

Heat-driven declines in Scots pine cone and seed quality contrast with long-term climate adjustment

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Abstract

Climate change can alter forest regeneration through effects on seed production, seed quality, and the structures that protect seeds, yet most evidence focuses on seed output alone. We used 15 years of cone and seed-quality data from 184 Scots pine (*Pinus sylvestris*) populations to test whether climate effects extend beyond fecundity to reproductive traits that determine viable propagule supply. We separated among-population differences along long-term climate gradients (spatial effects) from within-population responses to seasonal weather anomalies (temporal effects). Across space, warmer climates were associated with heavier seeds (by ~8%) but lighter cones (by ~15%), whereas wetter climates were associated with heavier seeds (by ~10%) and cones (by ~20%). Temporal analyses revealed additional constraints: at warmer sites, hotter-than-average years reduced seed mass (by ~8%), cone mass (by ~14%), and the number of seeds per cone (by ~23%). Thus, heat can constrain Scots pine regeneration before germination by reducing the number of filled seeds, their provisioning, and investment in surrounding cone tissue. Spatial gradients are consistent with long-term adjustment of Scots pine reproductive traits to local climate, potentially through acclimation, genetic adaptation, or both, whereas temporal anomalies reveal near-term constraints that may intensify under rapid warming. Because Scots pine is one of Europe's most important forest-forming species, these results point to near-term reproductive bottlenecks caused by heat and call for studies testing whether reduced seed number, seed size, and cone protection translate into lower regeneration under climate change.

Introduction

Forest regeneration depends on the quantity, quality, and protection of propagules produced by mature trees (Clark *et al.*, 2004; Moles *et al.*, 2004; Dalling *et al.*, 2020). Seeds number determines the supply of potential recruits, whereas seed quality determines how many propagules can germinate, establish, and contribute to recruitment (Maleki & Soltani, 2026). Seed mass is one component of quality: larger seeds often produce larger seedlings, survive better during early establishment, and perform better under hazards such as shade, drought, and herbivory (Moles *et al.*, 2006; Pawłowski *et al.*, 2024; Ammer *et al.*, 2026). Seed viability is another component of quality, because only viable seeds can germinate and produce seedlings (Walck *et al.*, 2011; Harmel *et al.*, 2026). Seed defenses add another filter. Seeds and the structures that enclose them are chemically defended with compounds that reduce palatability, while hard coats increase handling costs for consumers (Leslie, 2011; Dalling *et al.*, 2020). These reproductive

53 filters are likely to be environmentally sensitive because seed filling, viability, and protective tissue
54 formation depend on resource acquisition and allocation (Despland & Houle, 1997; Walck *et al.*, 2011;
55 Harmel *et al.*, 2026). Climate effects on regeneration therefore cannot be inferred from seed number
56 alone, because climate may also alter the quality of each seed and the protective structures that mediate
57 seed fate.

58 Tree reproduction is sensitive to climate change (Clark *et al.*, 2011; Pearse *et al.*, 2017), with most
59 evidence currently coming from seed production (Clark *et al.*, 2021; Foest *et al.*, 2026). For example,
60 climate warming and increasing aridity have been linked to declines in seed output in *Fagus sylvatica*,
61 *Pinus edulis*, *Pinus sibirica* (Goroshkevich *et al.*, 2021; Bogdziewicz *et al.*, 2023; Wion *et al.*, 2025),
62 although some species or communities appear resilient (reviewed in Foest *et al.*, 2026). Yet seed
63 production is only one regeneration filter, and evidence on seed quality and seed defensive investment
64 remains much more limited. On one hand, *Pinus banksiana* produces larger seeds in warm years (Despland
65 & Houle, 1997). On the other hand, *F. sylvatica* seed mass declined by 13% over five decades, with the
66 decline linked to summer warming and increasing drought (Bogdziewicz *et al.*, 2026). In *Abies alba*,
67 commercial seed-lot viability in Austria declined by over 40%, with warming without adequate water
68 supply likely constraining seed viability (Harmel *et al.*, 2026). These examples indicate that climate-
69 driven changes in regeneration traits may already be underway, but the scarcity of trait-level reproductive
70 data limits forecasts of climate-change effects on forest regeneration.

71 Compared with temporal changes in seed traits, spatial variation is better documented. Across
72 latitudinal gradients, intraspecific seed mass often varies with climate, although latitude also covaries with
73 soils, photoperiod, and biotic interactions (Frenne *et al.*, 2013). In boreal conifers, seeds were generally
74 larger in warmer or wetter climates across *Picea mariana*, *Picea glauca*, and *Pinus banksiana* (Liu *et al.*,
75 2013). In *Pinus yunnanensis*, populations from warmer and more humid climates produced heavier
76 cones and seeds, more filled seeds per cone, and fewer aborted seeds (Gao *et al.*, 2023). In *Quercus*
77 *macrocarpa*, acorn size declined with latitude, likely driven by temperature and rainfall constraints
78 (Koenig *et al.*, 2009). Such spatial patterns may reflect adaptive differentiation among populations or
79 adaptive plasticity when trait values improve performance under local conditions (Murray *et al.*, 2004;
80 Frenne *et al.*, 2013). Alternatively, reduced seed or cone investment under cold, dry, or resource-limited
81 conditions may also reflect direct developmental or resource constraints (Murray *et al.*, 2004; Frenne *et al.*,
82 2013). Nonetheless, because most evidence comes from among-population gradients, inferred climate
83 effects incorporate long-term adjustment of local populations to climate, including local adaptation (Evans

84 *et al.*, 2025). These spatial signals can guide forecasts of trait changes that unfold over decades, yet they
85 may misrepresent near-term responses to weather anomalies that determine whether existing populations
86 maintain viable seed supply under rapid climate change.

87 Temporal climate responses provide a complementary perspective. They describe how traits change
88 within the same population in unusually warm, cold, wet, or dry years, capturing faster processes such
89 as physiological plasticity (Felton *et al.*, 2022; Perret *et al.*, 2024; Stemkovski *et al.*, 2025; Evans *et al.*,
90 2025). Spatial and temporal sensitivities can therefore differ in magnitude or even direction (Stemkovski
91 *et al.*, 2025). For example, *Pinus ponderosa* growth is higher in warmer and wetter parts of its range,
92 yet hot years reduce growth within populations, leading spatial and temporal models to predict opposite
93 responses to warming (Perret *et al.*, 2024). Similar mismatches have been reported for rangeland
94 productivity (Felton *et al.*, 2022) and for reproductive dynamics in *F. sylvatica* (Foest *et al.*, 2025b,a).
95 For tree regeneration, comparing spatial and temporal climate responses can therefore separate short-
96 term sensitivity to weather anomalies from longer-term adjustment to local climate. Such comparison is
97 important as forecasts based only on temporal responses may overstate long-term vulnerability, whereas
98 forecasts based only on spatial gradients may understate near-term risks (Hastings, 2016; Francis *et al.*,
99 2021; Stemkovski *et al.*, 2025; Evans *et al.*, 2025). However, estimating both forms of sensitivity requires
100 long-term data replicated across broad climatic gradients, a design that remains uncommon in ecology
101 and especially rare for reproductive traits, which are monitored less consistently than growth, survival, or
102 species occurrence (Clark *et al.*, 2021; Hacket-Pain & Bogdziewicz, 2021; Evans *et al.*, 2025).

103 Scots pine (*Pinus sylvestris*) provides a suitable and important model system for testing whether
104 climate effects extend beyond fecundity to cone and seed quality, because the species combines a broad
105 range, ecological importance, and sensitivity to climate change. The species has major commercial,
106 ecological, and cultural importance in many European countries. Although Scots pine is frequently con-
107 sidered moderately drought-tolerant, recent evidence shows that drought is affecting both adult persistence
108 and regeneration (Vilà-Cabrera *et al.*, 2014; Buras *et al.*, 2018; Bose *et al.*, 2020). Drought-induced mor-
109 tality has increased over the last two decades, with high mortality now reported even near the species'
110 climatic optimum (Socha *et al.*, 2023; Bose *et al.*, 2024). Early life stages are also moisture-sensitive:
111 hotter drought reduces pine seedling performance and survival (Matías *et al.*, 2017; Tiebel & Karge,
112 2025). These findings indicate that intensifying drought may constrain population growth rates, espe-
113 cially where adult mortality increases the need for successful recruitment. Seed output also appears to
114 be declining, as suggested by seed harvest records linking reduced viable seed production to increasing

summer temperatures (Foest *et al.*, 2026). However, seed production captures only one component of regeneration. Climate effects on the cone and seed traits that determine viable propagule supply remain poorly understood.

Here, we used 15 years of cone and seed-quality data from 184 Scots pine (*Pinus sylvestris*) populations (Fig. 1) to test whether climate effects extend beyond fecundity to traits that determine viable propagule supply - which included seed mass, cone mass, number of seeds per cone, and seed germination rate. We quantified spatial and temporal climate effects on these traits. Spatial effects described how these traits varied among populations occupying contrasting long-term climates. Temporal effects described how traits changed when populations experienced anomalously warm, cold, wet, or dry seasons. We then used these two forms of climate sensitivity to project future trait values under future climate scenarios. Following the ecological acclimation framework, projections based on temporal anomaly effects represent near-term responses of current populations to future weather, whereas projections based on spatial climate effects represent longer-term expectations if reproductive traits track future climates through acclimation, local adaptation, or provenance turnover (Felton *et al.*, 2022; Perret *et al.*, 2024; Stemkovski *et al.*, 2025). We expected spatial climate gradients to reflect long-term differences in reproductive environments (Frenne *et al.*, 2013), with greater cone and seed investment under climates favourable for resource acquisition, i.e., warm and wet (Koenig *et al.*, 2009; Kondrat *et al.*, 2026). However, we expected temporal responses to diverge from these spatial patterns when annual weather anomalies pushed populations away from local reproductive optima, especially at sites that were already warm or dry. Consequently, we expected future projections based on spatial gradients and temporal anomalies to differ, with the magnitude of this difference indicating uncertainty about whether Scots pine reproductive traits can adjust quickly enough to keep pace with climate change.

Methods

Study species Scots pine (*Pinus sylvestris* L.) is one of the most widespread and economically important conifers in Europe, forming a large share of forests in northern, central, and eastern Europe. Its dominance reflects both broad ecological tolerance and extensive planting. Scots pine supports major timber industries and biodiversity (Mitchell *et al.*, 2026).

In Central Europe, Scots pine usually sheds pollen in May-June (Białobok *et al.*, 1993) and the cones mature the following year. Throughout the paper, we define t as the year in which cones were maturing;

therefore, spring $t - 1$ corresponds to the pollination period. After pollination, pollen tube growth slows or is suspended during winter, and fertilization occurs about 12 months later, usually in May-June of year t . Seed filling and cone maturation occur after fertilization during year t , whereas seed release often takes place the following spring. Thus, Scots pine reproduction integrates weather conditions across more than one year, from pollination in spring $t - 1$ through fertilization, seed filling, and cone maturation in year t .

Reproductive traits data We used cone and seed-quality data for Scots pine (*Pinus sylvestris* L.) collected in Poland across 184 sites and 15 years (2010 - 2024) as part of the State Forests monitoring programme of forest tree reproduction. The monitoring was commissioned by the State Forests and conducted by the Seed Testing Station of the Forest Research Institute. Scots pine stands were selected by Regional Directorates of the State Forests to represent seed-production areas used for reproductive monitoring and seed sourcing (Fig. 1). Mature cones were collected annually in October-November, prior to seed dispersal, from at least eight trees per stand and transported to the Forest Research Institute.

Cone and seed traits were derived from the laboratory processing of each cone sample (average N per site-year = 154, SD = 66.4) and represent site means. The number of cones in each sample was counted directly. To extract seeds, cones were dried in two stages: first at up to 35°C for 48 h, and then during intensive opening at up to 50°C. The mass of dry cones was measured after the second drying stage and represented cone mass with seeds before seed extraction. Mean cone mass, hereafter called cone mass, was calculated as (dry) cone mass divided by the number of cones measured. Seeds were then shaken out of the cones, and empty seeds and impurities were removed using a laboratory air separator. The mass of seeds therefore represented the mass of full seeds. The 1000-seed mass, hereafter called seed mass, was calculated from three replicate counts of 100 seeds, each weighed separately. The mean number of seeds per cone was estimated from seed mass, cone number, and 1000-seed mass. On average, full seeds represented approximately 1.6% of the dry cone mass (Fig. S2). Germination rate was tested by sowing 1000 seeds from each sample on Jacobsen germinators, and the percentage of germinated seedlings was calculated.

Climate data For all sites, we obtained daily climatic data (daily mean temperature TG, daily minimum temperature TN, daily maximum temperature TX, daily precipitation sum RR) from the Copernicus Climate Data Store [E-OBS datafiles, version 32.0e, 0.1 deg. regular grid, (Cornes *et al.*, 2018)]. Climatic variables included mean temperature and precipitation, which were aggregated to months and then phenological windows relevant to Scots pine reproduction. We defined t as the year of cone collection

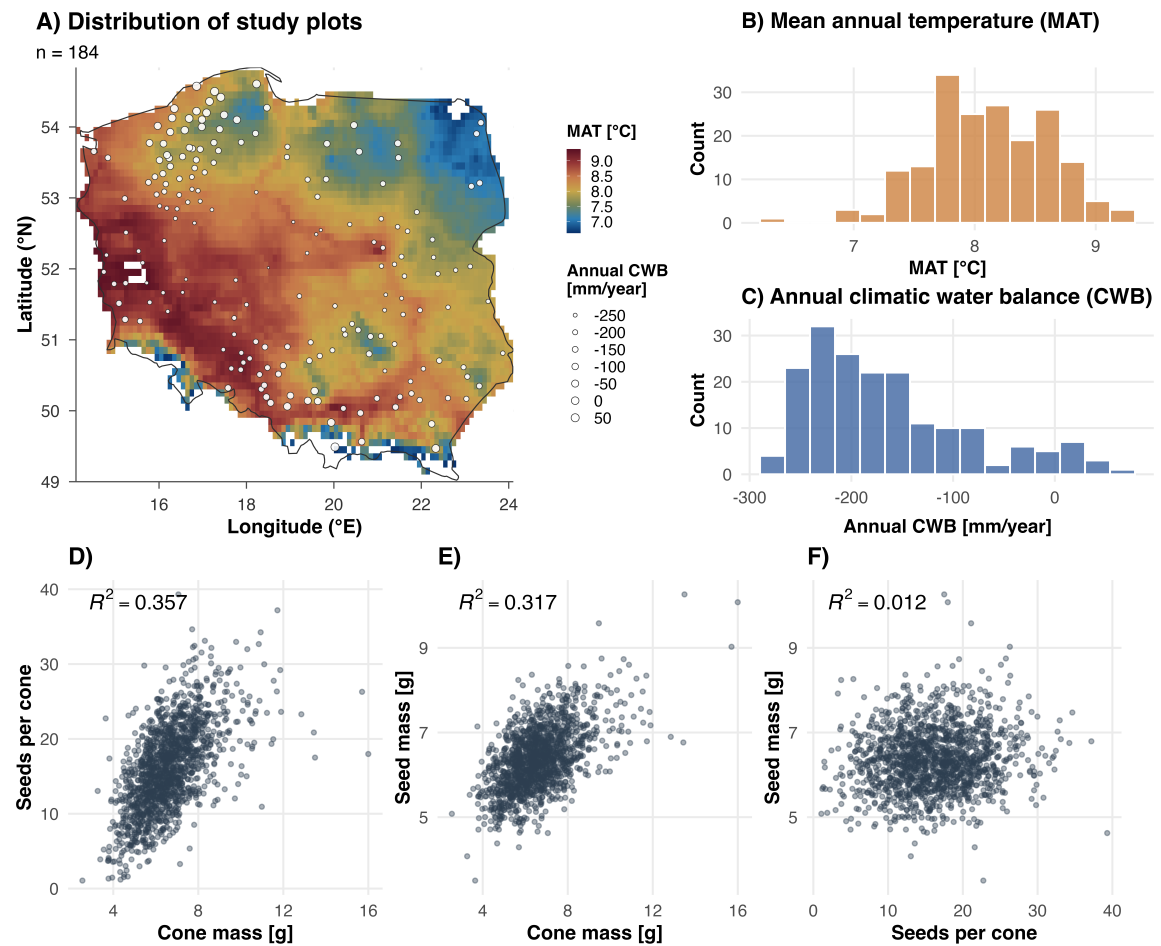


Figure 1: Study sites, their climatic gradients, and correlations among reproductive traits. Distribution of Scots pine study plots across Poland (A), site-level gradients in mean annual temperature (MAT; B) and annual climatic water balance (CWB; C), and pairwise relationships between selected reproductive traits analysed in this study: cone mass, seed number per cone, and seed mass (D-F). Data was collected across 184 sites and 15 years (2010-2024). Dots in D-F are site-level observations (N = 1475). Relationships with germination rate are provided in Fig. S1.

and seed-trait measurement, and calculated seasonal indices for spring t and $t - 1$ (May-June), summer t and $t - 1$ (July-August), and winter $t - 1/t$ (December-February). Mean temperature was averaged across months within each window. Climatic water balance (CWB) was calculated as the difference between total precipitation and potential evapotranspiration (PET) within each window. PET was estimated from monthly temperature data using the Hargreaves-Samani equation (Popa *et al.*, 2025; Hargreaves & Samani, 1985).

Future climate projections Historical climatic conditions were derived from the E-OBS gridded meteorological dataset, version 32.0e, at a spatial resolution of 0.1° (Cornes *et al.*, 2018). Monthly minimum temperature, maximum temperature and precipitation data were used aggregated from daily minimum temperature TN, daily maximum temperature TX. To ensure consistency with the future WorldClim data, mean temperature was calculated from minimum and maximum temperature as $T_{\text{mean}} = (T_{\text{min}} + T_{\text{max}})/2$. For each forest district, we extracted monthly temperature and precipitation projections and aggregated them to the same seasonal windows as in the analysis above. To project future cone and seed traits, we obtained monthly climate projections for 2070s, defined as the 2061-2080 period, under the SSP2-4.5 and SSP5-8.5 scenarios from WorldClim v. 2.1 (Fick & Hijmans, 2017) (30 arc-second resolution). We bilinearly resampled them to match the resolution of the historical climate data. Due to differences in projections resulting from different global climate model mechanics, we averaged projections from three global climate models: HadGEM3-GC31-LL, IPSL-CM6A-LR, and MPI-ESM1-2-HR. Poland's administrative boundaries were obtained and processed using the `rnaturalearth` v. 1.2.0 (Massicotte & South, 2026) and `rnaturalearthdata` v. 1.0.0 (South *et al.*, 2024) packages. Climatic water balance and mean temperature were calculated for future conditions using the same approach as for historical data. The summary of projected climate changes across seasons and scenarios is provided in Table S2.

Data Analysis

All analyses were performed in R (R Core Team, 2025), version 4.5.2. We fitted generalized linear mixed-effects models using the `glmmTMB` package (Brooks *et al.*, 2017), version 1.1.14. Response variables included cone mass, 1000-seed mass, number of seeds per cone, and germination rate (all at site-year level). Climatic predictors were mean temperature and climatic water balance (CWB), separately for winter, spring, and summer. Long-term site means were calculated for each season and used to estimate

spatial climate effects among forest districts. To estimate temporal variation, we calculated site-level yearly anomalies for each seasonal variable by subtracting the site's mean across all study years from the value observed in a given year. We evaluated these anomalies at lags corresponding to the Scots pine reproductive cycle: spring $t - 1$ for pollination, summer $t - 1$ and winter $t - 1/t$ for the post-pollination, pre-fertilization phase, spring t for fertilization, and summer t for seed filling and cone maturation. All climatic predictors were centred and scaled (Wickham *et al.*, 2025) before analysis. We also tested the interaction between each long-term seasonal mean and the corresponding anomaly for the same climate variable and season. Thus, each model separated spatial climate effects among forest districts from temporal weather effects within districts.

We fitted separate models for spring and summer seasonal anomalies because these temperature and CWB indices were strongly collinear. Thus, their effects should be interpreted as separate climate sensitivities rather than mutually adjusted effects. Forest district and measurement year were included as random intercepts to account for repeated sampling across space and time.

Model families were chosen according to the distribution of each response variable. Cone mass and seed mass effects were estimated using Gamma distributions because both traits are positive and right-skewed continuous variables. Germination rate was modelled using beta distributions because germination rate is a proportion bounded between 0 and 1. The number of seeds per cone was modelled with a Tweedie distribution because seed counts were non-negative and right-skewed. Model parameters were extracted and tidied using `broom.mixed` package (Bolker & Robinson, 2026), v. 0.2.9.7, and results were visualized using `ggplot2` package (Wickham, 2016), v. 4.0.3.

Future trait projections We projected future cone and seed traits using two climate-decomposition scenarios that correspond to different assumptions about ecological acclimation (Felton *et al.*, 2022; Perret *et al.*, 2024; Stemkovski *et al.*, 2025). Before prediction, all climatic predictors were standardized using the means and standard deviations derived from the model-fitting dataset, ensuring that present and future climatic conditions were expressed on the same scale as the predictors used to fit the models.

In the near-term anomaly scenario, mean climatic conditions were kept at their present-day values for 2010-2024, while future climate change was introduced as the difference between projected climate for 2061-2080 and present climate for 2010-2024. Because future projections represented average climatic conditions for 2061-2080, the same anomaly was used for years t and $t-1$.

In the long-term adjustment scenario, projected climatic conditions for 2061-2080 replaced present-day mean climate, while anomaly terms for years t and $t-1$ were set to zero.

Relative changes between future and present conditions were calculated as: $\% \Delta = 100 \times \frac{\hat{X}_{\text{future}} - \hat{X}_{\text{present}}}{\hat{X}_{\text{present}}}$, where: $\hat{X}_{\text{present}}$ is the predicted value for present (2010-2024) climate condition and $\hat{X}_{\text{future}}$ is the corresponding ensemble future (2061-2080) prediction.

To avoid predictions outside the climatic conditions represented by the study data, we applied the same climatic mask to all prediction rasters. The mask was based on baseline climate for 1950–2009 and excluded raster cells outside the climatic range represented in the model-fitting data.

Predictions were generated separately for each reproductive trait for present conditions (2010–2024) and for future conditions under SSP2-4.5 and SSP5-8.5 for 2061–2080. Because spring and summer climatic predictors were strongly collinear and were analysed in separate models (see Analysis), we generated separate future projections from the spring and summer models. The two sets of projections produced qualitatively similar results. We therefore present projections from the summer models in the main text and the corresponding projections from the spring models in the Appendix (Fig. S5). Final maps were generated using `ggplot2` v. 4.0.3 (Wickham, 2016), `terra` v. 1.8.93 (Hijmans, 2026), `sf` v. 1.1.1 (Pebesma & Bivand, 2023; Pebesma, 2018), `patchwork` v. 1.3.2 (Pedersen, 2025) and `scales` v. 1.4.0 (Wickham *et al.*, 2025) packages.

Results

Seed mass. Pines produced ~8-10% heavier seeds at warm and wet sites (Fig. 2A). For example, seed mass at sites where summers are relatively cold (15.5°C) had estimated seed mass at 6.1 g (95% CI: 5.83-6.30), which increased by 7.9%, to 6.5 g (95% CI: 6.38-6.70) at sites with warm summers (18.6°C). Similarly, seed mass at sites characterized by relatively cold springs (12.1°C) had estimated seed mass 6.1 g (95% CI: 5.84-6.29), which was higher by 7.8% (6.5 g, 95% CI: 6.38-6.69) at sites with warm springs (15.8°C).

Seed mass at sites where springs were dry (CWB = -164 mm) was 6.2 g (95% CI: 6.06-6.34), and was higher by 10%, (6.82 g, 95% CI: 6.53-7.13) at wetter sites (CWB = -19.7 mm). Similarly, seed mass at sites where summers were dry (CWB = -141.2 mm) was 6.2 g (95% CI: 6.06-6.37), which was higher by 9.5% (6.8 g, 95% CI: 6.47-7.15) at sites with relatively wetter summers (CWB = -3.6 mm).

Temporally, wetter springs (t) and summers (t-1) promote larger seeds. For example, seeds produced after wet springs (t) (365.2 mm; 6.8 g, 95% CI: 6.46-7.24) were 12.7% larger than those produced during dry springs (-265.8 mm; 6.1 g, 95% CI: 5.83-6.31). Seeds after wet previous-year summers (278.9 mm;

6.7 g, 95% CI: 6.38-6.92) were 7.6% larger than those produced during dry previous-year summers (-228 mm; 6.2 g, 95% CI: 5.98-6.38).

Warmer previous-year springs increased seed mass only at relatively cold sites, whereas the relationship became negative at warmer sites (Fig. 3). For example, at cold sites (12°C) seed mass increased by 7.7%, from 5.8 g to 6.3 g between cold (-0.5°C) and warm spring (3.5°C) springs t anomalies. In contrast, at hot sites (16°C) seed mass decreased by 7.8%, from 6.8 g to 6.3 g between cold and warm springs $t - 1$.

Wet summer conditions decreased seed mass at wet sites (Fig. 3). For example, seeds at relatively wet sites (CWB = -20 mm) decreased by 6.2%, from 7.2 g to 6.8 g, across summer moisture anomalies (from CWB of -180 to 180 mm). In turn, at dry sites, seeds were lighter, ~6.5 g, and showed little variation across summer moisture anomalies.

Cone mass. Scots pine produced ~14-20% larger cones in colder and wetter habitats (Fig. 2B). For example, cone mass at sites with cold springs (12.1°C) had an estimated cone mass of 7.4 g (95% CI: 6.91-7.95), and was higher by 15.4% (6.3 g, 95% CI: 6.00-6.55) at sites where springs were warm (15.8°C).

Sites characterized by dry springs (CWB = -164 mm) had a cone mass of 6.3 g (95% CI: 6.05-6.64), which was higher by 16.7% (7.4 g, 95% CI: 6.75-8.11) at wetter sites (CWB = -19.7 mm). Similarly, cone mass at sites where summers are dry (CWB = -141.2 mm) was 6.3 g (95% CI: 5.99-6.62), and was higher by 19.7% (7.5 g, 95% CI: 6.83-8.34) at sites with wetter summers (CWB = -3.6 mm).

Temporally, high previous-year spring and summer temperatures decreased cone mass (Fig. 2). For example, cones produced after cold summers (-0.74°C) were 5.6% larger (6.8 g; 95% CI: 6.33-7.31) than cones produced after warm summers (6.5 g; 95% CI: 6.01-6.93; 4.08°C). Cones produced after cold springs (-2.06°C) were 14.2% larger (7.1 g; 95% CI: 6.59-7.61) than cones produced after warm springs (6.2 g; 95% CI: 5.76-6.67; 4.04°C)

Similarly to the seed mass, wet summers decreased cone mass at wet sites (Fig. S3). For example, cones at relatively wet sites (CWB = -20) decreased by 19.8%, from 8.1 g to 6.5 g, across summer moisture anomalies (from CWB of -180 to 180). In turn, at dry sites, cones were lighter, ~6.5 g, and showed little variation across spring moisture anomalies.

Seeds per cone. Climate effects on seed number were thermal and often depended on background temperature (Fig. 2C). Spatially, seed number per cone was smaller at sites with cold winters (-4.1°C),

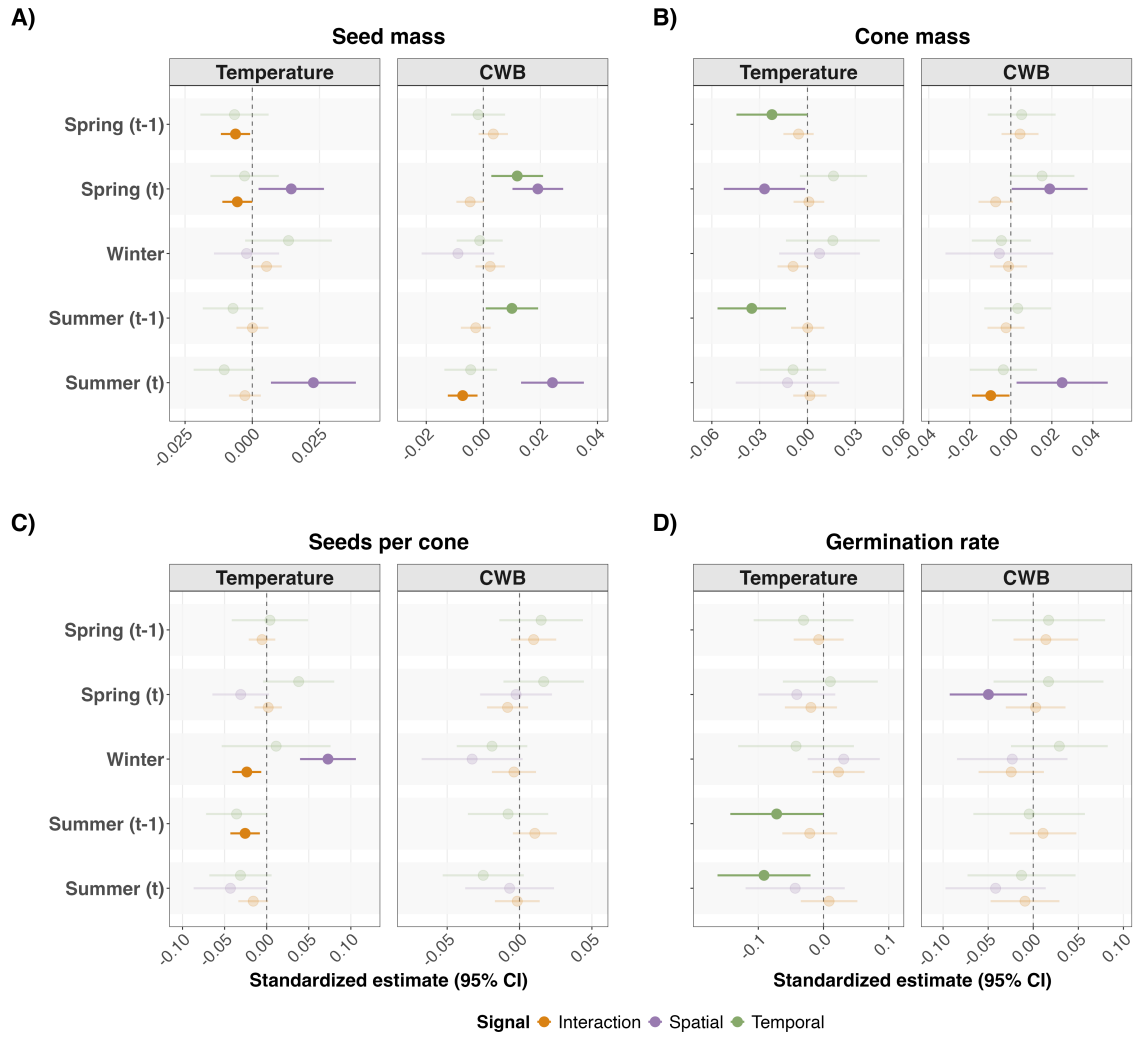


Figure 2: Spatial and temporal climate effects on seed mass, cone mass, seeds per cone, and germination rate in Scots pine. Points show standardized coefficient estimates and horizontal lines show 95% confidence intervals from GLMMs. Models included spatial climate effects, defined as long-term local climate means, temporal effects, defined as seasonal climate anomalies, and their interactions. To avoid collinearity among seasonal predictors, spring and summer climatic conditions were included in separate models (see Methods). Predictors were standardized to allow direct comparison of effect sizes. Transparent points indicate effects whose 95% confidence intervals overlapped zero. $N_{\text{sites}} = 184$; $N_{\text{observations}} = 1,475$ (Table S1).

i.e. 13.7 seeds (95% CI: 12.28-15.26), which was higher by 28.9% (17.6 seeds, 95% CI: 16.07-19.37) at sites with warm winters (0.3°C).

Temporally, effects varied across the climatic gradient (Fig. 3). Warmer winters increased seed number only at relatively cold sites, whereas the relationship became negative at warmer sites (Fig. S3). At sites with cold mean winter conditions (−3.5 °C), the number of seeds per cone increased by 24.0%, from 12.0 to 14.9, across winter temperature anomalies from −2 to +4.5 °C. In turn, at warmer sites (mean winter temperature = 0 °C), seeds number per cone decreased by 8.5%, from 18.8 to 17.2, across the same anomaly range. Similarly, hotter previous-year summers were associated with more seeds per cone at cold sites, but with fewer seeds per cone at hot sites (Fig. 3). For example, the number of seeds per cone at sites characterized by cold summers (15.5°C) increased by 17.7%, from 17 to 21, across summer temperature anomalies from 0.5°C to 2.5°C. In turn, at hot sites (18°C), the number of seeds per cone declined by 23.5%, from 17 to 14, across the same temperature range.

Germination rate. Germination rate was high (0.98 ± 0.03) and showed no spatial thermal sensitivity (Fig. 2D). Moisture effects were limited to spring and were minute, with germination rate at sites with dry springs (CWB = -164.0 mm) of 0.98 (95% CI: 0.97-0.98), which decreased by 1.0%, to 0.97 (95% CI: 0.96-0.98) at relatively wetter sites (CWB = -19.7 mm).

Temporally, warmer summers were associated with lower germination rate (Fig. 2D), although the effects were also minor. For example, germination rate in years with summer anomaly −0.7°C was estimated to be 0.98 (95% CI: 0.98-0.98), and decreased by 1.0%, to 0.97 (95% CI: 0.96-0.97) at years with summer anomaly of 4.7°C.

Future projections. Projected trait responses differed strongly depending on whether future climate change was treated as a shift in long-term climate or as anomalies experienced by current populations (Fig. 4). Under the long-term adjustment scenario, i.e., prediction based on spatial effects, seed mass increased across most of Poland, generally by approximately 5-10%, while the number of seeds per cone increased more strongly, commonly by 40-80%. In contrast, cone mass declined by approximately 5-10%. Under the near-term anomaly scenario, i.e., prediction based on temporal effects, all three traits declined: cone and seed mass generally decreased by approximately 5-10%, while the number of seeds per cone declined by approximately 40-80%. Thus, longer-term adjustment to future climate could maintain seed provisioning and increase the number of filled seeds per cone. In contrast, the response of current populations to future climate anomalies indicated substantial near-term losses in viable propagule supply.

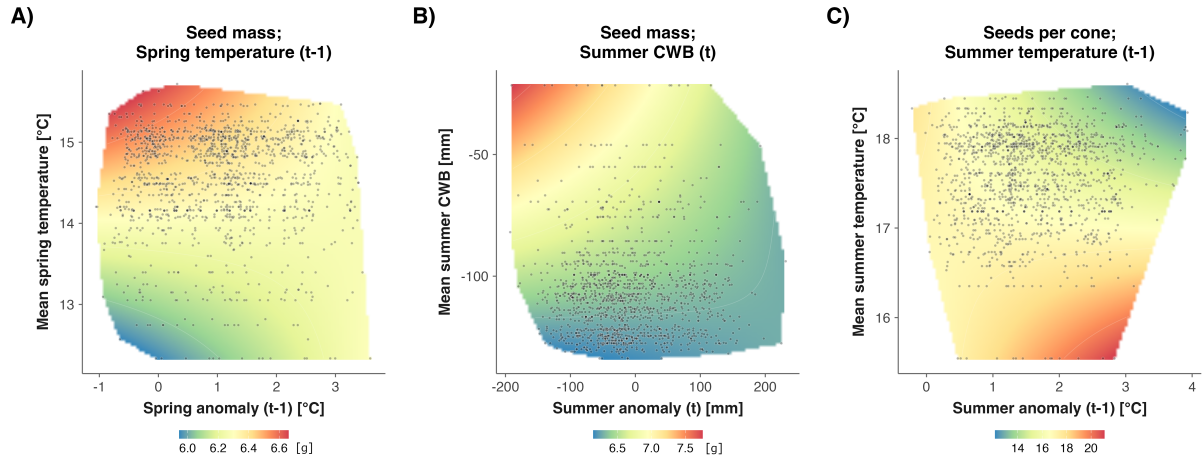


Figure 3: Background climate modifies temporal responses of Scots pine seed and cone traits to weather anomalies. Response surfaces show selected interactions between long-term local climate means and seasonal climate anomalies (see Fig. S3 for other interactions). Colours show model-predicted trait values from GLMMs, and grey points show observed combinations of spatial climate means and temporal anomalies. Panels show seed mass responses to previous-year spring temperature anomalies across the spring temperature gradient (A), seed mass responses to current-year summer CWB anomalies across the summer CWB gradient (B), and seed number per cone responses to previous-year summer temperature anomalies across the summer temperature gradient (C). Climate variables were back-transformed from the centred and scaled model scale to their original units. $N_{\text{sites}} = 184$; $N_{\text{observations}} = 1,475$.

Discussion

Our results show climate sensitivity of reproductive traits in Scots pine, highlighting their importance for forecasting climate effects on regeneration. Across space, pines produced more numerous and heavier seeds that were packaged in lighter cones in warmer climates. Temporal responses, however, diverged from these spatial patterns. Warm spring anomalies reduced seed and cone mass at warmer sites, and warm summer anomalies reduced the number of seeds per cone at warmer sites. Hot summers during seed maturation also reduced germination rate across the climatic gradient. Thus, although warmer sites can support heavier seeds, unusually hot years tended to produce lighter seeds, lighter cones, fewer seeds per cone, and seeds with a lower germination rate. The contrast between spatial and temporal signals suggests that Scots pine populations may adjust reproductive traits to long-term local climates, while short-term heat anomalies impose immediate constraints on seed and cone quality. Near-term climate warming may therefore create regeneration bottlenecks before longer-term adjustment can occur, especially in populations that already occupy warm parts of the climatic gradient.

Temperature effects indicate that reproductive traits respond to warming through a balance between relaxed cold limitation and increasing heat stress. Across sites, warmer climates were associated mainly with heavier seeds (by ~8%), consistent with the notion that long-term thermal conditions can favour seed filling by extending development or increasing resource acquisition (Frenne *et al.*, 2013; Kondrat

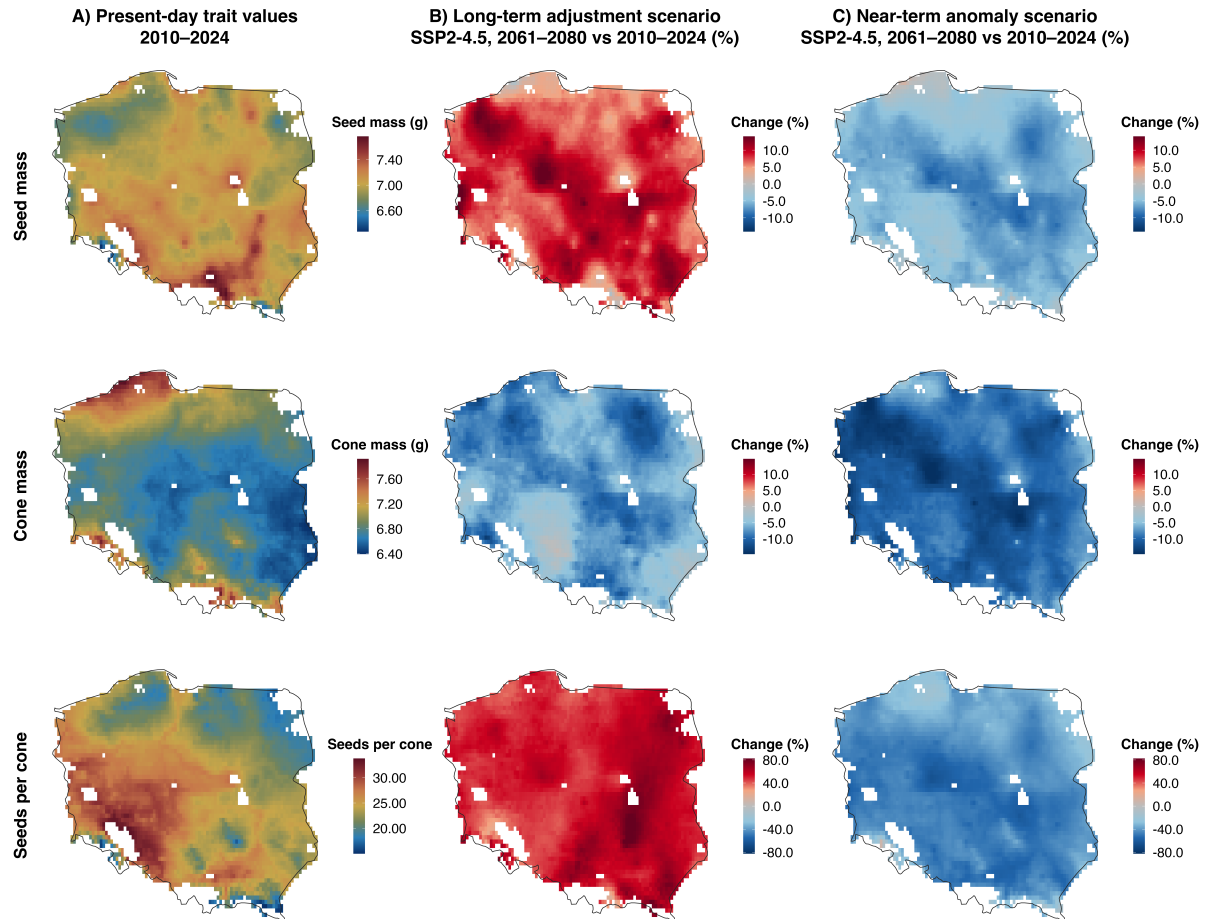


Figure 4: Projected changes in Scots pine reproductive traits under future climate. Rows show seed mass, cone mass, and the number of seeds per cone. Maps in the left column show trait values predicted under the present-day climate of 2010–2024. The middle column shows the percentage change projected for 2061–2080 under SSP2-4.5 when future climate replaces the historical long-term site climate, representing longer-term adjustment through acclimation, local adaptation, or provenance turnover. The right column shows the percentage change when future climate is expressed as an anomaly from each site’s historical climate, representing the near-term response of current populations before slower adjustment occurs. Temporal projections include interactions between historical site climate and future anomalies. White areas indicate climatic conditions outside the model calibration range. Projections based on models that included spring weather instead of summer are given in Fig. S5.

et al., 2026). At the same time, cones were lighter (by ~14%) in warmer habitats, suggesting that warmer long-term climates may shift reproductive allocation toward seed filling and away from cone tissue. In turn, temporal responses showed that warm anomalies can become detrimental within local populations. Spring warming increased seed mass only at colder sites (by ~8%), suggesting that additional heat may benefit reproduction where development remains thermally limited. At warmer sites, the same anomalies reduced seed mass (by ~8%), indicating that temperatures above local optima can constrain seed filling. Similar context dependence was observed for seed number per cone, with hot summers reducing seed number most strongly at warm sites (by ~23%). Cone mass declined in hot years as well (up to 14%), as did germination rates, although germination effects were minor (~1%). These negative temperature anomaly effects may arise through several mechanisms. High temperatures can impair pollen development, pollen germination, and pollen-tube growth, reducing fertilization success and seed set (Parantainen & Pulkkinen, 2002; Snider *et al.*, 2011; Müller & Rieu, 2016; Hsu & Kim, 2025). Heat can also reduce carbon gain, especially when high temperature coincides with water limitation. Scots pine closes stomata under drought, which limits carbon assimilation, and hot drought can reduce net carbon uptake to very low levels (Irvine *et al.*, 1998; Nadal-Sala *et al.*, 2021; Haberstroh *et al.*, 2022). Lower carbon gain during pollination, fertilization, seed filling, or cone maturation could therefore reduce the resources available for reproductive structures, leading to fewer filled seeds, smaller seeds, and lighter cones.

Water availability shaped reproductive investment through seed and cone mass. Across sites, pines produced heavier seeds and larger cones under wetter spring and summer climates, consistent with the expectation that greater water availability improves resource acquisition during cone development and seed filling (Walck *et al.*, 2011; Gao *et al.*, 2023; Kondrat *et al.*, 2026). Temporal moisture effects, however, did not mirror these spatial patterns. Seed and cone mass were highest at relatively wet sites, but within these sites, positive wet summer anomalies were associated with lower seed and cone mass. In contrast, dry sites produced small seeds and cones and showed little response to either wet or dry anomalies. This pattern suggests that populations in dry climates operate near a lower reproductive investment limit, whereas populations in wet climates retain greater capacity for variation in cone growth and seed filling. Short wet periods therefore do not necessarily increase reproductive investment, and may even reduce it at wet sites, potentially through reduced radiation or other conditions associated with wet summers. From a climate-change perspective, the moisture signal points to different near-term and long-term expectations. In the near term, drying anomalies may not further depress seed and cone mass at

371 already dry sites because reproductive investment is already low. Over longer periods, declining climatic
372 water balance may shift populations toward the smaller-seed and smaller-cone phenotype observed in
373 chronically dry sites.

374 Considering traits jointly shows that hot and wet years can alter regeneration potential through several
375 linked components of viable seed supply. Germination rate changed little, with hot summers reducing
376 germination by only about 1%. This small effect suggests that, once filled seeds are produced, Scots pine
377 seeds usually retain high germination capacity. The larger constraints occurred earlier in the reproductive
378 pathway. At warm sites, hot summer anomalies reduced the number of seeds per cone by more than 20%,
379 indicating that reproductive potential can decline substantially even without a change in cone production
380 itself. Cone counts alone would therefore miss an important component of fecundity variation, because
381 cones produced after hot years may contain fewer filled seeds. Hot years also reduced seed (~8%) and
382 cone mass (~14%) at warm sites, so lower seed number was accompanied by reduced seed provisioning
383 and, possibly, weaker protection against consumers. Greater investment in cone tissue may impede access
384 to seeds by consumers such as squirrels and crossbills, but the evidence is mixed: protection depends on
385 specific cone traits and consumer identity, while larger, more seed-rich cones may also be preferentially
386 selected (Benkman, 1999; Molinari *et al.*, 2006; Leslie, 2011).

387 These combined effects matter because larger seeds often improve early seedling performance,
388 especially under stressful establishment conditions such as drought (Castro, 1999; Landergott *et al.*,
389 2012). Moisture effects added a second dimension to this reduction in reproductive quality. Across sites,
390 wetter climates supported heavier seeds and larger cones, meaning that dry sites already produce smaller
391 seeds and less cone tissue. Climate effects on seed number, seed mass, and cone mass may reinforce
392 one another: unfavourable years can reduce the quantity of potential recruits, the provisioning of each
393 recruit, and the protective cone tissue around seeds. Combining cone mass, seed number, seed mass,
394 and germination therefore reveals a fuller picture of reproductive performance than any single trait could
395 provide.

396 Genomic data provide an additional dimension for interpreting these spatial gradients. Polish Scots
397 pine stands contain high genetic diversity within populations but show little genome-wide differentiation
398 among most provenance regions (Lasek *et al.*, 2024), consistent with weak range-wide genetic structure
399 in Scots pine (Bruxaux *et al.*, 2024). More recent analyses indicate that lowland stands form an admixed
400 genetic mosaic derived from multiple European lineages, whereas mountain populations are more strongly
401 differentiated and represent an important exception to the otherwise weak structure (Lasek *et al.*, 2026).

Our spatial trait relationships should therefore not be read as direct evidence of fixed genetic differentiation among provenances; they may instead integrate acclimation and polygenic local adaptation that cannot be separated by our observational design. The high standing genetic diversity documented among Polish populations of Scots pine could provide capacity for evolutionary responses to changing climate, but whether such responses can proceed rapidly enough to buffer the near-term reproductive losses identified here remains uncertain (Alberto *et al.*, 2013; Lasek *et al.*, 2024, 2026).

Forecasting reproductive responses to climate change requires matching the climate signal to the forecast horizon. Ecological acclimation theory distinguishes fast responses to weather anomalies from slower adjustment to long-term climate, and stresses that these sensitivities can differ in magnitude or direction (Stemkovski *et al.*, 2025). Our future projections made this distinction explicit. Spatial-gradient projections suggested that longer-term adjustment to warmer climates could partly maintain or increase seed mass and number of seeds per cone, whereas temporal-anomaly projections indicated near-term reductions. If Scots pine reproductive traits track future climates slowly, current populations may experience the stronger losses predicted by temporal anomaly models before any longer-term adjustment occurs. A similar contrast was reported for Scots pine seed production across Poland: pine produced more seeds at warmer sites, yet seed production declined over time as summers warmed (Foest *et al.*, 2026). Together, these results suggest that warming may reduce pine reproductive capacity through multiple pathways: fewer cones (Foest *et al.*, 2026), fewer filled seeds per cone, and reduced seed provisioning. These effects are likely to interact with climate-sensitive seedling establishment, because smaller seed crops and smaller seeds can reduce the capacity of populations to compensate for mortality during hot and dry recruitment years (Davis *et al.*, 2019, 2023). Forecasts of Scots pine persistence therefore need to move beyond adult growth, mortality, or cone counts alone, and integrate seed production, seed quality, and recruitment. Long-term recruitment studies are a priority, because they can determine whether the decline in reproductive potential documented here is already translating into reduced population growth rates.

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Author Contributions Statement

SB and MB conceived and designed the study. MD, SJ, AG collected and curated the data. SB conducted the analysis. MB wrote the first draft of the manuscript. All authors contributed to the interpretation of the analysis, revised the draft, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data availability statement

The data supporting the results are archived in the Open Science Framework and are available at: <https://doi.org/10.17605/OSF.IO/K53ZN>.

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628 **Supporting Information**

629 **Heat-driven declines in Scots pine cone and seed quality contrast with spatial evidence of adaptive**
630 **potential**

631

Table S1: Generalized linear mixed-effects models of the effects of mean temperature (Temperature) and climatic water balance (CWB), expressed as long-term means, anomalies, and interactions between means and anomalies, on reproductive traits of Scots pine.

Predictor	Estimate	SE	<i>z</i>	<i>p</i>
Seed mass — spring model				
<i>N</i> = 1475; <i>sites</i> = 184; <i>years</i> = 15; <i>AIC</i> = 3120.3; <i>BIC</i> = 3226.2; <i>logLik</i> = −1540.2.				
<i>Random SD: site</i> = 0.0340, <i>year</i> = 0.0259; <i>Gamma family with log link; dispersion</i> = 0.0108.				
(Intercept)	1.851	0.008	237.35	$< 2 \times 10^{-16}$
Spring Temperature mean	0.014	0.006	2.34	0.019
Winter Temperature mean	0.005	0.005	0.91	0.361
Spring Temperature anomaly (<i>t</i>)	−0.003	0.006	−0.44	0.658
Winter Temperature anomaly (<i>t</i>)	0.006	0.008	0.77	0.443
Spring Temperature anomaly (<i>t</i> − 1)	−0.007	0.006	−1.02	0.306
Spring CWB mean	0.019	0.005	4.21	< 0.001
Winter CWB mean	−0.006	0.006	−1.10	0.271
Spring CWB anomaly (<i>t</i>)	0.012	0.005	2.56	0.010
Winter CWB anomaly (<i>t</i>)	−0.002	0.004	−0.51	0.612
Spring CWB anomaly (<i>t</i> − 1)	−0.002	0.005	−0.38	0.703
Spring Temperature mean × Spring Temperature anomaly (<i>t</i>)	−0.006	0.003	−1.97	0.049
Spring Temperature mean × Spring Temperature anomaly (<i>t</i> − 1)	−0.006	0.003	−2.25	0.024
Winter Temperature mean × Winter Temperature anomaly (<i>t</i>)	0.004	0.003	1.50	0.133
Spring CWB mean × Spring CWB anomaly (<i>t</i>)	−0.005	0.002	−1.89	0.059
Spring CWB mean × Spring CWB anomaly (<i>t</i> − 1)	0.003	0.003	1.33	0.183
Winter CWB mean × Winter CWB anomaly (<i>t</i>)	0.003	0.003	1.24	0.214
Cone mass — spring model				
<i>N</i> = 1475; <i>sites</i> = 184; <i>years</i> = 15; <i>AIC</i> = 4862.8; <i>BIC</i> = 4968.8; <i>logLik</i> = −2411.4.				
<i>Random SD: site</i> = 0.0830, <i>year</i> = 0.0458; <i>Gamma family with log link; dispersion</i> = 0.032.				
(Intercept)	1.891	0.015	129.90	$< 2 \times 10^{-16}$
Spring Temperature mean	−0.027	0.013	−2.07	0.039
Winter Temperature mean	0.009	0.011	0.84	0.402

Continued on next page

Table S1 – continued

Predictor	Estimate	SE	<i>z</i>	<i>p</i>
Spring Temperature anomaly (<i>t</i>)	0.016	0.011	1.52	0.129
Winter Temperature anomaly (<i>t</i>)	0.013	0.013	0.97	0.331
Spring Temperature anomaly (<i>t</i> – 1)	–0.022	0.011	–1.96	0.050
Spring CWB mean	0.019	0.009	2.01	0.044
Winter CWB mean	–0.006	0.012	–0.49	0.626
Spring CWB anomaly (<i>t</i>)	0.015	0.008	1.90	0.058
Winter CWB anomaly (<i>t</i>)	–0.002	0.007	–0.27	0.791
Spring CWB anomaly (<i>t</i> – 1)	0.005	0.008	0.63	0.531
Spring Temperature mean × Spring Temperature anomaly (<i>t</i>)	0.001	0.005	0.19	0.852
Spring Temperature mean × Spring Temperature anomaly (<i>t</i> – 1)	–0.006	0.005	–1.16	0.248
Winter Temperature mean × Winter Temperature anomaly (<i>t</i>)	–0.012	0.005	–2.43	0.015
Spring CWB mean × Spring CWB anomaly (<i>t</i>)	–0.007	0.004	–1.73	0.083
Spring CWB mean × Spring CWB anomaly (<i>t</i> – 1)	0.004	0.005	0.98	0.329
Winter CWB mean × Winter CWB anomaly (<i>t</i>)	0.001	0.005	0.15	0.879

Seeds per cone — spring model

N = 1475; sites = 184; years = 15; AIC = 8991.3; BIC = 9102.6; logLik = –4474.7.

Random SD: site = 0.0889, year = 0.1594; Tweedie family with log link; dispersion = 1.3.

(Intercept)	2.769	0.043	64.90	$< 2 \times 10^{-16}$
Spring Temperature mean	–0.031	0.017	–1.80	0.072
Winter Temperature mean	0.061	0.014	4.26	< 0.001
Spring Temperature anomaly (<i>t</i>)	0.038	0.022	1.76	0.078
Winter Temperature anomaly (<i>t</i>)	–0.028	0.037	–0.75	0.451
Spring Temperature anomaly (<i>t</i> – 1)	0.004	0.023	0.17	0.867
Spring CWB mean	–0.002	0.013	–0.19	0.848
Winter CWB mean	–0.025	0.016	–1.54	0.124
Spring CWB anomaly (<i>t</i>)	0.017	0.014	1.18	0.240
Winter CWB anomaly (<i>t</i>)	–0.018	0.013	–1.40	0.161
Spring CWB anomaly (<i>t</i> – 1)	0.015	0.015	1.01	0.311

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Table S1 – continued

Predictor	Estimate	SE	<i>z</i>	<i>p</i>
Spring Temperature mean × Spring Temperature anomaly (<i>t</i>)	0.002	0.008	0.22	0.829
Spring Temperature mean × Spring Temperature anomaly (<i>t</i> – 1)	–0.006	0.008	–0.69	0.490
Winter Temperature mean × Winter Temperature anomaly (<i>t</i>)	–0.037	0.009	–4.21	< 0.001
Spring CWB mean × Spring CWB anomaly (<i>t</i>)	–0.008	0.007	–1.15	0.252
Spring CWB mean × Spring CWB anomaly (<i>t</i> – 1)	0.010	0.008	1.22	0.222
Winter CWB mean × Winter CWB anomaly (<i>t</i>)	–0.001	0.008	–0.12	0.904

Germination rate — spring model

N = 1475; sites = 184; years = 15; AIC = –8031.6; BIC = –7925.7; logLik = 4035.8.

Random SD: site = 0.0000, year = 0.1339; Beta family with logit link; dispersion = 52.3.

(Intercept)	3.691	0.042	88.58	< 2 × 10 ^{–16}
Spring Temperature mean	–0.041	0.030	–1.36	0.173
Winter Temperature mean	0.016	0.025	0.67	0.506
Spring Temperature anomaly (<i>t</i>)	0.010	0.037	0.28	0.778
Winter Temperature anomaly (<i>t</i>)	–0.068	0.042	–1.61	0.108
Spring Temperature anomaly (<i>t</i> – 1)	–0.031	0.039	–0.78	0.434
Spring CWB mean	–0.050	0.022	–2.27	0.023
Winter CWB mean	–0.015	0.029	–0.50	0.615
Spring CWB anomaly (<i>t</i>)	0.017	0.031	0.54	0.587
Winter CWB anomaly (<i>t</i>)	0.022	0.027	0.82	0.413
Spring CWB anomaly (<i>t</i> – 1)	0.017	0.032	0.53	0.595
Spring Temperature mean × Spring Temperature anomaly (<i>t</i>)	–0.019	0.020	–0.95	0.342
Spring Temperature mean × Spring Temperature anomaly (<i>t</i> – 1)	–0.007	0.020	–0.38	0.704
Winter Temperature mean × Winter Temperature anomaly (<i>t</i>)	0.012	0.020	0.61	0.541
Spring CWB mean × Spring CWB anomaly (<i>t</i>)	0.003	0.017	0.16	0.875
Spring CWB mean × Spring CWB anomaly (<i>t</i> – 1)	0.014	0.018	0.76	0.445
Winter CWB mean × Winter CWB anomaly (<i>t</i>)	–0.016	0.018	–0.87	0.385

Seed mass — summer model

N = 1475; sites = 184; years = 15; AIC = 3121.8; BIC = 3227.7; logLik = –1540.9.

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Table S1 – continued

Predictor	Estimate	SE	<i>z</i>	<i>p</i>
<i>Random SD: site = 0.0357, year = 0.0295; Gamma family with log link; dispersion = 0.0107.</i>				
(Intercept)	1.852	0.009	213.51	$< 2 \times 10^{-16}$
Summer Temperature mean	0.023	0.008	2.82	0.005
Winter Temperature mean	-0.002	0.006	-0.35	0.730
Summer Temperature anomaly (<i>t</i>)	-0.010	0.006	-1.80	0.071
Winter Temperature anomaly (<i>t</i>)	0.013	0.008	1.64	0.102
Summer Temperature anomaly (<i>t</i> - 1)	-0.007	0.006	-1.25	0.212
Summer CWB mean	0.024	0.006	4.31	< 0.001
Winter CWB mean	-0.009	0.006	-1.37	0.170
Summer CWB anomaly (<i>t</i>)	-0.004	0.005	-0.94	0.347
Winter CWB anomaly (<i>t</i>)	-0.001	0.004	-0.31	0.757
Summer CWB anomaly (<i>t</i> - 1)	0.010	0.005	2.14	0.032
Summer Temperature mean × Summer Temperature anomaly (<i>t</i>)	-0.003	0.003	-0.91	0.364
Summer Temperature mean × Summer Temperature anomaly (<i>t</i> - 1)	0.000	0.003	0.02	0.984
Winter Temperature mean × Winter Temperature anomaly (<i>t</i>)	0.005	0.003	1.84	0.065
Summer CWB mean × Summer CWB anomaly (<i>t</i>)	-0.007	0.003	-2.72	0.006
Summer CWB mean × Summer CWB anomaly (<i>t</i> - 1)	-0.003	0.003	-1.00	0.319
Winter CWB mean × Winter CWB anomaly (<i>t</i>)	0.002	0.003	0.91	0.362

Cone mass — summer model

N = 1475; *sites* = 184; *years* = 15; *AIC* = 4859.7; *BIC* = 4965.6; *logLik* = -2409.8.

Random SD: site = 0.0844, year = 0.0628; Gamma family with log link; dispersion = 0.0317.

(Intercept)	1.891	0.018	103.14	$< 2 \times 10^{-16}$
Summer Temperature mean	-0.013	0.017	-0.76	0.450
Winter Temperature mean	0.008	0.013	0.59	0.558
Summer Temperature anomaly (<i>t</i>)	-0.009	0.011	-0.85	0.393
Winter Temperature anomaly (<i>t</i>)	0.016	0.015	1.06	0.288
Summer Temperature anomaly (<i>t</i> - 1)	-0.035	0.011	-3.18	0.001

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Table S1 – continued

Predictor	Estimate	SE	<i>z</i>	<i>p</i>
Summer CWB mean	0.025	0.011	2.21	0.027
Winter CWB mean	−0.006	0.013	−0.42	0.677
Summer CWB anomaly (<i>t</i>)	−0.004	0.008	−0.43	0.665
Winter CWB anomaly (<i>t</i>)	−0.005	0.007	−0.62	0.532
Summer CWB anomaly (<i>t</i> − 1)	0.003	0.008	0.40	0.686
Summer Temperature mean × Summer Temperature anomaly (<i>t</i>)	0.002	0.005	0.29	0.774
Summer Temperature mean × Summer Temperature anomaly (<i>t</i> − 1)	0.000	0.005	0.03	0.978
Winter Temperature mean × Winter Temperature anomaly (<i>t</i>)	−0.009	0.005	−1.81	0.071
Summer CWB mean × Summer CWB anomaly (<i>t</i>)	−0.010	0.005	−2.09	0.036
Summer CWB mean × Summer CWB anomaly (<i>t</i> − 1)	−0.002	0.005	−0.51	0.610
Winter CWB mean × Winter CWB anomaly (<i>t</i>)	−0.001	0.005	−0.24	0.809

Seeds per cone — summer model

$N = 1475$; sites = 184; years = 15; AIC = 8981.5; BIC = 9092.7; logLik = −4469.8.

Random SD: site = 0.0928, year = 0.1660; Tweedie family with log link; dispersion = 1.29.

(Intercept)	2.771	0.044	62.47	$< 2 \times 10^{-16}$
Summer Temperature mean	−0.043	0.022	−1.93	0.053
Winter Temperature mean	0.073	0.017	4.30	< 0.001
Summer Temperature anomaly (<i>t</i>)	−0.031	0.019	−1.65	0.099
Winter Temperature anomaly (<i>t</i>)	0.011	0.033	0.34	0.733
Summer Temperature anomaly (<i>t</i> − 1)	−0.036	0.018	−1.94	0.053
Summer CWB mean	−0.007	0.016	−0.44	0.660
Winter CWB mean	−0.033	0.018	−1.84	0.066
Summer CWB anomaly (<i>t</i>)	−0.025	0.014	−1.75	0.079
Winter CWB anomaly (<i>t</i>)	−0.019	0.012	−1.53	0.126
Summer CWB anomaly (<i>t</i> − 1)	−0.008	0.014	−0.56	0.575
Summer Temperature mean × Summer Temperature anomaly (<i>t</i>)	−0.016	0.009	−1.76	0.078

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Table S1 – continued

Predictor	Estimate	SE	<i>z</i>	<i>p</i>
Summer Temperature mean × Summer Temperature anomaly (<i>t</i> – 1)	–0.026	0.009	–2.86	0.004
Winter Temperature mean × Winter Temperature anomaly (<i>t</i>)	–0.024	0.009	–2.69	0.007
Summer CWB mean × Summer CWB anomaly (<i>t</i>)	–0.002	0.008	–0.20	0.843
Summer CWB mean × Summer CWB anomaly (<i>t</i> – 1)	0.011	0.008	1.36	0.173
Winter CWB mean × Winter CWB anomaly (<i>t</i>)	–0.004	0.008	–0.50	0.618
Germination rate — summer model				
<i>N</i> = 1475; <i>sites</i> = 184; <i>years</i> = 15; <i>AIC</i> = –8039.3; <i>BIC</i> = –7933.4; <i>logLik</i> = 4039.7.				
<i>Random SD: site</i> = 0.0000, <i>year</i> = 0.1543; <i>Beta family with logit link; dispersion</i> = 52.7.				
(Intercept)	3.696	0.046	80.09	$< 2 \times 10^{-16}$
Summer Temperature mean	–0.043	0.039	–1.12	0.262
Winter Temperature mean	0.031	0.028	1.10	0.272
Summer Temperature anomaly (<i>t</i>)	–0.091	0.036	–2.51	0.012
Winter Temperature anomaly (<i>t</i>)	–0.042	0.045	–0.93	0.351
Summer Temperature anomaly (<i>t</i> – 1)	–0.072	0.036	–1.98	0.047
Summer CWB mean	–0.042	0.028	–1.47	0.141
Winter CWB mean	–0.023	0.031	–0.75	0.456
Summer CWB anomaly (<i>t</i>)	–0.013	0.031	–0.43	0.670
Winter CWB anomaly (<i>t</i>)	0.029	0.027	1.06	0.291
Summer CWB anomaly (<i>t</i> – 1)	–0.005	0.032	–0.14	0.885
Summer Temperature mean × Summer Temperature anomaly (<i>t</i>)	0.009	0.022	0.39	0.700
Summer Temperature mean × Summer Temperature anomaly (<i>t</i> – 1)	–0.021	0.021	–0.98	0.325
Winter Temperature mean × Winter Temperature anomaly (<i>t</i>)	0.023	0.020	1.12	0.262
Summer CWB mean × Summer CWB anomaly (<i>t</i>)	–0.009	0.019	–0.47	0.638
Summer CWB mean × Summer CWB anomaly (<i>t</i> – 1)	0.011	0.019	0.57	0.566
Winter CWB mean × Winter CWB anomaly (<i>t</i>)	–0.024	0.018	–1.32	0.186

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Table S1 – continued

Predictor	Estimate	SE	z	p
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Notes: t = current year (year of fertilization, seed filling, and seed dispersal); $t - 1$ = previous year (year of pollination). SE = standard error. Estimates are reported on the model link scale. All continuous predictors were standardized.

Table S2: Projected seasonal changes in mean temperature and climatic water balance.

Scenario	Variable	Mean	SD	Median	Min.	Max.	Unit
SSP2–4.5	Spring Tmean	1.67	0.385	1.66	-0.61	6.05	°C
SSP2–4.5	Summer Tmean	2.21	0.394	2.19	-0.16	6.94	°C
SSP2–4.5	Winter Tmean	2.06	0.451	2.03	-0.94	5.28	°C
SSP2–4.5	Spring CWB	5.24	19.3	6.71	-183	115	mm
SSP2–4.5	Summer CWB	-32.1	17.9	-32.0	-260	66.2	mm
SSP2–4.5	Winter CWB	-8.08	18.1	-8.28	-220	98.9	mm
SSP5–8.5	Spring Tmean	2.95	0.383	2.93	0.08	7.76	°C
SSP5–8.5	Summer Tmean	4.32	0.454	4.31	1.08	9.36	°C
SSP5–8.5	Winter Tmean	3.50	0.485	3.49	0.37	6.75	°C
SSP5–8.5	Spring CWB	-12.3	19.3	-10.9	-225	126	mm
SSP5–8.5	Summer CWB	-67.1	19.0	-66.1	-335	12.4	mm
SSP5–8.5	Winter CWB	-7.32	18.0	-8.08	-221	104	mm

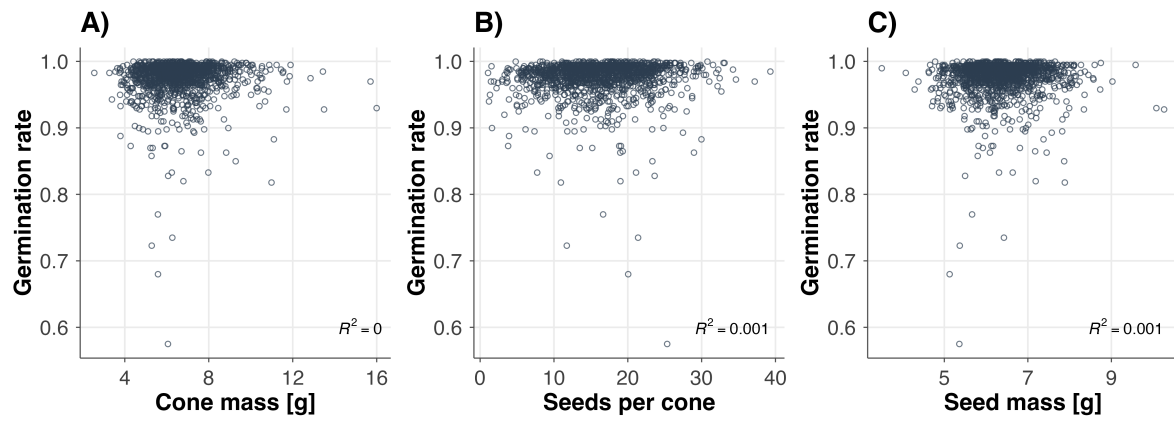


Figure S1: Additional pairwise relationships among the germination rate and other reproductive traits analysed in this study: A) cone mass, B) seed number per cone, and C) seed mass. Data was collected across 184 sites and 15 years (2010-2024). Dots in A-C are site-level observations (N = 1475)

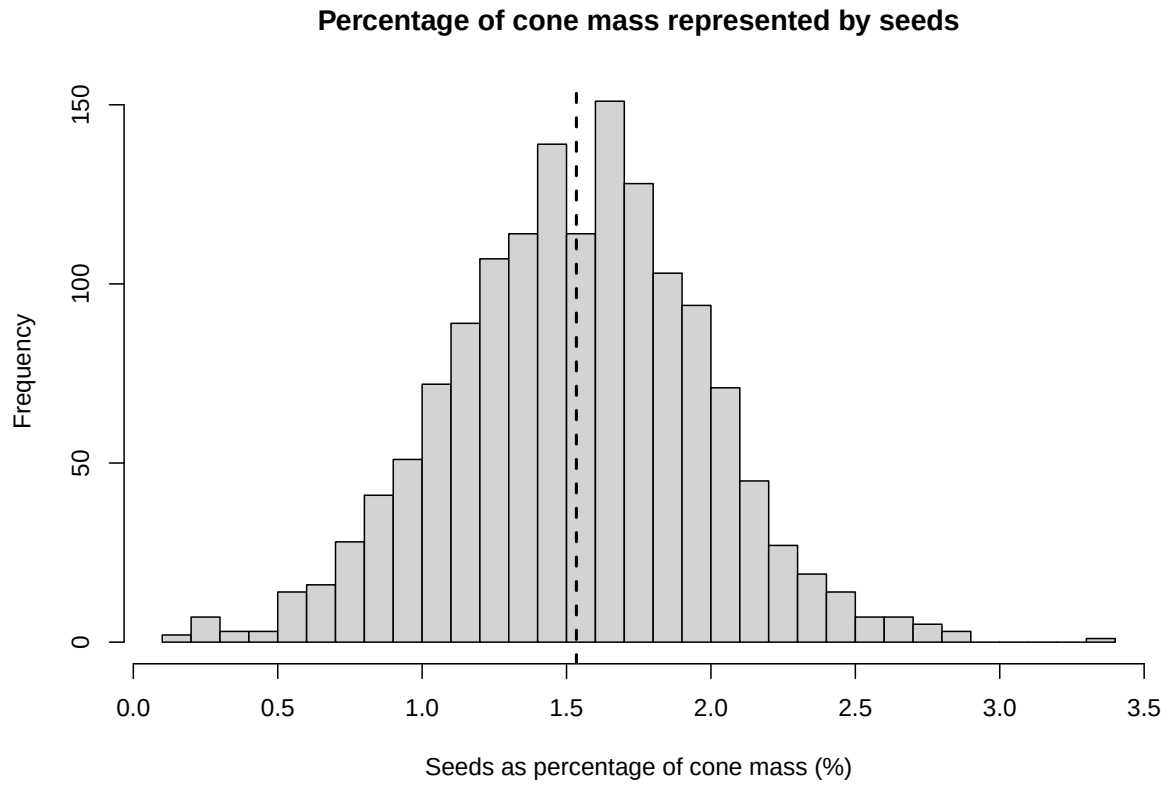


Figure S2: Distribution of the percentage of dry cone mass represented by seeds across cone samples. Bars show the frequency of observations, and the dashed vertical line indicates the overall mean (approximately 1.6%).

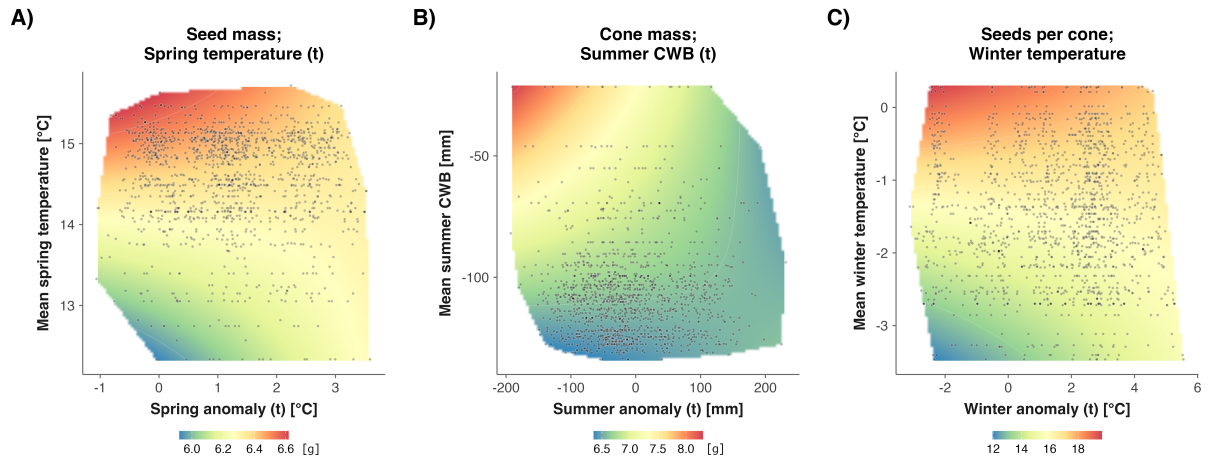


Figure S3: Additional interactions between background climate and weather anomalies for Scots pine cone and seed traits. Response surfaces show selected significant interactions between long-term local climate means and seasonal climate anomalies (see Fig. 3 for others). Colours show model-predicted trait values from GLMMs, and grey points show observed combinations of spatial climate means and temporal anomalies. Panels show (A) cone mass responses to current-year summer CWB anomalies across the summer CWB gradient, and (B) seed number per cone responses to winter temperature anomalies across the winter temperature gradient. Data was collected across 184 sites and 15 years (2010–2024). Dots in A–C are site-level observations ($N = 1475$)

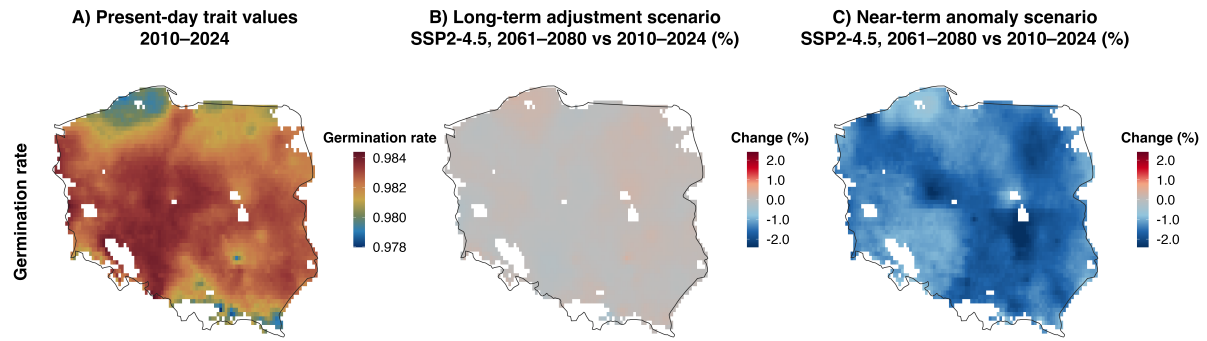


Figure S4: Projected changes in Scots pine germination rate under future climate. Maps in the left column show trait values predicted under the present-day climate of 2010–2024. The middle column shows the percentage change projected for 2061–2080 under SSP2-4.5 when future climate replaces the historical long-term site climate, representing longer-term adjustment through acclimation, local adaptation, or provenance turnover. The right column shows the percentage change when future climate is expressed as an anomaly from each site’s historical climate, representing the near-term response of current populations before slower adjustment occurs. Temporal projections include interactions between historical site climate and future anomalies. White areas indicate climatic conditions outside the model calibration range. Projections based on models that included the other traits for summer are given in Fig. 4.

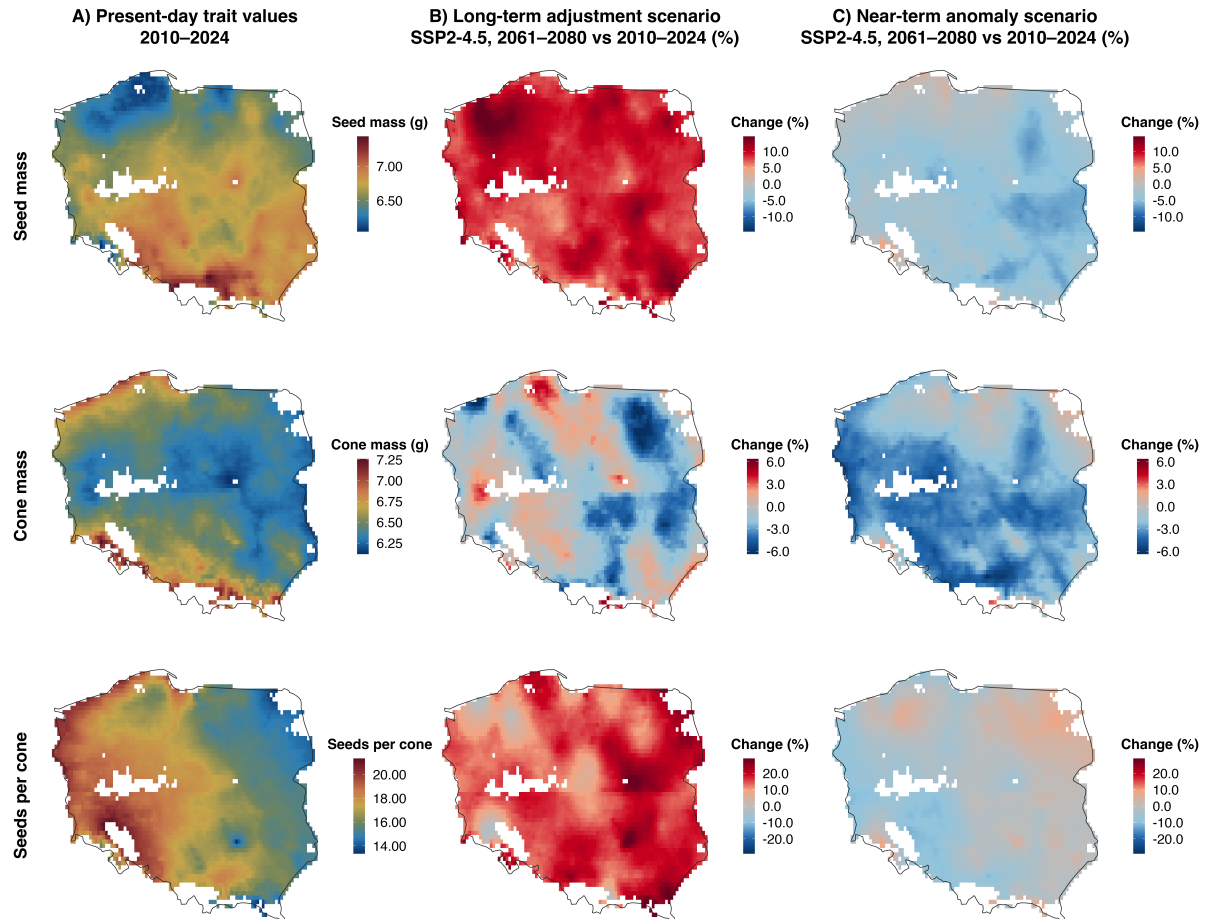


Figure S5: Projected changes in Scots pine reproductive traits under future climate. Rows show cone mass, seed mass, and the number of seeds per cone. Maps in the left column show trait values predicted under the present-day climate of 2010–2024. The middle column shows the percentage change projected for 2061–2080 under SSP2–4.5 when future climate replaces the historical long-term site climate, representing longer-term adjustment through acclimation, local adaptation, or provenance turnover. The right column shows the percentage change when future climate is expressed as an anomaly from each site’s historical climate, representing the near-term response of current populations before slower adjustment occurs. Temporal projections include interactions between historical site climate and future anomalies. White areas indicate climatic conditions outside the model calibration range. Projections based on models that included summer weather instead of spring are given in Fig. 4.

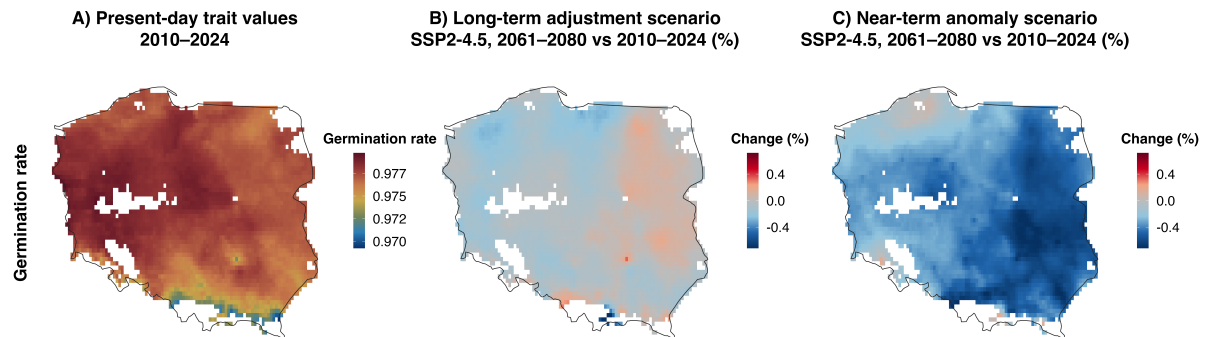


Figure S6: Projected changes in Scots pine germination rate under future climate. Maps in the left column show trait values predicted under the present-day climate of 2010–2024. The middle column shows the percentage change projected for 2061–2080 under SSP2-4.5 when future climate replaces the historical long-term site climate, representing longer-term adjustment through acclimation, local adaptation, or provenance turnover. The right column shows the percentage change when future climate is expressed as an anomaly from each site’s historical climate, representing the near-term response of current populations before slower adjustment occurs. Temporal projections include interactions between historical site climate and future anomalies. White areas indicate climatic conditions outside the model calibration range. Projections based on models that included summer weather instead of spring are given in Fig. 4.

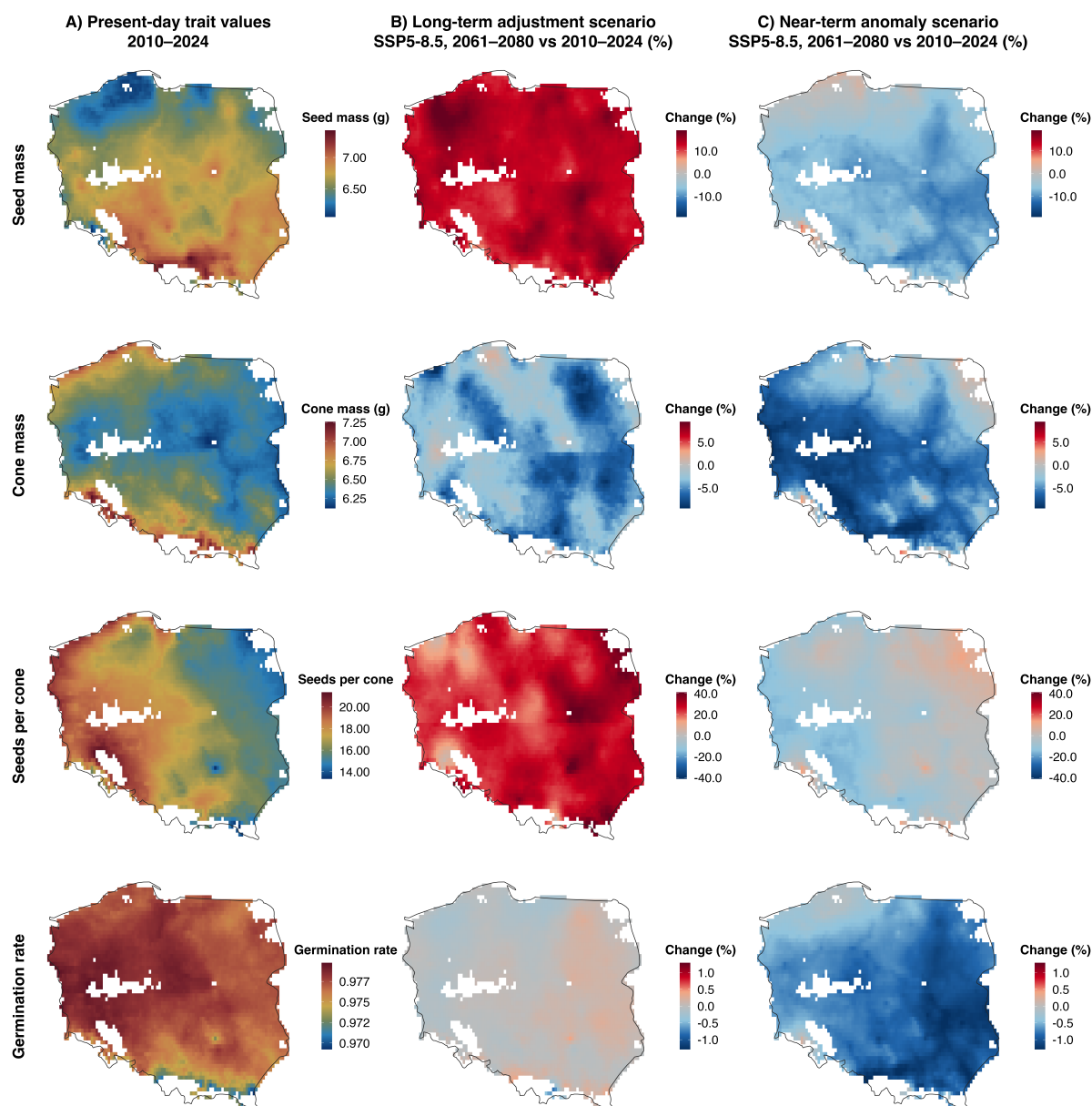


Figure S7: Projected changes in Scots pine reproductive traits under future climate. Rows show seed mass, cone mass, the number of seeds per cone, and germination rate. Maps in the left column show trait values predicted under the present-day climate of 2010–2024. The middle column shows the percentage change projected for 2061–2080 under SSP5-8.5 when future climate replaces the historical long-term site climate, representing longer-term adjustment through acclimation, local adaptation, or provenance turnover. The right column shows the percentage change when future climate is expressed as an anomaly from each site’s historical climate, representing the near-term response of current populations before slower adjustment occurs. Temporal projections include interactions between historical site climate and future anomalies. White areas indicate climatic conditions outside the model calibration range. Projections based on models that included summer weather and made for scenario SSP2-4.5 are given in Fig. 4.

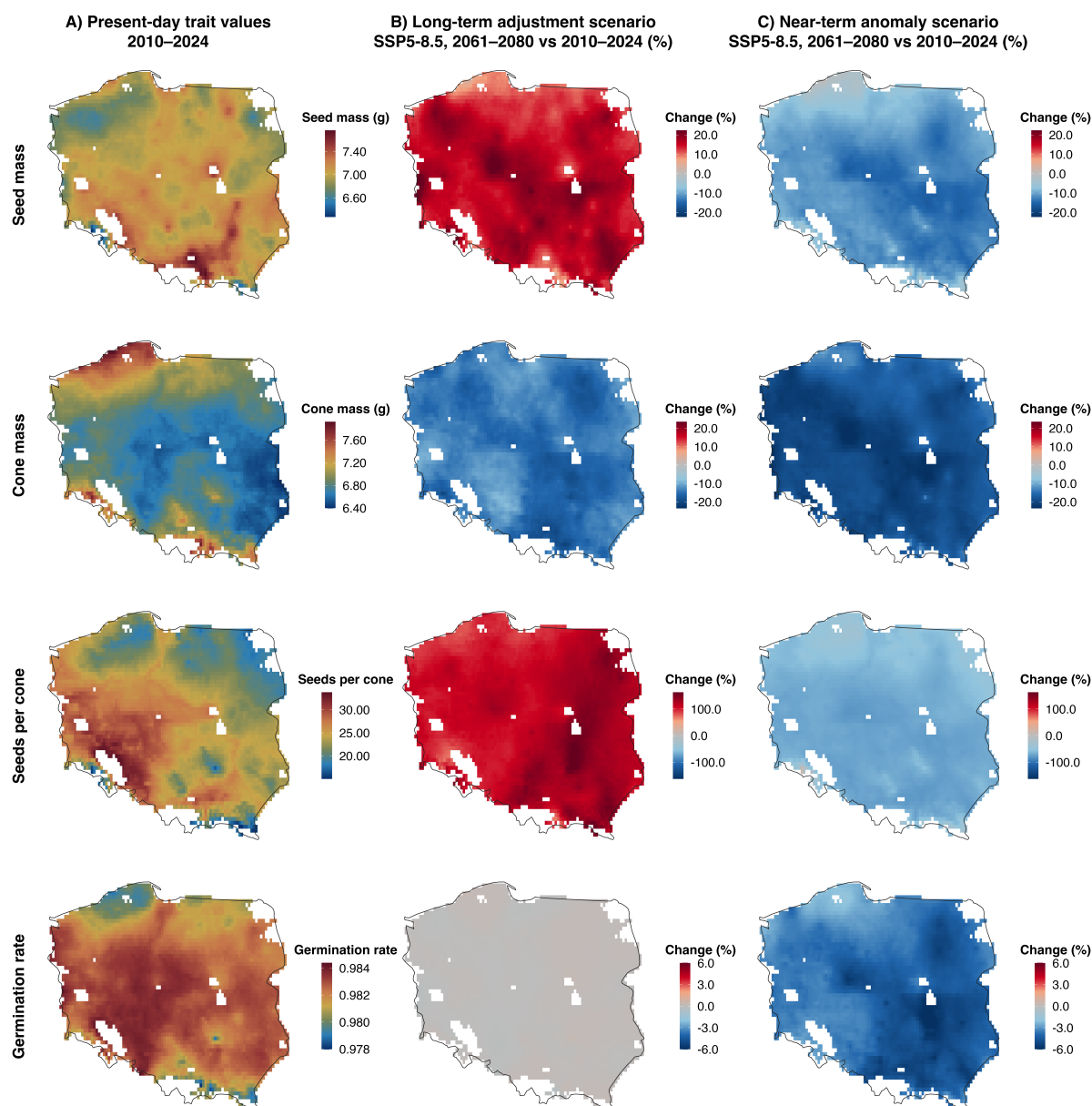


Figure S8: Projected changes in Scots pine reproductive traits under future climate. Rows show seed mass, cone mass, the number of seeds per cone, and germination rate. Maps in the left column show trait values predicted under the present-day climate of 2010–2024. The middle column shows the percentage change projected for 2061–2080 under SSP5-8.5 when future climate replaces the historical long-term site climate, representing longer-term adjustment through acclimation, local adaptation, or provenance turnover. The right column shows the percentage change when future climate is expressed as an anomaly from each site’s historical climate, representing the near-term response of current populations before slower adjustment occurs. Temporal projections include interactions between historical site climate and future anomalies. White areas indicate climatic conditions outside the model calibration range. Projections based on models that included summer weather and made for scenario SSP2-4.5 are given in Fig. 4.