

Abrupt reproductive responses to weather and shifting climatic signals across thermal contexts in trees

Jessie J. Foest^{*1}, Emilie Fleurot², Maria Bogdańska¹, Jakub Szymkowiak¹, Michał Bogdziewicz¹

¹Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland.

². Department of Soil and Forest Sciences, Institute of Forest Ecology, BOKU University of Natural Resources and Life Sciences, Vienna, 1180 Austria

*corresponding author: Jessie J. Foest jjfoest_articles@protonmail.com

keywords: masting | climate sensitivity | tree fecundity | reproductive history | environmental gradients | boosted regression trees

Abstract

Large inter-annual variation in tree seed production is widespread and closely linked to weather. Yet, we know little about the shape of these relationships, their dependence on resources, or their spatial consistency. We fitted boosted regression trees (eight species; 6,491 population-level observations; 352 sites), using prior seeding as proxy for resource status. Predictive performance ranged from $r_{CV} = 0.33$ to 0.72, yet climatic signals emerged in most species. Non-linear responses to weather were common, often showing sharp transitions over narrow climatic ranges. Prior seeding was influential and frequently modified weather responses, with species ranging from predominantly climatically controlled to strongly resource-dependent. Leading predictors generally remained influential across sites within species, but their strength or relative importance shifted along a gradient from warmer, less thermally variable to colder, more variable sites. Consequently, small climatic shifts may coincide with large changes in reproduction, with the magnitude depending on prior seeding and climatic context.

Large inter-annual variation in tree seed production, or masting, is a major feature of forest ecosystems, shaping regeneration, population dynamics, and food webs [1–3]. Weather is closely linked to variation in seed production, affecting reproductive processes from flower initiation to seed maturation [4, 5]. Weather signals are thought to 'cue' or 'veto' reproductive effort, and spatially synchronous signals can generate population-level or even regional seed-production pulses [5–8]. Decades of research have identified many species-specific weather predictors of seed production [4, 5, 7], but whether these relationships are non-linear, depend on previous reproductive effort, or vary across climatic ranges remains unclear. These features directly determine how reliably weather–reproduction relationships can be extrapolated across populations and into future climates.

Tree species may differ not only in which weather conditions act as environmental signals for reproduction [4], but also in how seed production responds to these signals. In particular, responses to weather variation may be non-linear, as is common for ecological responses to environmental drivers [9, 10]. For instance, seed crops may remain low across a wide range of weather conditions, increasing sharply once reproduction is 'cued' by favourable weather conditions [11]. In European beech (*Fagus sylvatica*), reproduction responds non-linearly to previous-summer temperature cues [12], while seed production in temperate oaks (*Quercus robur*, *Quercus petraea*) increases steeply when spring temperatures exceed 12 °C [13]. Environmental vetoes provide another source of possible non-linearity, causing reproductive failure once conditions become too severe [14–16]. We lack a systematic understanding of how frequently seed production responds non-linearly to weather, whether response shapes are consistent across species, and how often these relationships contain thresholds. The implications of thresholds are generally underappreciated in tree reproduction, but important for climate-change forecasting. If prevailing weather conditions lie close to a reproductive threshold, even a small climatic shift could cause a disproportionately large change in seed output and, if sustained, substantially alter reproductive dynamics [5, 17, 18].

Predictions of seed production from weather variation alone may be unreliable if trees' responses also depend on endogenous resource status. The idea that resource status modifies sensitivity to weather cues has been invoked to explain inter-annual variation in tree reproduction

[4, 19–21]. Reproduction can carry resource costs: in high-seeding years, *F. sylvatica* allocated up to half of aboveground NPP to reproduction [22], and heavy seed production is often followed by reduced reproduction in the subsequent year [23–25]. In *F. sylvatica*, seed production responses to summer temperatures during flower initiation interacted with the reconstructed resource state [21]. By suppressing reproduction after high seed crops and amplifying responses as resources recover, resource–cue interactions may ‘fine-tune’ intervals between high-seeding years [21]. This mechanism may also affect how seed production responds to warming. If weather cues become more frequent under climate change, reproduction may occur too often for resources to replenish, weakening subsequent responses to cues and producing frequent but smaller seed crops [21, 26]. This, in turn, may reduce viable seed supply through increased seed predation and constrain tree growth through sustained resource allocation to reproduction [26–28]. However, empirical tests of resource-dependent sensitivity to weather cues remain limited [19, 21, 29]. Testing resource–cue interactions across species will show how widely this framework applies and when including past seed production improves predictions of seed crop responses to altered weather cues.

Local context could affect how well species-level weather–reproduction relationships predict seed production across populations, as the drivers of reproduction may shift over space [4, 30, 31]. Earlier work emphasised species-level differences in the reproductive stages driving seed production, distinguishing species in which reproductive variation is driven primarily by flowering conditions from those in which conditions during fruit maturation play a greater role [7]. However, studies are increasingly revealing intraspecific variation in drivers [30–32]. Fleuret et al. [30] found that acorn production in semi-continental oak populations is strongly driven by spring temperatures, which often limit pollination and fruit set. In contrast, in milder oceanic and Mediterranean climates, acorn production depends more on flowering synchrony, determined earlier in the reproductive cycle. Establishing whether such context dependence follows general patterns will help to predict seed production responses to climate change [31]. The same weather cues could operate across populations if trees can adjust their sensitivity to local conditions through adaptation or phenotypic plasticity [33]. For example, in beech, seed production across populations responds to warm summer temperatures following the summer

solstice, even though absolute temperatures during this period differ widely among sites [33]. This apparent sensitivity to locally warm conditions may arise through local adaptation or phenotypic plasticity. Conversely, local climate could change which stage of the reproductive cycle is most limiting, resulting in different observed relationships between climate and seed production across sites [34].

The complexity of weather–reproduction relationships across species, endogenous resource states, and local environments makes it difficult to identify all relevant predictors, response shapes, and interactions in advance. Boosted regression trees (BRTs) are useful in this setting; although primarily optimised for prediction rather than causal inference, they can accommodate complex non-linear relationships and interactions and quantify predictor importance [35, 36]. When predictors are selected based on biological hypotheses, the resulting patterns can also be mechanistically informative [35–37]. Here, we fitted species-specific BRTs for eight spatially well-replicated tree species using long-term reproductive-effort time-series from MASTREE+ [38, 39]. We first assessed how well seasonal climate and previous reproductive effort predicted seed production, expecting the identity and timing of the strongest predictors to vary among species. We then used the flexibility of BRTs to evaluate whether (1) non-linear responses of seed production to climatic and reproductive predictors are common, including threshold-like responses with abrupt changes over narrow predictor ranges, (2) previous reproductive effort modifies responses to leading climatic predictors, and (3) the predictive importance of individual drivers varied within species across local climatic contexts or remained stable along spatial climatic gradients.

Results

Seed production is unevenly coupled to weather variation across species. The predictive performance of models combining seasonal weather and previous seed production varied among species (Table 1). Spatially blocked cross-validation correlations ranged from $r_{CV} = 0.33 \pm 0.04$ in *P. ponderosa* to 0.72 ± 0.02 in *F. sylvatica*, while $RMSE_{CV}$ ranged from 0.68 to 0.91 on the seed production z -score scale. Predicted time-series generally captured the broad temporal variation in seed production but tended to underestimate the magnitude of year-to-year fluctuations,

Table 1 | Cross-validation (CV) performance of species-specific Boosted Regression Tree (BRT) models

Species	Dataset			BRT settings		CV performance		
	N	Median length	Time-series (unique sites)	lr	Selected trees	r (SE)	Deviance (SE)	RMSE
<i>F. sylvatica</i>	1475	20	61 (60)	0.010	3500	0.72 (0.02)	0.46 (0.03)	0.68
<i>P. abies</i>	529	14	33 (30)	0.005	2900	0.45 (0.04)	0.76 (0.04)	0.87
<i>P. glauca</i>	745	16	38 (35)	0.010	1050	0.54 (0.04)	0.68 (0.05)	0.82
<i>P. albicaulis</i>	1201	20	59 (59)	0.010	1350	0.55 (0.04)	0.67 (0.04)	0.82
<i>P. edulis</i>	582	14	38 (38)	0.005	1000	0.65 (0.03)	0.54 (0.04)	0.74
<i>P. ponderosa</i>	852	15	57 (56)	0.001	4350	0.33 (0.04)	0.84 (0.02)	0.91
<i>P. sylvestris</i>	689	13	50 (39)	0.010	1750	0.53 (0.03)	0.67 (0.03)	0.82
<i>Q. petraea</i>	418	11	35 (35)	0.001	3100	0.45 (0.05)	0.73 (0.04)	0.86

Note: 'N' indicates annual observations included in each model, and 'Median length' summarises the median time-series length per species. 'Time-series' gives the number of site-level time series, with the number of unique MASTREE+ coordinates in parentheses. Learning rates ('lr') were initially set to 0.01 and then reduced until the CV-selected number of trees exceeded 1000, with tree complexity held constant at 3. Species were evaluated using five 50-km spatial CV blocks.

particularly in *P. ponderosa* (Fig. S3).

Predictor importance varies in concentration and timing, but previous seed production is consistently important. Species fell into two broad groups depending on whether predictor importance was concentrated in a few variables or spread across many (Fig. 1). A small set of predictors accounted for much of the relative influence in five of eight species, whereas importance was more diffusely distributed in *P. albicaulis*, *P. ponderosa*, and *P. sylvestris*.

Important climatic predictors generally occurred before the seed dispersal year, most often at $t - 1$ or $t - 2$, with *Q. petraea* as an exception (Fig. 1). Seasonally, summer temperature weather conditions were among the top predictors in all species, either as temperature (*F. sylvatica*, *P. abies*, *P. glauca*, *P. albicaulis*, *P. sylvestris*, *Q. petraea*), or VPD (*P. edulis*, *P. ponderosa*). Spring weather was also consistently among the top predictors across species studied.

Previous seed production ranked among the four most influential predictors in all but one species (*P. glauca*).

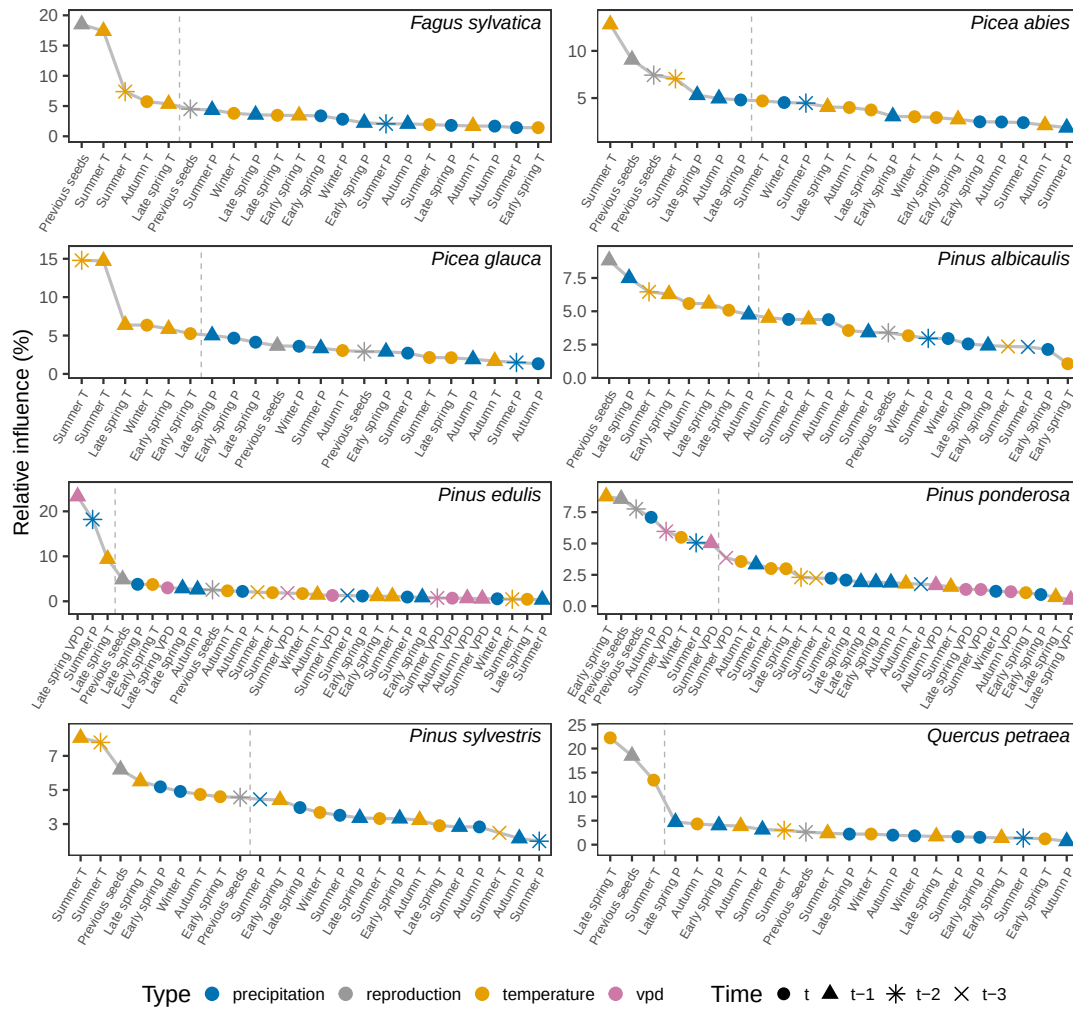


Figure 1: Lagged summer and spring weather are leading seed production predictors, with previous seeding generally important. Points show the relative influence of all predictors in species-specific boosted regression tree models of reproduction. Predictor relative influence reflects split frequency and improvement in model fit, rescaled to sum to 100 within each model. The dashed vertical line is placed after the smallest set of top-ranked predictors needed to reach $\geq 50\%$ of cumulative relative influence. Symbols indicate the time lag relative to the seed maturation year (t). Species' specific N provided in Table 1.

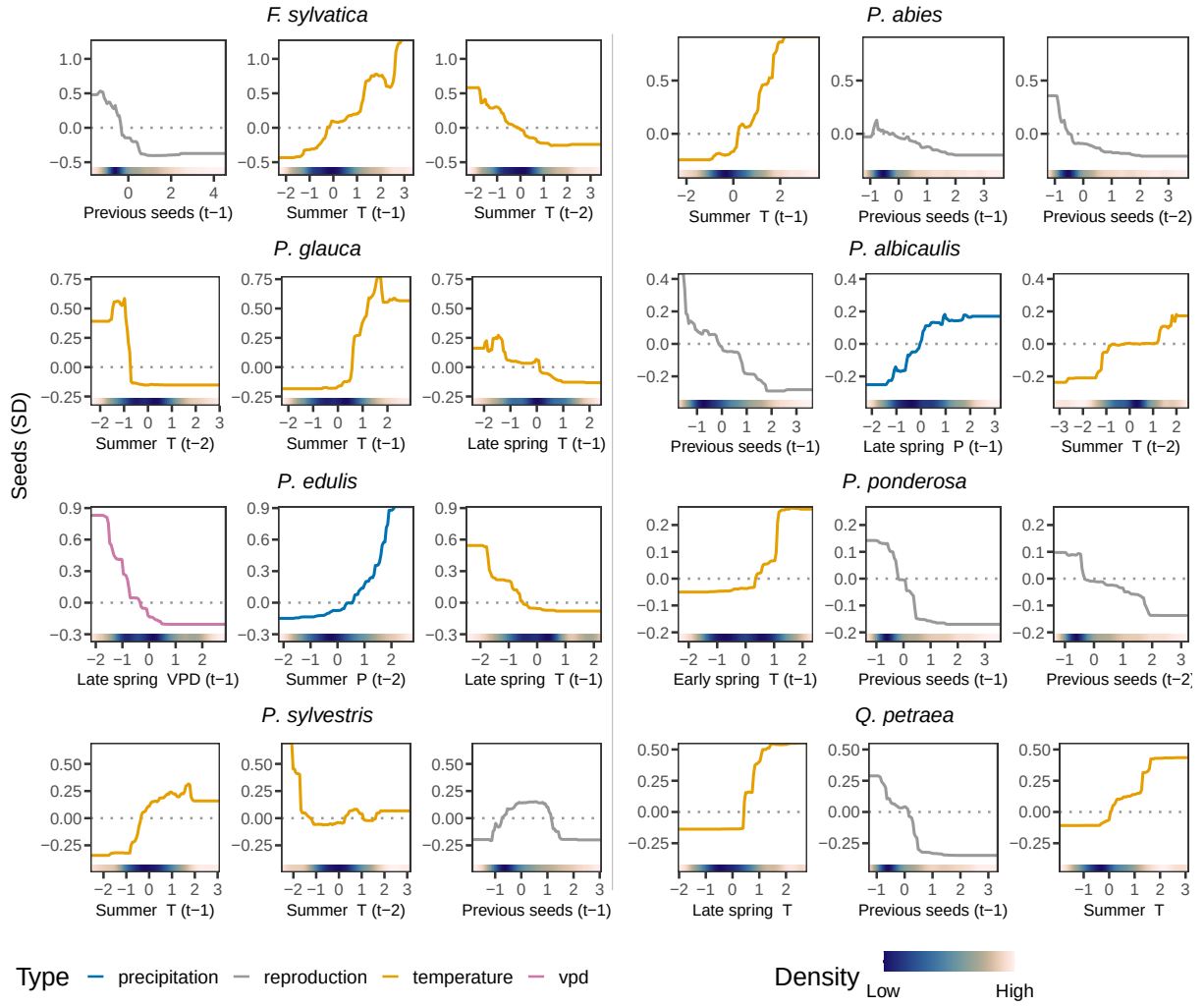


Figure 2: Seed-production responses frequently show sharp transitions across predictors and species. Partial-dependence curves from species-specific machine-learning models, shown for the three predictors with the highest relative importance in each species. Lines show fitted seed production across the standardised range of each predictor. The colour strip along the bottom of each panel shows the within-panel relative density of observed predictor values. Predictor labels indicate season and variable, with T = temperature, P = precipitation, t = seed year, $t - 1$ = one year before seed production, and $t - 2$ = two years before seed production. Ranked pairwise interactions among predictors for each species are shown in Fig. S4. Species' specific N provided in Table 1.

Climatic responses are often non-linear and include sharp transitions. Partial-dependence curves showed that non-linear seed-production responses to predictors were common (Fig. 2), often involving abrupt changes followed by plateaus. In *F. sylvatica*, *P. abies*, *P. ponderosa*, and *Q. petraea* predicted seed production increased sharply as previous-year seed production fell below the long-term mean. In *P. glauca*, predicted seed production increased abruptly as summer temperature at $t - 2$ fell below approximately -1 SD, or as summer temperature at $t - 1$ rose above the long-term mean. Colder springs were associated with low predicted seed production, which increased sharply only when temperatures exceeded approximately $+1$ SD above the long-term

mean in early spring at $t - 1$ in *P. ponderosa*, or the long-term mean in current-year late spring in *Q. petraea*. The density of predictor values showed that sharp transitions occurred under both commonly observed conditions and towards less frequent climatic extremes, suggesting that populations differ in how frequently climatic variation may move them between low- and high-seed-production states.

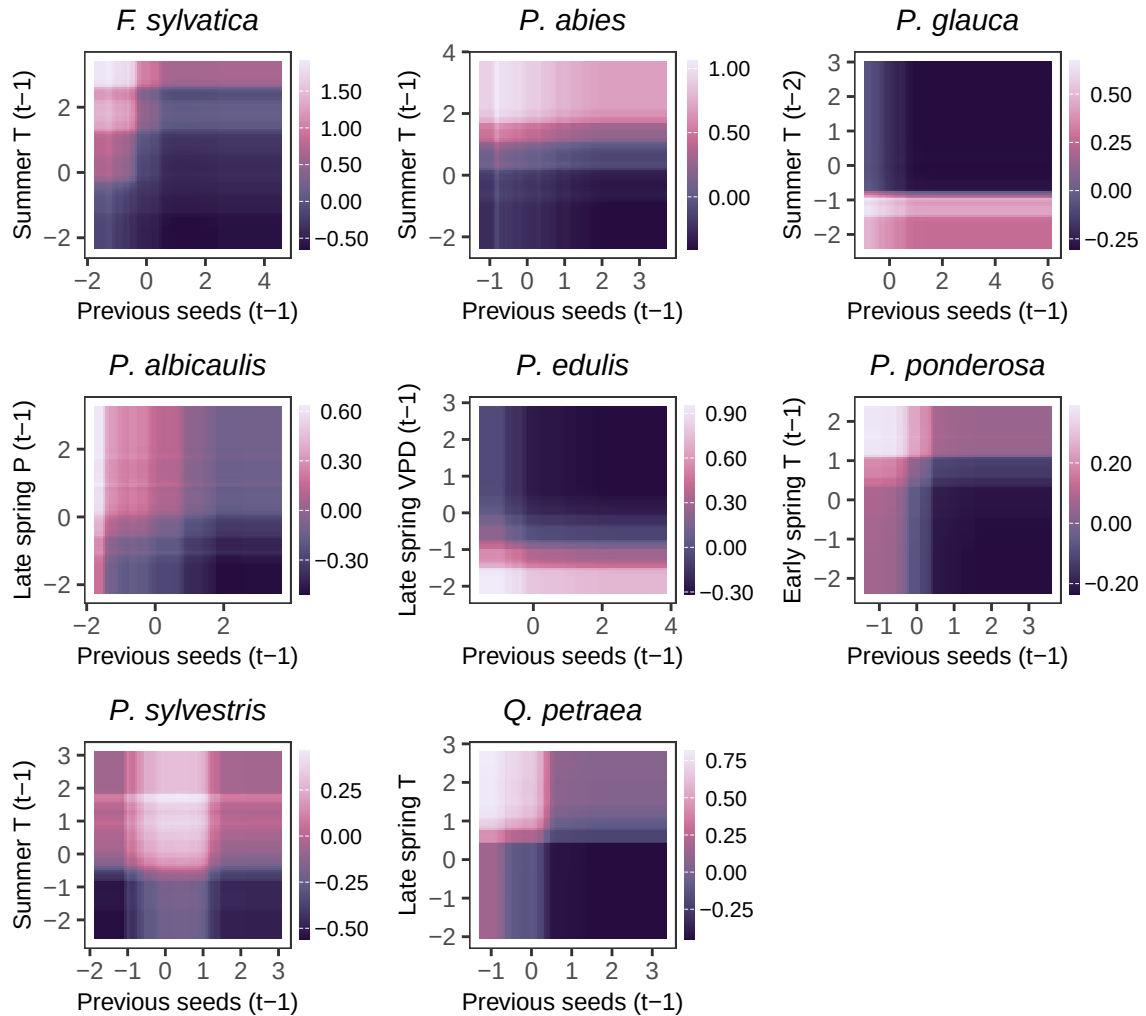


Figure 3: Previous seed production modifies seed crop predictions, with responses ranging from climate-dominated to strongly interactive. Heatmap colours show fitted seed production (SD from the site mean) for each species-specific BRT. Weather predictors are expressed as SD from the site mean. Predictor labels indicate season and variable, with T = temperature, P = precipitation, t = seed year, $t - 1$ = one year before seed production, and $t - 2$ = two years before seed production. Fig S5 shows a version of this plot along variation in previous seed crop at $t - 2$. Species' specific N provided in Table 1.

Joint climate-resource effects contrast with climate-dominated responses. Across species, previous seed production modulated fitted climatic responses (Fig. 3, Fig. S5). In several

species, including *F. sylvatica*, *P. albicaulis*, *P. ponderosa*, and *Q. petraea*, high seed production in the previous year was associated with suppressed responses to otherwise favourable weather cues. For instance, in *Q. petraea*, warm late springs (> 1 SD above the site mean) were associated with large seed crops when previous-year reproduction was below or around the reproductive average (≤ 0 SD), but intermediate crops were predicted when previous-year reproduction was higher. Additionally, after low previous-year reproduction, weaker cues were sufficient to trigger high predicted seed production. For other species, *P. abies*, *P. glauca*, and *P. edulis*, fitted seed production varied with previous reproduction to a smaller extent. In these species, the largest seed crops were predicted when previous reproduction was low, but after a low seed crop weaker cues were insufficient to increase predicted seed production. Instead, reproductive variation was more pronounced along the climatic predictor axes.

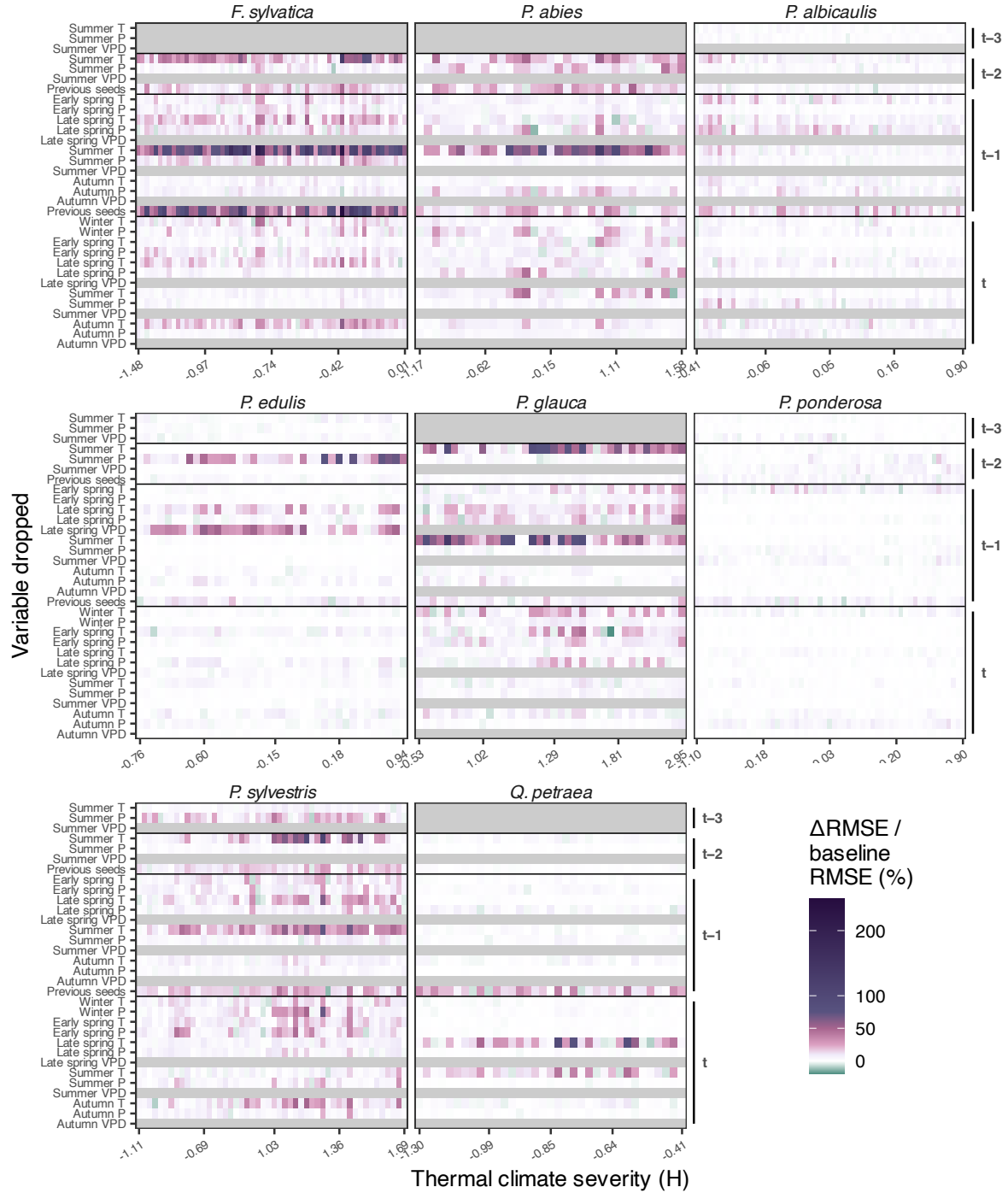


Figure 4: Main predictor identity is conserved, but predictive importance shifts across thermal climate severity gradients. Heatmaps show permutation-based predictor importance from species-specific BRT models for individual time-series ordered from lower to higher thermal climate severity (H). Higher H represents colder and more thermally variable sites. For each predictor and time-series, importance was quantified as the mean change in prediction error (ΔRMSE) across 1000 within-time-series permutations and expressed as a percentage of the baseline RMSE of the unpermuted model. Larger positive values indicate a greater increase in prediction error (in %) after permutation and therefore greater local predictive importance; values near or below zero indicate little or no predictive contribution. Grey cells mark predictors that were not assessed for a given species. Predictor labels specify season and variable, with T = temperature, P = precipitation, t = seed year, and $t - 1$ to $t - 3$ denoting one to three years before the seed year. Species' specific N for the BRT models are provided in Table 1. An alternative scatterplot visualisation of the three highest-ranking variables per species is provided in Fig. S6.

Predictor identity persists, but strength or relative importance shifts along thermal gra-

dients. Permutation-based importance showed that predictor strength varied systematically across thermal climate severity (H). Comparable patterns were less evident along MAT or MAP alone (Figs. S7, S8), suggesting that thermal variability helps to structure predictive importance. For most species, the predictors with the largest permutation-based influence (highest $\frac{\Delta RMSE}{RMSE_{baseline}}$) remained influential across climate gradients, indicating that predictor identity was generally retained (Fig. 4). However, in *P. edulis*, *P. glauca*, and *P. sylvestris*, a relative shift occurred between dominant predictors. For instance, in *P. edulis*, lagged summer precipitation became more prominent towards higher H (colder, more thermally variable climates), whereas late-spring VPD was relatively more important at lower H (warmer, less thermally variable climates). In *Q. petraea* and *P. abies*, the main predictors, late-spring temperature and summer temperature respectively, tended to be more important towards colder, more thermally variable sites (i.e. higher H). In *P. sylvestris*, weather predictors were generally strongest at intermediate to high H , but weakened at the most extreme values. By contrast, the dominant predictors in *F. sylvatica* were comparatively stable across the gradient.

When spatial variability in predictor importance was summarised across time-series, species ranged from relatively stable importance of the dominant predictors in *F. sylvatica* to strong spatial variation in *Q. petraea* (Fig. 5). *P. edulis* and *P. glauca* showed intermediate patterns, with high variability restricted to some important predictors such as late spring VPD (t-1) and summer P (t-2) in the former, or summer T (t-1) in the latter.

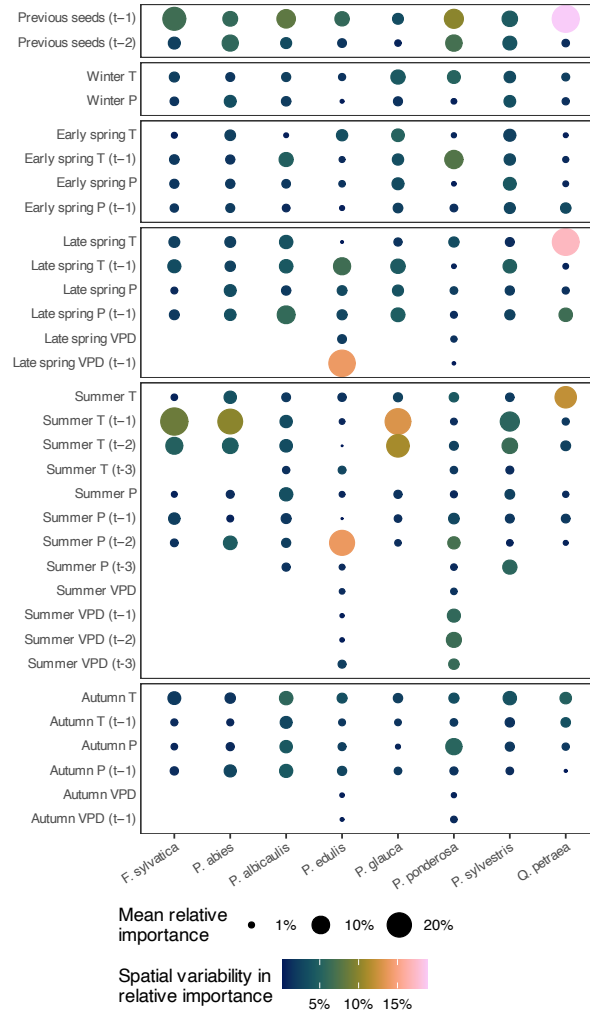


Figure 5: Oak shows the strongest context dependency in its dominant predictors. Point size shows species-mean relative predictor importance across time-series. For each time-series of a species, the mean ΔRMSE (from 1000 permutations) was set to zero when negative, and rescaled so that the positive importance values across predictors summed to 100%. Point colour shows the standard deviation of this relative importance among time-series. Species' specific N for the BRT models are provided in Table 1.

Discussion

Our results reveal strong, recurring patterns in the shape of weather-reproduction relationships and in how they vary with reproductive history and climatic context. First, seed production - weather relationships were frequently non-linear, with sharp transitions indicating that small changes in weather conditions may coincide with large changes in predicted seed production. Second, we revealed a continuum from predominantly climate-dominated variation in seed production to patterns strongly conditioned by previous reproductive effort, suggesting that climate change may alter reproduction differently among species [16, 21]. Third, spatial variation

in predictor importance was structured along thermal climate severity, or ‘harshness’: leading climatic predictors generally remained informative, but their predictive strength and, in some species, relative importance shifted across the gradient, extending evidence that climatic context can alter the importance of reproductive weather signals [30]. Together, these results help clarify how, when, and where weather matters for tree reproduction across our focal species, indicating that robust predictions of future seed production will need to account for non-linear climatic relationships, cue sensitivity to previous seed production, and local thermal context.

Our models revealed a gradient in how tightly annual seed production was coupled to weather variation and previous reproduction across species. For instance, predictability was relatively low in *P. ponderosa* ($r_{CV} = 0.33 \pm 0.04$ SE) but considerably higher in *P. edulis* ($r_{CV} = 0.65 \pm 0.03$ SE), consistent with previous work showing a greater importance of local tree and stand attributes in *P. ponderosa* and a clearer weather signals in *P. edulis* [40–42]. More generally, model performance fell within the range reported for regression-based models of annual seed production [43, 44], leaving considerable temporal variation in seeding unexplained even after accounting for non-linearities and interactions. Identifying the processes underlying this unexplained variation should therefore be a priority. Integrating seed-production records with tree age and size, stand structure, neighbourhood competition, and growth could reveal whether apparently weak weather coupling instead reflects modulation by tree- and stand-level processes, as observed in *P. ponderosa* [41]. Importantly, weak coupling to inter-annual weather does not imply a lower sensitivity to long-term climate change: climate also influences seed production indirectly through changes in tree growth, demography, and stand dynamics [1]. Such differences among species could also inform management. Where seed production depends more strongly on tree and stand attributes, interventions that alter stand density, size structure, or neighbourhood competition may offer greater scope to support reproduction than in species whose seed crops are tightly coupled to weather.

Non-linear relationships between seed production and weather predictors were the dominant pattern across species. At the same time, species differed in which parts of these fitted response curves they commonly experienced, suggesting that the implications of response shape for masting may depend on how frequently weather conditions favour high seed production. In *P.*

glauca, for example, most observed summer temperatures ($t-1$, $t-2$) fell within the portion of the response associated with low seed production, whereas climatic conditions associated with high seed production occurred only rarely. Such a pattern is consistent with the relatively high inter-annual variability in seed production (CVp) reported for this species [45]: large crops may emerge when populations only occasionally encounter the climatic conditions associated with the upper part of the response. In contrast, commonly experienced summer temperatures at $t - 1$ in *P. sylvestris* spanned much of the sharp transition from low to high predicted seed production. Consequently, these populations commonly experience conditions associated with high production. This is consistent with the lower CVp and greater probability of large seed crops reported for this species [45]. Testing how both response curves (i.e. sensitivity to cueing) and the distribution of experienced weather conditions (i.e. cueing frequencies) link to temporal reproductive indices may thus be a fruitful avenue towards explaining intraspecific variation in masting.

Climate change will likely shift where populations fall along non-linear climate-reproduction response curves [5]. The abrupt transitions documented here across species bring into focus how small climatic shifts could translate into disproportionately large reproductive changes. Populations near steep transitions may show large changes in predicted seed production following relatively small climatic shifts, whereas populations occupying flatter portions of the response may change little until conditions move into a more responsive part of the curve. How such shifts translate into temporal reproductive patterns may also depend on the underlying cueing mechanism. *F. sylvatica* and *P. glauca*, for example, showed similar fitted responses to temperatures in successive summers, yet continued warming could have different consequences depending on whether reproduction responds to the thermal contrast between years (ΔT) or to absolute temperatures. In *P. glauca*, ΔT cueing has been proposed, which could allow the cue to remain informative under directional warming and may help explain the apparent stability of masting patterns [46, 47]. Consistent with this, our model identified a strong interaction between summer temperatures in the two preceding years. In *F. sylvatica*, by contrast, ΔT appears to explain less variation than absolute temperature cues [21], while recent changes in masting have been associated with warming relative to local climatic conditions [39]. A further

uncertainty is whether the response curves themselves remain stable through time. In *F. sylvatica*, sensitivity to climatic cues has weakened under warming [12], which could explain the more gradual summer $t - 1$ response we observed as cooler summers become less constraining for reproduction. Continued long-term monitoring is needed to assess the temporal stability of response curves among species and cueing mechanisms, and improve our understanding of divergent reproductive responses to climate change.

Previous reproductive effort was not only an important predictor of seed production across species, but also frequently modified responses to leading weather predictors. Thus, the same weather conditions may lead to different reproductive outcomes depending on previous seed production. This dependence was strong in *F. sylvatica*, *P. albicaulis*, *P. ponderosa*, and *Q. petraea*, for which favourable climatic conditions were associated with the highest predicted seed production after years of low seed production. In *P. glauca* and *P. edulis*, climatic responses were less dependent on previous reproduction. Such species-level differences may matter under climate change because warming can alter both cue frequency and resource availability [20]. Where climatic responses depend strongly on resource status, more frequent favourable cues may not produce more frequent large seed crops if resources cannot recover in time, as proposed for the decline in *F. sylvatica* mast seeding under summer warming [12, 21, 39]. Conversely, where dependence on previous seed production is weaker, seed production may track favourable climatic conditions more directly. Whether this reflects greater resource acquisition, or stronger allocation away from other sinks such as growth or defence remains unclear [48, 49]. Previous seed production is only a proxy for resource status, and resolving these mechanisms will require direct measurements of resource dynamics that are difficult to obtain at the scale of our study.

Spatial variation in predictor importance supports two ways in which reproductive responses are shaped by climatic context: the same climatic predictor may vary in importance among populations, or different predictors may become dominant under different climatic conditions. In *F. sylvatica*, the same dominant predictors persisted across thermal climate severity gradients and varied only slightly in strength, consistent with populations responding to a conserved climatic signal [33]. In other species, climatic context appeared to change which predictor was most important. In *Q. petraea*, for example, spring temperature became more important towards

colder, more thermally variable sites (higher H). This closely matches the pattern reported by Fleurot et al. [30], who found that spring temperature was strongly associated with pollination success and fruit set in semi-continental populations. This relationship was much weaker in warmer, less thermally variable oceanic populations, where crop size depended more strongly on synchronous flower production. In *P. edulis*, late-spring VPD was more prominent at lower H , whereas lagged summer precipitation became more important at higher H ; in *P. glauca*, the relative importance of successive-summer temperatures also shifted, albeit in opposing directions. A greater importance of summer temperature at higher H may reflect stronger limitation by growing-season warmth, affecting resource acquisition or temperature-dependent reproductive development. Together, these patterns show that local thermal context can reshape which climatic conditions matter for reproduction, limiting the transferability of species-level relationships across populations and future climates.

Confidence in the biological relevance of the BRT results was strengthened by the recovery of several well-established climatic signals. These included lagged summer temperature in *F. sylvatica* [29, 43], *P. abies* [29], and *P. glauca* [8, 50]; lagged VPD and precipitation in *P. edulis* [40]; and late-spring temperature in *Q. petraea* [29, 30, 34]. Similarly, diffuse climatic signals in *P. sylvestris* and *P. ponderosa* agreed with previous reports of spatially variable climatic relationships [29, 41]. Against this background, several less well-studied signals emerged, including current-summer temperature in *Q. petraea* and current-autumn temperature in *F. sylvatica*, meriting mechanistic testing.

In closing, clear climatic signals emerged in most species, but their predictive relationships with seed production were strongly conditional. Seed production was associated with non-linear climatic responses and previous reproductive effort, while the strength and relative importance of climatic predictors varied across populations. Under continued climate change, shifts in both mean conditions and climatic variability may therefore alter where populations fall along these fitted climate-reproduction relationships and change which climatic predictors are most informative. Forecasts of future tree reproduction will consequently need to jointly consider non-linear climatic responses, interactions between weather and reproductive history, and spatial climatic context.

Methods

Reproductive data

We extracted annual reproductive time-series from MASTREE+ v.2 [38, 39]. We retained time-series reporting seed, fruit, or cone production and at least 10 annual records. To link reproductive and climatic data spatially, we selected stand- and patch-level series with sampling location-specific coordinates. We kept only continuous measures of reproductive effort, such as seeds m^{-2} , and excluded indices or spatial synchrony-based measures such as the percentage of individuals reproducing. Because we aimed to quantify spatial variation in weather cueing, we restricted analyses to species sampled at > 20 sites.

The final dataset comprised two broadleaved species, *F. sylvatica* and *Q. petraea*, and six conifers: *Picea abies*, *Picea glauca*, *Pinus albicaulis*, *Pinus edulis*, *Pinus ponderosa* and *Pinus sylvestris*. It contained 6,491 observations across 352 sites, with a mean time-series length of 17.5 years (range: 10-57 years). Fig. S1 shows the geographical distribution of the study sites. The number of observations and time-series per species is given in Table 1. Although reproductive output was quantified using different measures across datasets, including cones, acorns and seeds, we refer to these as seed production for simplicity.

Annual seed production was standardised to z -scores within sites to isolate temporal variation in reproductive effort and to reduce among-site differences caused by variation in sampling methods [39].

Climate data

We obtained monthly climate data from ERA5 single-level reanalysis [51]. For each site and month, we extracted 2-m air temperature (K), dewpoint temperature (K) and total precipitation (m). Temperatures were converted to $^{\circ}\text{C}$, and precipitation to mm. Because vapour pressure deficit (VPD; hPa) has been linked to North American pine reproduction [40, 41], we calculated monthly mean VPD from air temperature and dewpoint temperature following equations in Park Williams et al. [52].

Monthly climate data were aggregated to seasonal predictors. Seasons were defined from

winter onwards as December (of the previous calendar year) to February, March to May, June to August and September to November in the Northern Hemisphere, and June to August, September to November, December to February and March to May in the Southern Hemisphere. Spring was split into early spring (the first month), and late spring (the second and third months), because these periods may capture different reproductive constraints, including frost risk and pollen dispersal [53]. Temperature and VPD were summarised as seasonal means, and precipitation as seasonal totals. All weather predictors were subsequently standardised to z -scores within sites. This isolated temporal weather anomalies from among-site climatic differences [39]. Strong collinearity ($r \geq 0.7$) was restricted to temperature and VPD within the same period (Fig. S2).

Analysis

All analyses were performed in R version 4.5.2 [54]. To identify strong predictors of seed production, we modelled seed production as a function of weather and lagged seed production using species-specific Gaussian boosted regression models (BRMs) fitted with `gbm.step` in the *dismo* package v. 1.3-16. We quantified the spatial consistency of weather cueing using a site-level permutation importance analysis.

Predicting seed production from weather and previous seed production

The response variable was annual seed production expressed as z -scores within sites. Predictors represented processes linked to the reproductive developmental cycle; we restricted predictors to those with an *a priori* hypothesised link to reproductive development, to maintain an interpretable predictor set rather than searching for any predictive association. We included lagged scaled seed production one and two years before seed maturation ($t-1$ and $t-2$) to account for potential multi-year suppression of subsequent crop size, and various predictors capturing seasonal weather anomalies during the reproductive year and two preceding years (for *Pinus* spp.: 3 preceding years). Mean temperature and precipitation predictors were included for all species, while VPD predictors were included only for *P. edulis* and *P. ponderosa*, since sensitivity to drought was specified *a priori* [40, 41]. Predictor sets and relative importance are shown in Fig. 1, with importance reflecting each predictor's contribution to reducing model error across all trees and

scaled to sum to 100%.

BRMs used a bag fraction of 0.5, such that each regression tree was fitted to a random 50% subset of the data, and a tree complexity of 3, permitting up to three-way interactions among predictors [35]. We began with a learning rate of 0.01, which controls the contribution of each tree to the final model, and reduced it in increments of 0.005 until the model selected by `gbm.step` contained ≥ 1000 trees, following Elith et al. [35].

Predictive performance was evaluated with five-fold spatial cross-validation in `gbm.step`, using spatial blocks generated with the *blockCV* package (v. 3.2-0). Observations were first grouped into 50-km spatial blocks, which were then assigned to five cross-validation folds. In each iteration, one fold was held out for validation and the remaining four folds were used for model training. This reduced spatial dependence between training and validation data and prevented observations from the same or nearby sites from contributing to both sets.

Spatial consistency of predictor importance

We estimated local predictor importance using a repeated within-time-series permutation procedure. For each time-series, we first calculated the baseline root mean square error (RMSE) between observed seed production and predictions from the fitted species-specific BRTs. Each predictor included in the model was then randomly permuted within the focal time-series 1000 times while all other predictors and the fitted model were left unchanged. For each permutation, we generated new predictions and calculated the change in prediction error relative to baseline ($\Delta\text{RMSE} = \text{RMSE}_{\text{permuted}} - \text{RMSE}_{\text{baseline}}$). We averaged ΔRMSE across the 1000 permutations to obtain a single estimate of local predictive importance for each time-series $\times$ predictor combination. Larger positive ΔRMSE values indicate a greater deterioration in predictive performance following permutation and, therefore, greater local predictive importance of the focal predictor. Values close to zero indicate little contribution to local predictions, whereas negative values indicate that prediction error decreased following permutation.

To examine whether local predictor importance changed along broad climatic gradients, we expressed mean ΔRMSE as a percentage of the baseline RMSE of the corresponding time-series. This metric captures how much prediction error increased after permuting a predictor relative

to the error of the unpermuted model. For example, a 20% value indicates that permuting the predictor increased RMSE by 20% of the baseline RMSE. A non-linear colour transformation was applied only to the graphical scale to improve visual discrimination across the skewed distribution of relative Δ RMSE values. Thus, the results quantify predictor importance relative to the prediction error of each individual time-series.

Predictor importance was compared for each time-series along species-specific mean annual temperature and precipitation (MAT & MAP) gradients, as well as along a gradient of thermal climate severity (H). This index was inspired by Fleurot et al. [30], who distinguished sites using mean temperature together with thermal variability within and among years. For each site and year, we obtained the mean temperature (T) and thermal amplitude (A), defined as the difference between the warmest and coldest seasonal mean temperatures. For each time-series, we then calculated the mean and standard deviation of both T and A . These four variables were standardised using z -scores across sites and combined into a thermal climate severity index H . Higher H values indicate colder sites with greater inter-annual temperature variability, stronger seasonal temperature contrasts, and greater inter-annual variation in those contrasts (See Fig. S1).

$$H = \frac{1}{4}(-z(T_{\text{mean}}) + z(T_{\text{SD}}) + z(A_{\text{mean}}) + z(A_{\text{SD}}))$$

To quantify both the relative contribution of each predictor and its spatial consistency within species, we expressed the importance of each predictor relative to the combined importance of all predictors within the same time-series. Negative mean Δ RMSE values were set to zero, and each positive Δ RMSE value was divided by the sum of positive Δ RMSE values across all predictors. The resulting percentages therefore sum to 100% within each time-series. For each species and predictor, we then calculated the mean relative importance across time-series and its standard deviation. The mean describes the average contribution of a predictor relative to the other predictors, whereas the standard deviation quantifies how much this relative importance varies among time-series, with lower values indicating greater spatial consistency.

Data availability

The data supporting the findings of this study are openly available.

Code availability

Upon acceptance of the manuscript, the code supporting the results will be deposited in the Open Science Framework (OSF) and made publicly accessible.

References

- [1] Clark, J. S. *et al.* Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications* 2021 12:1 **12**, 1–11 (2021). URL <https://www.nature.com/articles/s41467-020-20836-3>.
- [2] Silveira, F. A. O. *et al.* Open letter: A call to integrate plant regeneration into sustainability science and policy. *PLANTS, PEOPLE, PLANET* ppp3.70201 (2026). URL <https://nph.onlinelibrary.wiley.com/doi/10.1002/ppp3.70201>.
- [3] Pang, S. E. H. *et al.* From niche theory to demographic realities: the demographic niche concept for understanding range-wide population dynamics. *Ecography* **2026**, e07774 (2026). URL <https://onlinelibrary.wiley.com/doi/abs/10.1002/ecog.07774>.
- [4] Bogdziewicz, M. *et al.* Evolutionary ecology of masting: mechanisms, models, and climate change. *Trends in Ecology & Evolution* **39**, 851–862 (2024). URL <https://linkinghub.elsevier.com/retrieve/pii/S0169534724001174>.
- [5] Journé, V. *et al.* Weather drivers of reproductive variability in perennial plants and their implications for climate change risks. *Nature Communications* **16**, 9226 (2025).
- [6] Kelly, D. & Sork, V. L. Mast seeding in perennial plants: Why, how, where? *Annual Review of Ecology and Systematics* **33**, 427–447 (2002).

- [7] Pearse, I. S., Koenig, W. D. & Kelly, D. Mechanisms of Mast Seeding: Resources, Weather, Cues, and Selection. *New Phytologist* **212**, 546–562 (2016).
- [8] LaMontagne, J. M., Pearse, I. S., Greene, D. F. & Koenig, W. D. Mast seeding patterns are asynchronous at a continental scale. *Nature Plants* **6**, 460–465 (2020). URL <http://www.nature.com/articles/s41477-020-0647-x>.
- [9] Kreyling, J. *et al.* To replicate, or not to replicate – that is the question: how to tackle nonlinear responses in ecological experiments. *Ecology Letters* **21**, 1629–1638 (2018). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13134>.
- [10] Fernández-Martínez, M., Bogdziewicz, M., Espelta, J. M. & Peñuelas, J. Nature beyond linearity: Meteorological variability and jensen’s inequality can explain mast seeding behavior. *Frontiers in Ecology and Evolution* **5**, 134 (2017).
- [11] Szymkowiak, J. *et al.* Tail-dependence of masting synchrony results in continent-wide seed scarcity. *Ecology Letters* **27**, e14474 (2024).
- [12] Bogdziewicz, M. *et al.* Climate warming causes mast seeding to break down by reducing sensitivity to weather cues. *Global Change Biology* **27**, 1952–1961 (2021). URL <https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.15560><https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.15560><https://onlinelibrary.wiley.com/doi/10.1111/gcb.15560>.
- [13] Schermer, E. *et al.* Flower phenology as a disruptor of the fruiting dynamics in temperate oak species. *New Phytologist* **225**, 1181–1192 (2020).
- [14] Crone, E. E. & Rapp, J. M. Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences* **1322**, 21–34 (2014). URL <https://onlinelibrary.wiley.com/doi/full/10.1111/nyas.12465><https://onlinelibrary.wiley.com/doi/abs/10.1111/nyas.12465><https://nyaspubs.onlinelibrary.wiley.com/doi/10.1111/nyas.12465>.
- [15] Bogdziewicz, M., Marino, S., Bonal, R., Zwolak, R. & Steele, M. A. Rapid aggregative and

reproductive responses of weevils to masting of north american oaks counteract predator satiation. *Ecology* **99**, 2575–2582 (2018).

[16] Bogdziewicz, M., Kelly, D., Zwolak, R., Szymkowiak, J. & Hacket-Pain, A. Dynamics, Mechanisms, and Consequences of Mast Seeding. *Annual Review of Ecology, Evolution, and Systematics* **56**, 119–144 (2025). URL <https://www.annualreviews.org/content/journals/10.1146/annurev-ecolsys-102723-052948>.

[17] Ratajczak, Z. *et al.* Abrupt Change in Ecological Systems: Inference and Diagnosis. *Trends in Ecology & Evolution* **33**, 513–526 (2018). URL <https://www.sciencedirect.com/science/article/pii/S0169534718300910>.

[18] Bogdziewicz, M., Kelly, D., Thomas, P. A., Lageard, J. G. A. & Hacket-Pain, A. Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nature Plants* **6**, 88–94 (2020). URL <https://doi.org/10.1038/s41477-020-0592-8>.

[19] Smaill, S. J., Clinton, P. W., Allen, R. B. & Davis, M. R. Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology* **99**, 870–877 (2011). URL <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2745.2011.01803.x><https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2745.2011.01803.x><https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2745.2011.01803.x>.

[20] Monks, A., Monks, J. M. & Tanentzap, A. J. Resource limitation underlying multiple masting models makes mast seeding sensitive to future climate change. *New Phytologist* **210**, 419–430 (2016). URL <https://onlinelibrary.wiley.com/doi/full/10.1111/nph.13817><https://onlinelibrary.wiley.com/doi/abs/10.1111/nph.13817><https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.13817>.

[21] Kelly, D., Szymkowiak, J., Hacket-Pain, A. & Bogdziewicz, M. Fine-tuning mast seeding: as resources accumulate, plants become more sensitive to weather cues. *New Phytologist* **246**, 1975–1985 (2025). URL <https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.70092>.

- [22] Müller-Haubold, H., Hertel, D., Seidel, D., Knutzen, F. & Leuschner, C. Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: A transect study in mature forests. *Ecosystems* **16**, 1498–1516 (2013).
- [23] Sork, V. L., Bramble, J. & Sexton, O. Ecology of mast-fruiting in three species of north american deciduous oaks. *Ecology* **74**, 528–541 (1993). URL <http://www.jstor.org>URL:<http://www.jstor.org/stable/1939313>http://www.jstor.org/stable/1939313?seq=1&cid=pdf-reference#references_tab_contents.
- [24] Pearse, I. S., LaMontagne, J. M., Lordon, M., Hipp, A. L. & Koenig, W. D. Biogeography and phylogeny of masting: do global patterns fit functional hypotheses? *New Phytologist* **227**, 1557–1567 (2020).
- [25] Roncé, I. L. *et al.* Reproduction alternation in trees: testing the resource depletion hypothesis using experimental fruit removal in quercus ilex. *Tree Physiology* **43**, 952–964 (2023). URL <https://academic.oup.com/treephys/advance-article/doi/10.1093/treephys/tpad025/7074166>.
- [26] Hacket-Pain, A. *et al.* Growth decline in european beech associated with temperature-driven increase in reproductive allocation. *PNAS* **122**, e2423181122 (2025).
- [27] Bogdziewicz, M. *et al.* Reproductive collapse in European beech results from declining pollination efficiency in large trees. *Global Change Biology* **29**, 4595–4604 (2023).
- [28] Jantzen, C. C., Burant, J. B., Gamelon, M., Bakker, E. S. & Visser, M. E. Mast-ing Breakdown in European Beech Reduces Fitness Benefits of Masting, Partly Explained by Climate Change. *Ecology and Evolution* **16**, e73809 (2026). URL <https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.73809>.
- [29] Nussbaumer, A. *et al.* Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in europe. *Forest Ecology and Management* **429**, 336–350 (2018).

- [30] Fleurot, E. *et al.* Oak Masting Drivers Vary between Populations Depending on Their Climatic Environments. *Current Biology* S0960982223000684 (2023).
- [31] Kelly, D. Mast Seeding: Study of Oak Mechanisms Carries Wider Lessons. *Current Biology* **33**, R231–R233 (2023).
- [32] Koenig, W. D., Pearse, I. S., Pesendorfer, M. B., Carmen, W. J. & Knops, J. M. H. Flowering and flower maturation in valley oak *quercus lobata*. *Ecology and Evolution* **16**, e73720 (2026). URL <https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.73720>. E73720 ECE-2026-04-01206.
- [33] Journé, V. *et al.* Summer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature Plants* **10**, 367–373 (2024). URL <https://doi.org/10.21203/rs.3.rs-3369033/v1>.
- [34] Bogdziewicz, M., Szymkowiak, J., Fernández-Martínez, M., Peñuelas, J. & Espelta, J. M. The effects of local climate on the correlation between weather and seed production differ in two species with contrasting masting habit. *Agricultural and Forest Meteorology* **268**, 109–115 (2019).
- [35] Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *Journal of Animal Ecology* **77**, 802–813 (2008).
- [36] Pichler, M. & Hartig, F. Machine learning and deep learning—A review for ecologists. *Methods in Ecology and Evolution* **14**, 994–1016 (2023). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.14061>. _eprint: <https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/2041-210X.14061>.
- [37] Davis, K. T. *et al.* Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences* **116**, 6193–6198 (2019). URL <https://www.pnas.org/doi/abs/10.1073/pnas.1815107116>.

- [38] Hacket-Pain, A. *et al.* Mastree+: Time-series of plant reproductive effort from six continents. *Global Change Biology* **28**, 3066–3082 (2022). URL <https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.16130><https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.16130><https://onlinelibrary.wiley.com/doi/10.1111/gcb.16130>.
- [39] Foest, J. *et al.* Widespread breakdown in masting in European beech due to rising summer temperatures. *Global Change Biology* **30**, e17307 (2024).
- [40] Wion, A. P., Weisberg, P. J., Pearse, I. S. & Redmond, M. D. Aridity drives spatiotemporal patterns of masting across the latitudinal range of a dryland conifer. *Ecography* **43**, 569–580 (2020). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.04856>.
- [41] Wion, A. P., Pearse, I. S., Rodman, K. C., Veblen, T. T. & Redmond, M. D. Masting is shaped by tree-level attributes and stand structure, more than climate, in a rocky mountain conifer species. *Forest Ecology and Management* **531**, 120794 (2023). URL <https://linkinghub.elsevier.com/retrieve/pii/S0378112723000270>.
- [42] Wion, A. P., Pearse, I. S., Broxson, M. & Redmond, M. D. Mast hindcasts reveal pervasive effects of extreme drought on a foundational conifer species. *New Phytologist* **246**, 450–460 (2025). URL <https://nph-1onlinelibrary-1wiley-1com-110kllgga01cc.han.amu.edu.pl/doi/10.1111/nph.20321>.
- [43] Journé, V., Hacket-Pain, A., Oberklammer, I., Pesendorfer, M. B. & Bogdziewicz, M. Forecasting seed production in perennial plants: identifying challenges and charting a path forward. *New Phytologist* **239**, 466–476 (2023).
- [44] Oberklammer, I. *et al.* Towards weather-based forecasting of annual seed production in six European forest tree species. *Journal of Applied Ecology* **63**, e70437 (2026). URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.70437>.
- [45] Foest, J. J., Caignard, T., Pearse, I. S., Bogdziewicz, M. & Hacket-Pain, A. Intraspecific variation in masting across climate gradients is inconsistent with the environmental stress hypothesis. *Ecology* **106**, e70076 (2025).

- [46] Kelly, D. *et al.* Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters* **16**, 90–98 (2013). URL <https://onlinelibrary.wiley.com/doi/full/10.1111/ele.12020><https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12020><https://onlinelibrary.wiley.com/doi/10.1111/ele.12020>.
- [47] LaMontagne, J. M., Redmond, M. D., Wion, A. P. & Greene, D. F. An assessment of temporal variability in mast seeding of north american Pinaceae. *Philosophical Transactions of the Royal Society B: Biological Sciences* **376**, 20200373 (2021).
- [48] Redmond, M. D., Davis, T. S., Ferrenberg, S. & Wion, A. P. Resource allocation trade-offs in a mast-seeding conifer: Piñon pine prioritizes reproduction over defence. *AoB PLANTS* **11** (2019).
- [49] Gonzalez, A. D., Pearse, I. S. & Redmond, M. D. Increased aridity is associated with stronger tradeoffs in ponderosa pine vital functions. *Ecology* **104**, e4120 (2023).
- [50] Krebs, C., LaMontagne, J., Kenney, A. & Boutin, S. Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. *Botany* **90**, 113–119 (2012). URL <http://www.nrcresearchpress.com/doi/10.1139/b11-088>.
- [51] Copernicus Climate Change Service. ERA5 monthly averaged data on single levels from 1940 to present (2019). URL <https://cds.climate.copernicus.eu/doi/10.24381/cds.f17050d7>.
- [52] Park Williams, A. *et al.* Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* **3**, 292–297 (2013). URL <https://www.nature.com/articles/nclimate1693>.
- [53] Fleurot, E. *et al.* Oak masting under climate change: when spatially heterogeneous shifts in flowering phenology reshape pollen limitation. *New Phytologist* (2026).
- [54] R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria (2025). URL <https://www.R-project.org/>.

Acknowledgments

We thank Maciej Barczyk for helpful comments on the manuscript.

Funding

The study was funded by the European Union and supported by grant no. 2024/54/E/NZ8/00007 from the Polish National Science Centre. JF was supported by the MSCA Postdoctoral Fellowship FECUND (ID: 101244227). Views and opinions expressed are however those of the author(s) only and do not necessarily reflect those of the European Union or the European Research Executive Agency (REA). Neither the European Union nor the granting authority can be held responsible for them.

Author Contributions

JF and MB: Conceptualisation, Methodology, Writing – original draft. JF: Formal analysis, Data curation, Visualisation. MB: Supervision. JF, MB, EF, MaB, JS: Writing – review & editing. All authors have read and approved the final manuscript and agreed to its submission.

Competing interests

No competing interests to declare.

Supplementary Information

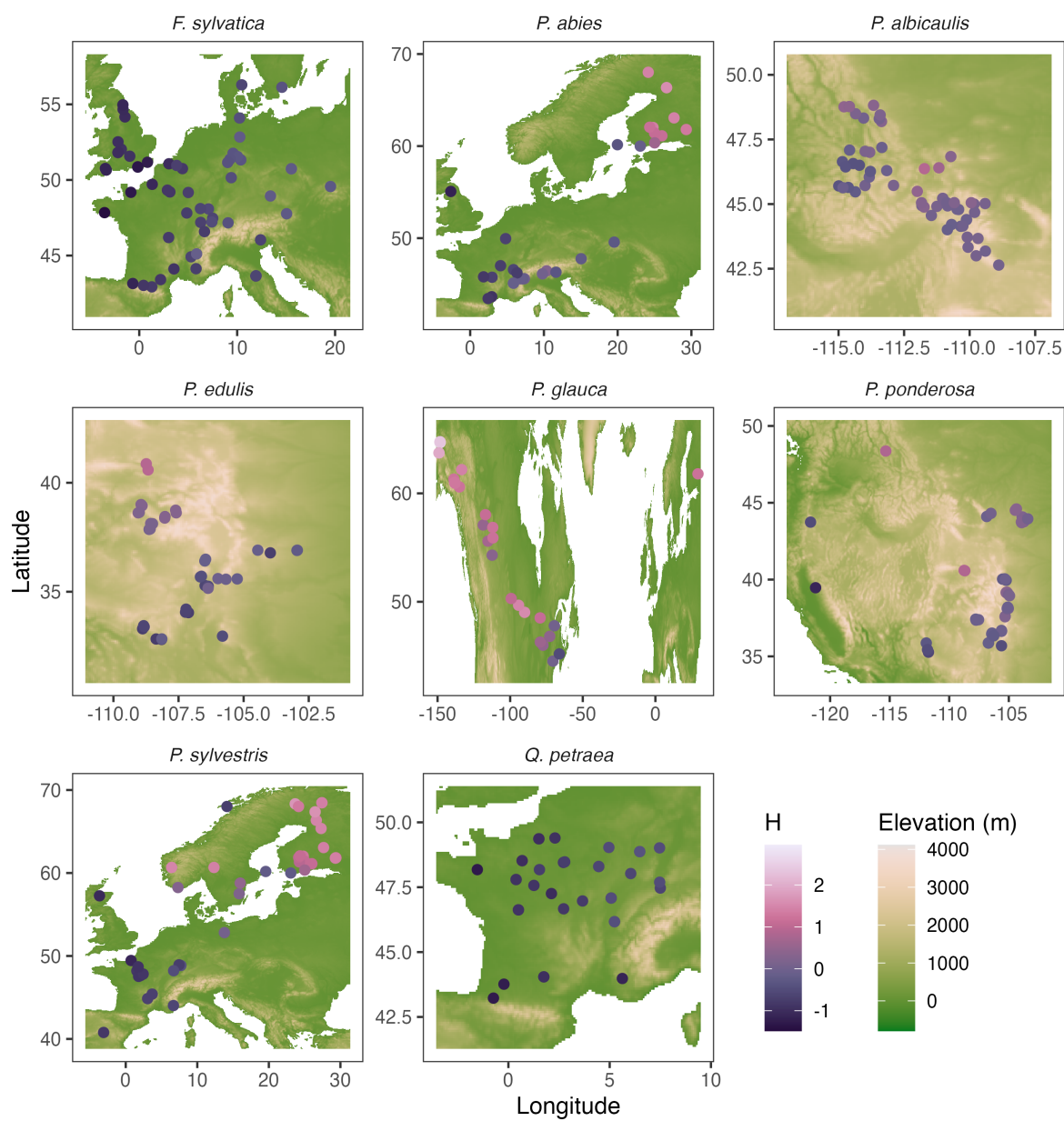


Figure S1: Geographic distribution of study populations for each species, shown against elevation. Points indicate sampled populations. Point colour shows thermal climate severity index H .

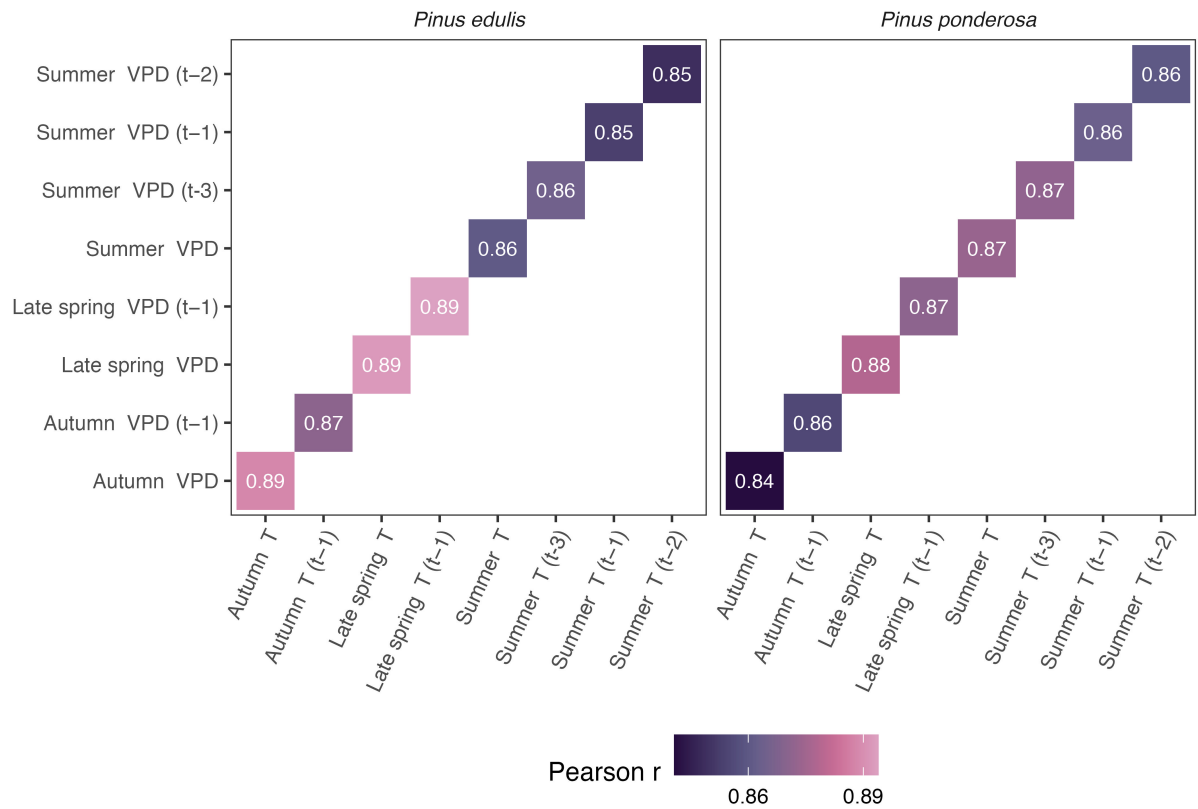


Figure S2: Strong correlations among predictors ($|r| \geq 0.7$). These occurred only between VPD and mean temperature within the same seasonal and lagged periods in two species.

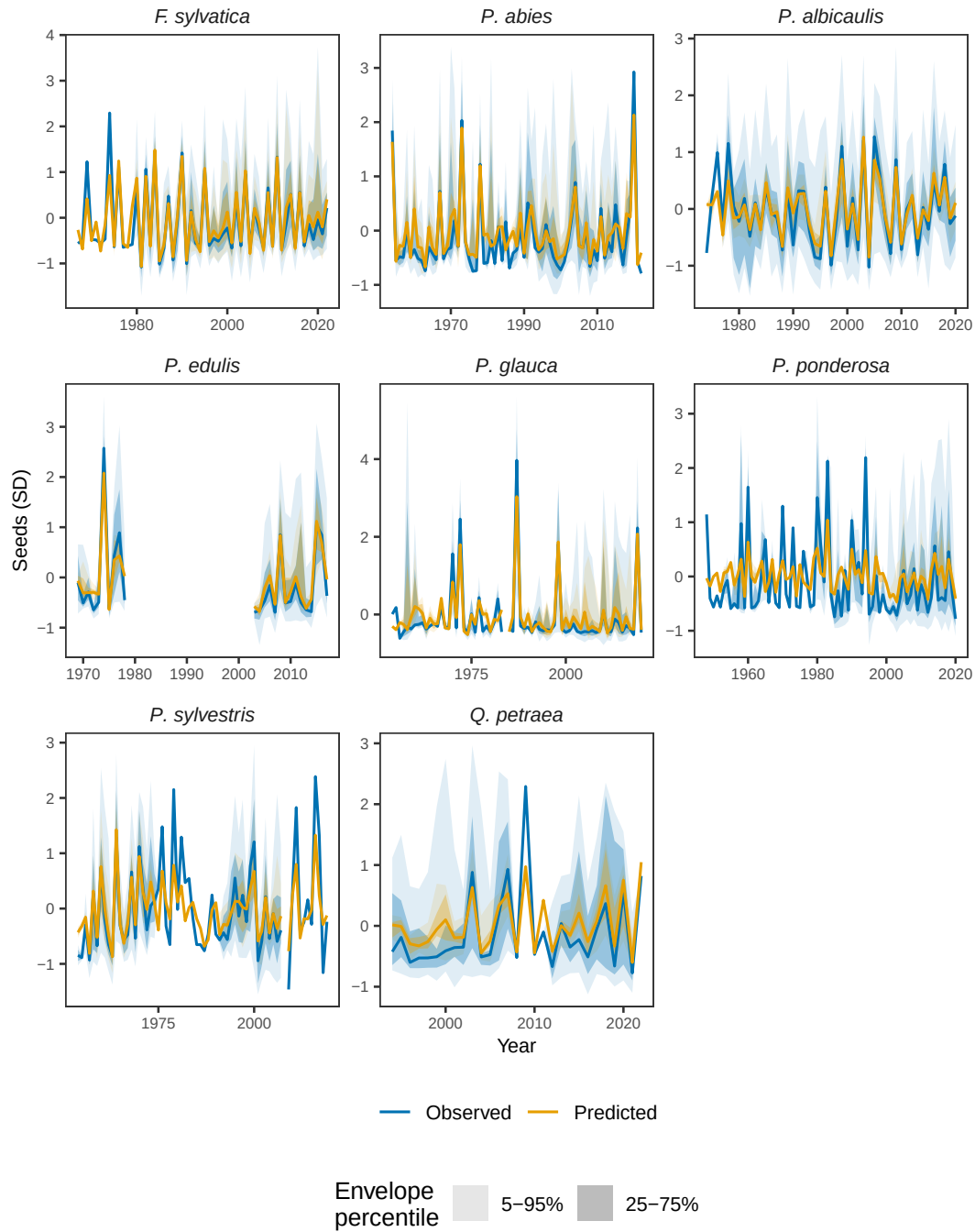


Figure S3: Observed and predicted temporal variation in seed production across species. Blue and orange lines show the median observed and BRT-predicted seed production, respectively, across available time-series in each year. Seed production is expressed as standard deviations from the site mean. Dark and light shaded envelopes show the 25-75% and 5-95% percentiles, respectively, of values across time-series.

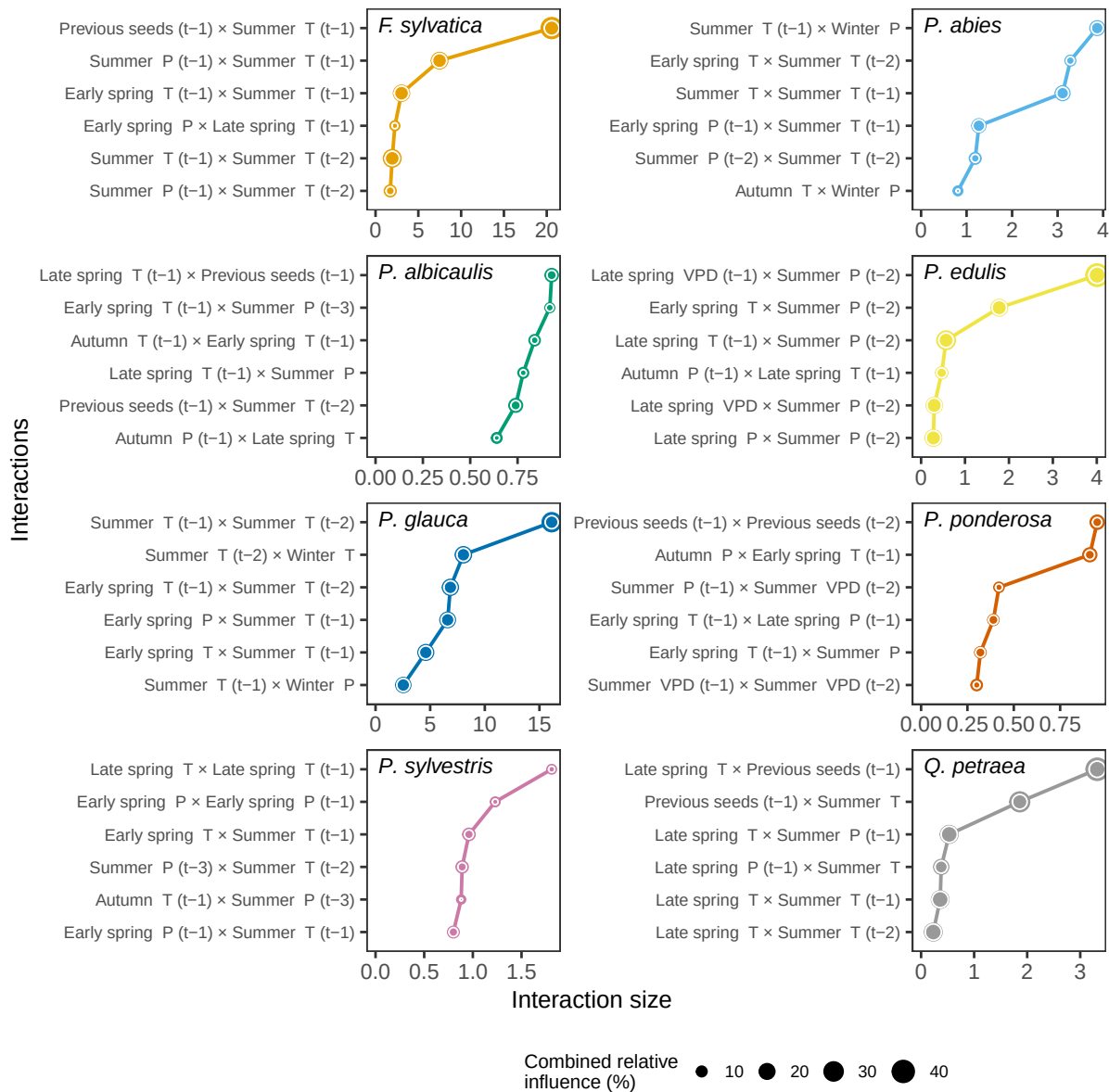


Figure S4: Ranked pairwise interactions among predictors. Interaction strength from species-specific machine-learning models is shown for the strongest predictor pairs in each species. Within each panel, interactions are ranked from strongest to weakest. Point size represents the summed relative influence of the two predictors forming each interaction, while the white inner circle represents the relative influence of the more influential of the two predictors. Predictor labels indicate season and variable, with T = temperature, P = precipitation, t = seed year, $t - 1$ = one year before seed production, and $t - 2$ = two years before seed production.

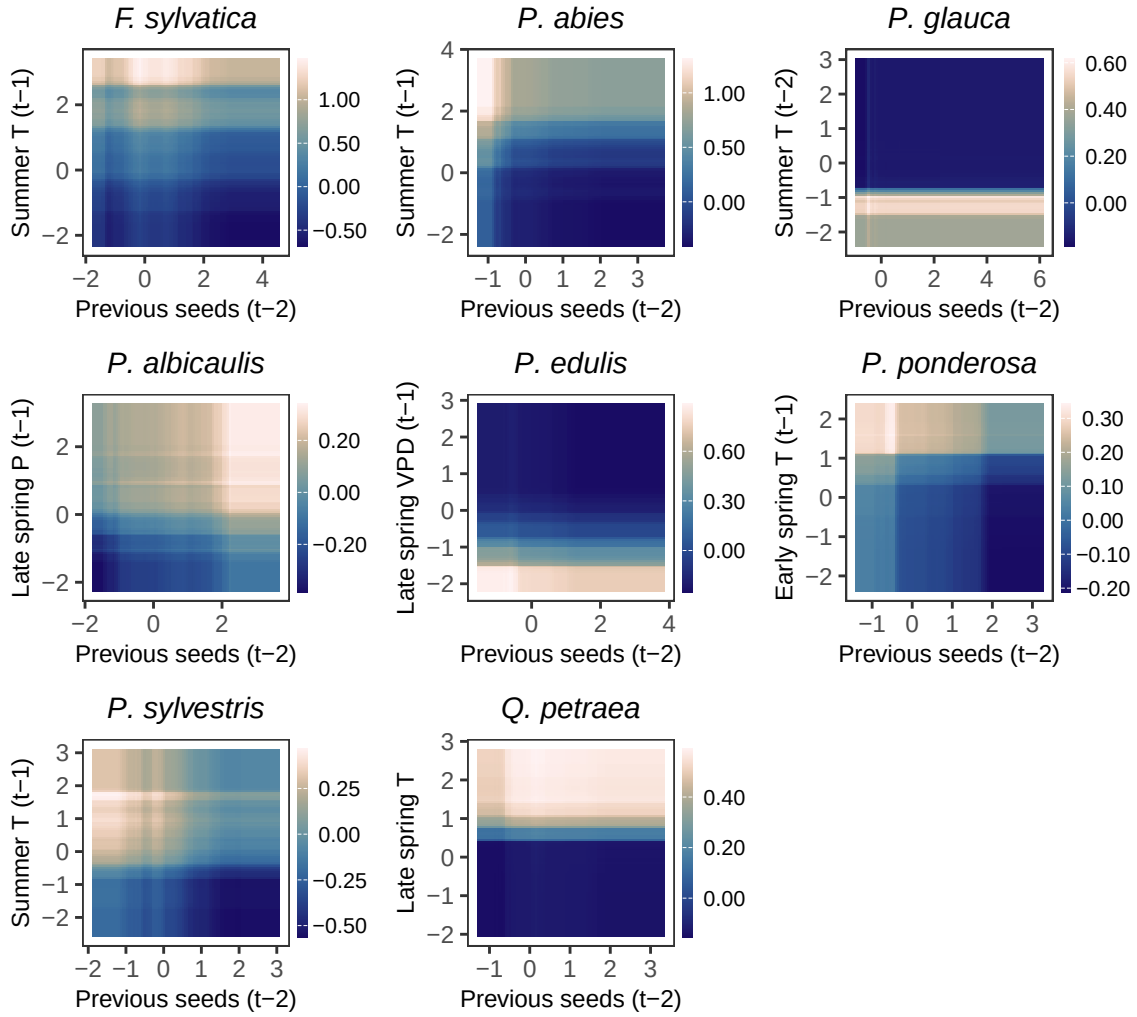


Figure S5: Two-way partial dependence between the strongest weather predictor and previous seed crop ($t - 2$) across species. Heatmap colours show fitted seed production (SD from the site mean) for each species-specific BRT. Weather predictors are expressed as SD from the site mean. Predictor labels indicate season and variable, with T = temperature, P = precipitation, t = seed year, $t - 1$ = one year before seed production, and $t - 2$ = two years before seed production.

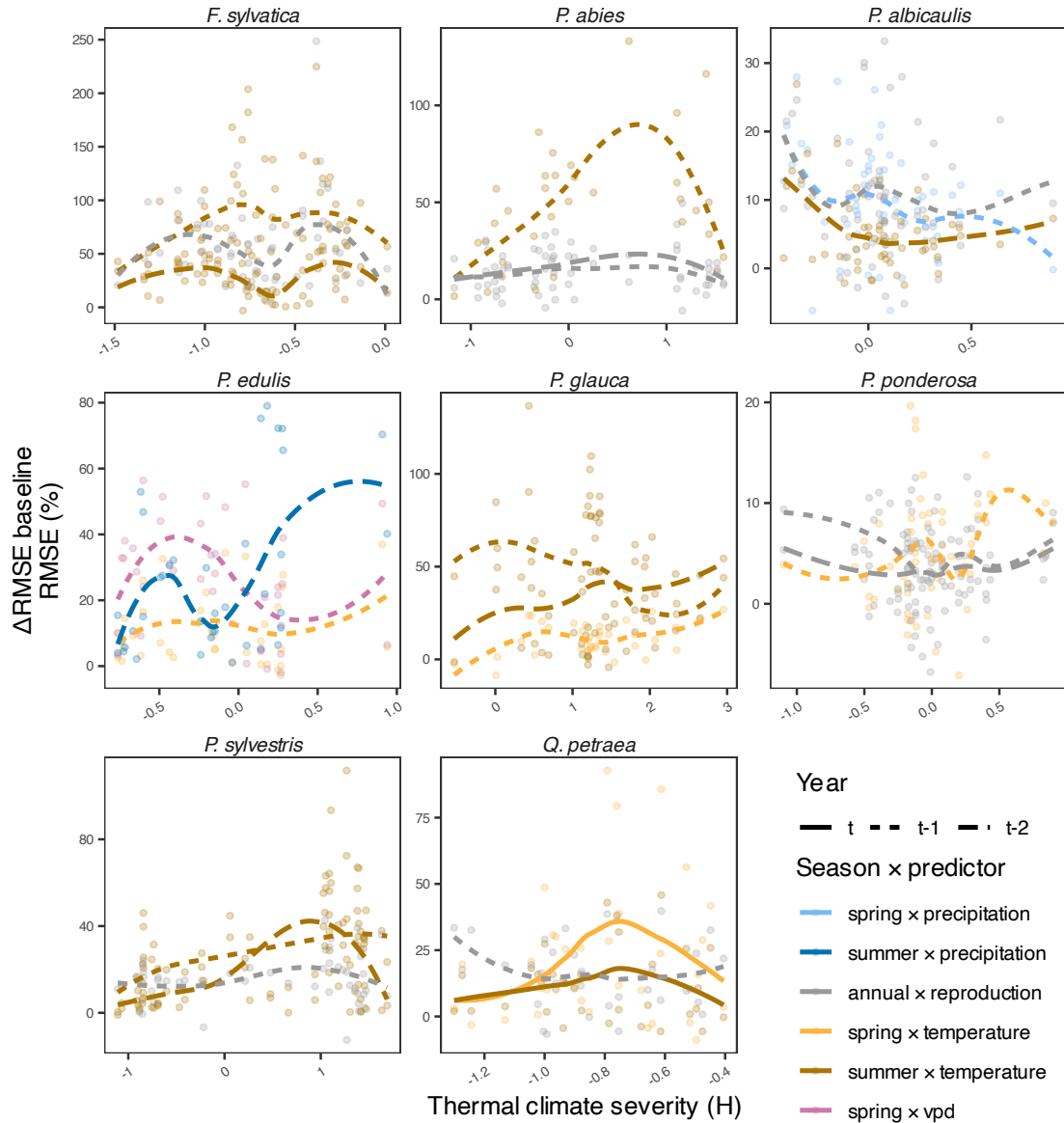


Figure S6: Predictive importance varies across thermal climate severity gradients. Scatterplots show permutation-based predictor importance from species-specific BRT models across thermal climate severity (H), with higher H representing colder and more thermally variable sites. Points represent individual time-series, and lines show loess smoothers fitted for each predictor for visualisation purposes. Predictor importance is expressed as the mean increase in prediction error (Δ RMSE) following within-time-series permutation, relative to the baseline RMSE of the unpermuted model (%). Larger positive values indicate greater local predictive importance. Colours distinguish season and predictor type, whereas line types indicate temporal lag relative to the seed year. Only the three predictors with the highest relative influence per species are shown.

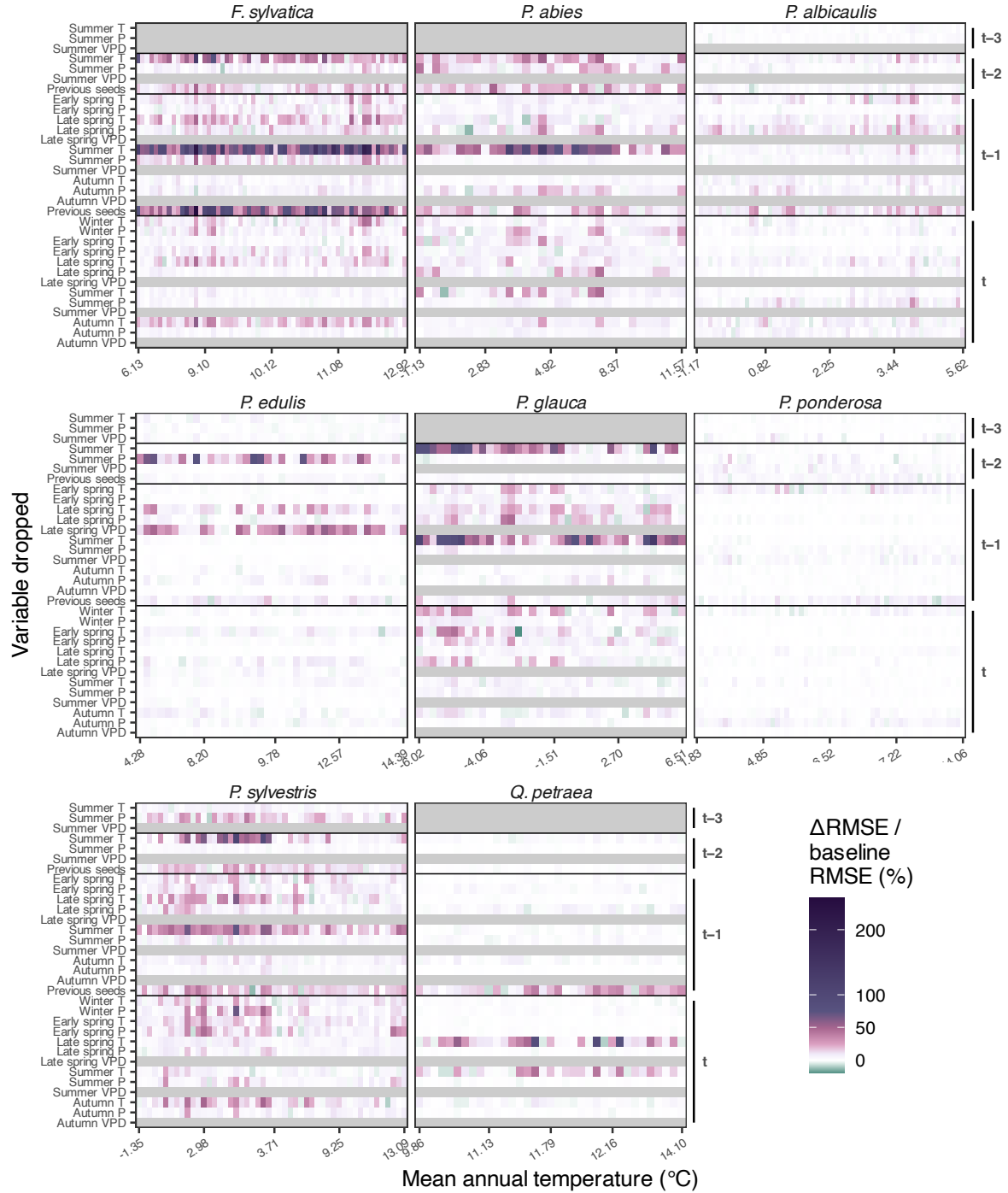


Figure S7: Predictor importance is broadly stable along MAT gradients, with localised shifts among time series. Heatmaps show local permutation-based predictor importance from species-specific machine-learning models for individual time-series ordered from lower to higher mean annual precipitation. For each predictor and time-series, importance was quantified as the mean change in prediction error (Δ RMSE) across 1000 within-time-series permutations and expressed as a percentage of the baseline RMSE of the unpermuted model. Larger positive values indicate a greater increase in prediction error (in %) after permutation and therefore greater local predictive importance; values near or below zero indicate little or no predictive contribution. Grey cells mark predictors that were not assessed for a given species. Predictor labels specify season and variable, with T = temperature, P = precipitation, t = seed year, and $t - 1$ to $t - 3$ denoting one to three years before the seed year.

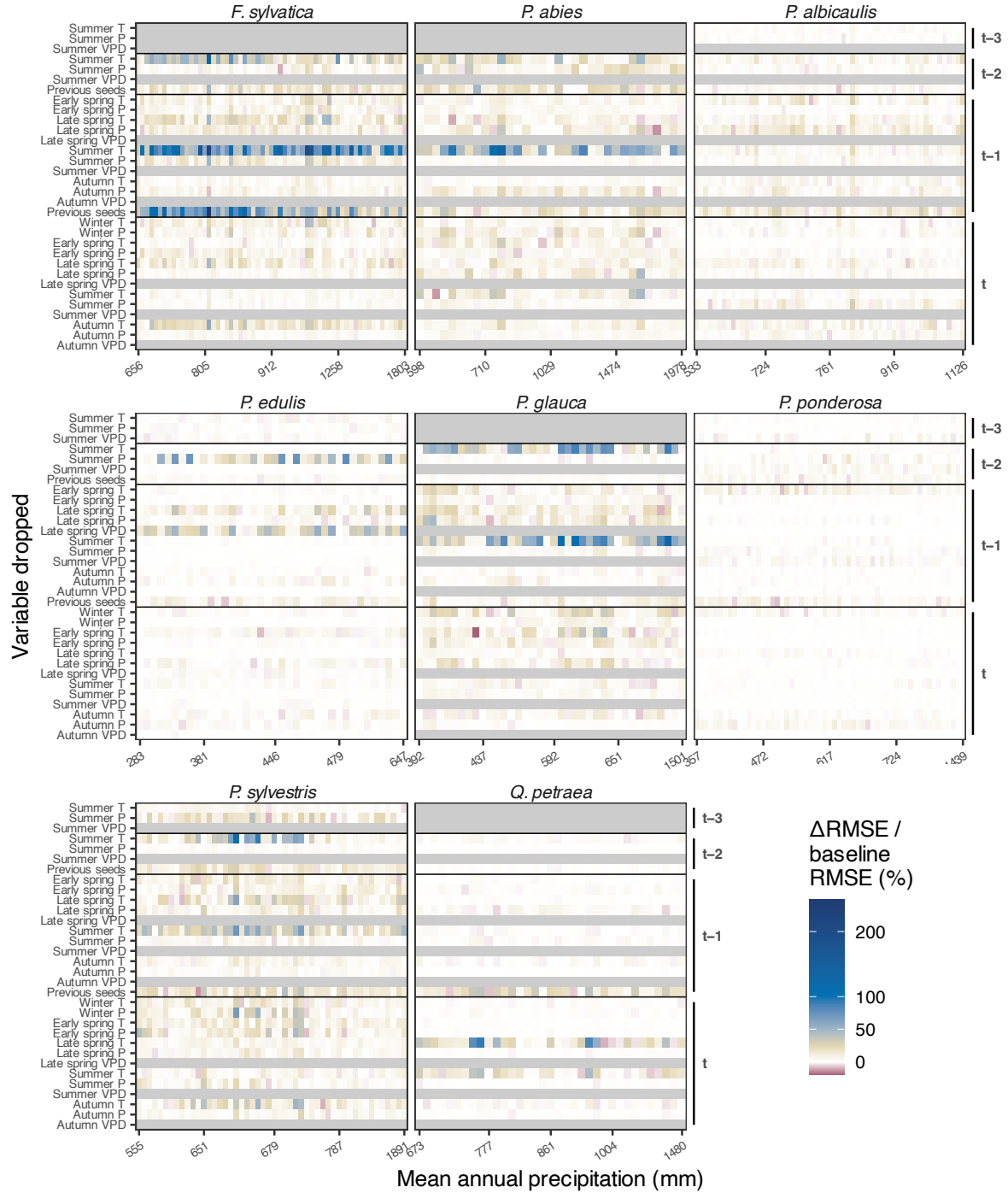


Figure S8: Predictor importance is broadly stable along MAP gradients, with localised shifts among time series. Heatmaps show local permutation-based predictor importance from species-specific machine-learning models for individual time-series ordered from lower to higher mean annual precipitation. For each predictor and time-series, importance was quantified as the mean change in prediction error (Δ RMSE) across 1000 within-time-series permutations and expressed as a percentage of the baseline RMSE of the unpermuted model. Larger positive values indicate a greater increase in prediction error (in %) after permutation and therefore greater local predictive importance; values near or below zero indicate little or no predictive contribution. Grey cells mark predictors that were not assessed for a given species. Predictor labels specify season and variable, with T = temperature, P = precipitation, t = seed year, and $t - 1$ to $t - 3$ denoting one to three years before the seed year.