother cushion area, from the mother-plant models. Cushion area was not significantly related to any response, and the warming effect did not vary with it (all cushion-area and treatment $\times$ cushion-area terms non-significant; smallest $p = 0.21$). Germination probability, timing and size are shown for each treatment; the dashed line in (c) marks a hazard ratio of 1, and shaded areas are 95% confidence intervals.