Woody plant phenological responses are strongly associated with key functional traits

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Running title: Budburst responses associated with traits

Summary

Species-level variation in phenology—the timing of recurring life history events—can vary seasonally with changes in climatic risk, light, and nutrients. This favours acquisitive growth strategies early in the spring season and conservative growth strategies under the more climatically benign, but competitive, environment later in the season. This framework infers suites of traits that may co-vary with phenologies, but high trait variability across environments makes this challenging to test. Here, we combine a new joint modeling approach to accommodate this variability with global data on plant traits and budburst responses in controlled environment experiments. We find that earlier species—which are generally most responsive to anthropogenic warming—are generally shorter with denser, lower nitrogen leaves. These results suggest warming may reshape the trait structure of plant communities, and could help improve predictions of how growth strategies and phenologies together may shift with continued climate change.

Key Words: Budburst, spring phenology, functional traits, trees, climate change, forest communities

Introduction

The timing of life history events—phenology—can shape both ecosystem services and community dynamics. Spring phenology, for example, defines the start and overall length of the growing season—shaping forest carbon storage and species interactions [3,9,18]. Shifts in phenology with climate change across systems [31,45] have thus led to growing concerns over their possible impacts.

Predicting these changes requires understanding the drivers of phenology both at a proximate scale—the environmental triggers of phenology each year, such as temperature and daylength—and at an ultimate scale, where long-term environmental pressures may select for different phenologies across species e.g., certain species are early or late relative to other species each year, [33,51]. At the proximate level, environmental conditions throughout the winter and spring cause species to start growth at different times. This is well documented for the start of growth in woody plants each year [15,24]. Similar environmental conditions appear to trigger spring phenological events across taxa, including in the timing of egg laying in birds [11,12] and the advance of spawning in amphibians [23,43], but current work provides limited insights into the drivers of species differences [6,15,24].

At the ultimate level, species phenologies may vary due to changing pressures across the growing season. Species that start growth early often risk high tissue loss—due to frost damage [2,37] or high herbivore apparency [46]—but benefit from higher resource availability [21,34]. In contrast, later species face greater biotic pressures, especially from high competition for resources [27,52]. For plants, this variation in early to late season growth, may mirror the stressors from early to late successional communities, and may similarly shape phenology [24].

Different pressures could shape a number of species attributes related to their growth strategies, including phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced if damaged [36], while species with later phenology may benefit from investing in tissues that infer greater resource retention [16]. Differences in traits, and trade-offs in allocation of resources to growth and tissue quality, can be related to a broader framework of species growth strategies and functional traits [52] (Fig 1), where species range from acquisitive (fast) to more conservative (slow) growth [5,53].

Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation of the leaf economic and the wood economic spectra [5,13,47,48,53], but they can make limited predictions of trait variability [44]. As a result, highly variable traits like phenology are often excluded from trait studies, leaving the relationships between broader trait syndromes and phenology largely unknown. Understanding these relationships is critical to forecasting community dynamics and responses to climate change. To date, studies have generally only examined the relationship between traits and phenology within a single site, as reviewed by Wolkovich and Cleland[50] and Wolkovich and Donahue[51], where the problem of proximate drivers causing phenological variation can be more easily ignored. Adding phenology to broader trait frameworks becomes more complex when high levels of variation ocurrs across large spatial and temporal ranges.

Consistently defining early to late phenology is possible using the underlying cues that predict gradients in phenology which do not generally vary strongly across space and time,[7,15,20]. For many plants, early species generally have small in magnitude responses to all three major cues of spring leafout: warm spring temperatures (forcing), cool winter temperatures (chilling) and daylength (photoperiod). In contrast, later species have larger responses to chilling and/or photoperiod[15,24], and likely larger forcing responses.

Studies of spring phenology in temperate forests may provide the best opportunity to integrate phenology into functional trait research. In addition to how well we understand the environmental cues that trigger early versus late leafout, spring in many forests includes strong gradients in potential selective environments (Fig 1). Based on trade-offs between early and late spring phenologies, we predict acquisitive species to be shorter, with leaf traits favourable to higher light availability and tolerance of late spring frost (high specific leaf area, SLA, and leaf nitrogen content, LNC; Fig 1). Such species should exhibit early phenology, with small cue responses. Canopy species that budburst later via larger cue responses, when competition for soil resources is greater, would then have traits associated with conservative growth—taller with denser wood[25]—with leaf traits suited for more variable light (low SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative continuum, as acquisitive species produce smaller seeds and conservative species produce larger—better provisioned—seeds (Fig 1).

To test our predicted relationships between budburst responses to environmental cues and common functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases—BIEN[29] and TRY[22]—with budburst data from the OSPREE database of controlled environment studies[14]. We developed a hierarchical Bayesian joint model that predicts phenological responses to forcing, chilling and photoperiod treatments based on species-level trait values, while allowing additional variation due to species. This approach takes a step towards predicting variation via species traits instead of species identity (when traits explain a significant portion of the variation, species identity will explain only a small amount), which could help forecast species phenological responses based on trait values alone.

Methods

We merged three major databases for our analysis. We gathered phenological data from the OSPREE database[14], which contains budburst data for woody, deciduous species from experiments of forcing, chilling and photoperiod. We updated this database since its initial publication, the methods of which are discussed by Morales-Castilla et al.[32]. We gathered trait data from TRY and BIEN (v. 4.0)[22,29], both of which are large trait databases that include plant trait data across many individuals, species, and studies (Table S1). We obtained data from both databases on 5 December, 2018, with an updated version of the TRY data obtained 10 April, 2019. We focused our search for trait data on the subset of 234 OSPREE species used in Morales-Castilla et al.[32]. Using the BIEN R package, version 1.2.5[29], we downloaded trait data for the 94 species available, for which there were 13 traits. The TRY database included data for 10 traits for 96 of our focal species[22]. Given our focus on phenology of adult trees, we included trait data from adult individuals with a minimum height of 1.38 m. We further removed all data from experiments or from plants growing in non-natural habitats. We also grouped trait values where appropriate, for example categorizing trait values for "SLA", "SLA with petioles", and "SLA without petioles" as simply "SLA" in our analysis (see Table S1). Duplicated data in both the TRY and BIEN datasets were also removed (n = 434905). Based on our selection criteria, our final dataset included data for 11 traits from 91 of the species also represented in the OSPREE database, with each species differing in the number and types of traits measured.

For our analysis, we only include species for which we had a complete trait profile (i.e., all traits measured for all species). We initially considered six commonly measured traits—SLA, leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species had at least one trait measurement for each trait. We then used a principle component analysis to understand trait correlations and adjusted which traits we included. A PCA of our six initial traits identified high correlations between SLA and LDMC, and between height and SSD (see Supplementary material). The first principal component explained 32% of variation while the second explained 24.2% of the variation (Fig. S1). By excluding one trait from each of these highly correlated trait pairs(specifically LDMC and SSD) we increased the number of species in our dataset from the 26 species with six traits, to 37 species for which we had complete datasets for four traits. The data for these 37 species were from 24 unique studies (height n = 47781, seed mass n = 281, LNC n = 3853, SLA n = 7656). We subsampled height measurements to reduce the influence the 13 most frequently measured tree species had on our height model. Since these 13 species were measured 19 times more frequently than other species, for each species, we randomly sampled 3000 height measurements.

Joint model of trait and phenology

To understand connections between phenology and species traits, we developed and then parameterized a joint model for each trait: height, SLA, LNC, and seed mass. Our model is a joint model insofar as it involves two types of data—trait observations and phenological observations—that arise from shared latent processes. In particular, we assume that species "true" trait values determine observed trait values across different studies (trait sub-model), and separately, that the same "true" trait values interact with phenological cues (forcing, chilling, and photoperiod) to determine observed phenology, specifically day of year of budburst (phenology sub-model). Below we describe the two sub-models, noting which parameters are shared across sub-models and which are independent.

Trait sub-model

The trait sub-model describes the processes that determine trait observations for 1 to n species across each of the 1 to m studies in our trait dataset (TRY and BIEN data). We use hierarchical modeling to partitions trait variation by measurement error, species identity, and study identity. In particular, we assume that a trait observation for species i from study j, $Y_{\text{trait}_{i,j}}$, has the following normal distribution:

$$Y_{\text{trait}_{i,j}} \sim \mathcal{N}(\mu_{i,j}, \sigma^2_{\text{m}}) \tag{1}$$

with

$$\mu_{i,j} = \alpha_{\text{grand trait}} + \alpha_{\text{trait}_i} + \alpha_{\text{study}_j} \tag{2}$$

where α_{trait_i} and α_{study_j} are elements of the normal random vectors:

$$\begin{aligned} \boldsymbol{\alpha}_{\text{trait}} &= \{\alpha_{\text{trait}_1}, ..., \alpha_{\text{trait}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{trait}} \sim \mathcal{N}(0, \sigma^2_{\text{trait}}) \\ \boldsymbol{\alpha}_{\text{study}} &= \{\alpha_{\text{study}_1}, ..., \alpha_{\text{study}_m}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \mathcal{N}(0, \sigma^2_{\text{study}}) \end{aligned} \tag{3}$$

The latent parameter $\alpha_{\text{grand trait}}$ represents a trait value that is independent of study and species, $\alpha_{\text{species},i}$ and $\alpha_{\text{study},j}$ are species- and study-level offsets from that trait value, σ^2_{m} is measurement error, and σ^2_{trait} and σ^2_{study} represent species and study-level variances in trait values. Of these parameters, $\boldsymbol{\alpha}_{\text{trait}}$ are shared by the phenology sub-model.

Phenology sub-model

The phenology sub-model describes the processes that determine phenological observations for 1 to n species, specifically the timing (day of year) of budburst from the updated OSPREE dataset. We assume that an observation of budburst day for species k under set g of chilling, forcing, and photoperiod treatments, which we z-scored to allow direct comparison of cues (c_g, f_g, p_g), $Y_{\text{pheno}_{k,g}}$, has the following normal distribution:

$$Y_{\text{pheno}_{k,g}} \sim \mathcal{N}(\mu_{k,g}, \sigma^2_{\text{d}}) \tag{4}$$

with

$$\mu_{k,g} = \alpha_{\text{pheno},k} + \beta_{\text{chill}_k} \cdot c_g + \beta_{\text{force}_k} \cdot f_g + \beta_{\text{photo}_k} \cdot p_g \tag{5}$$

and

$$\begin{aligned} \beta_{\text{chill},k} &= \alpha_{\text{chill},k} + \beta_{\text{trait.chill}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{force},k} &= \alpha_{\text{force},k} + \beta_{\text{trait.force}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{photo},k} &= \alpha_{\text{photo},k} + \beta_{\text{trait.photo}} \cdot \alpha_{\text{trait},k} \end{aligned} \tag{6}$$

where α_{pheno_k}, α_{chill_k}, α_{force_k}, and α_{photo_k} are elements of the normal random vectors:

$$\begin{aligned} \boldsymbol{\alpha}_{\text{pheno}} &= \{\alpha_{\text{pheno}_1}, ..., \alpha_{\text{pheno}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \mathcal{N}(\mu_{\text{pheno}}, \sigma^2_{\text{pheno}}) \\ \boldsymbol{\alpha}_{\text{chill}} &= \{\alpha_{\text{chill}_1}, ..., \alpha_{\text{chill}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chill}} \sim \mathcal{N}(\mu_{\text{chill}}, \sigma^2_{\text{chill}}) \\ \boldsymbol{\alpha}_{\text{force}} &= \{\alpha_{\text{force}_1}, ..., \alpha_{\text{force}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{force}} \sim \mathcal{N}(\mu_{\text{force}}, \sigma^2_{\text{force}}) \\ \boldsymbol{\alpha}_{\text{photo}} &= \{\alpha_{\text{photo}_1}, ..., \alpha_{\text{photo}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photo}} \sim \mathcal{N}(\mu_{\text{photo}}, \sigma^2_{\text{photo}}) \end{aligned} \tag{7}$$

Parameter $\alpha_{\text{pheno},k}$ represents the day of budburst for species k without the influence of chilling, forcing, or photoperiod treatments. Average day of budburst (independent of treatments) is μ_{pheno}, and σ^2_{pheno} is the variance across species. The parameters $\alpha_{\text{chill},k}$, $\alpha_{\text{force},k}$, and $\alpha_{\text{photo},k}$ represent the trait-independent responses of species k to chilling, forcing, and photoperiod treatments respectively, each with an associated mean (μ_{chill}, μ_{force}, μ_{photo}) and variance (σ^2_{chill}, σ^2_{force}, σ^2_{photo}) across species. The effect of the species trait value, $\alpha_{\text{trait},k}$ (parameter shared with trait sub-model above), on its responses to chilling, forcing, and photoperiod are described by parameters $\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$. Finally, σ^2_{d} is the variance arising from measurement error.

We chose weakly informative priors, and validated them using a series of prior predictive checks. The model was coded in the Stan programming language, fit using the rstan package version 3.3.6 [41], with 1,000 iterations per chain across 4 chains (4,000 total sampling iterations), and all models met basic diagnostic checks, including no divergences, high effective sample size (n_eff), and $\hat{R}$ close to 1, fitting the data well (Fig S2). Here we present our model estiamtes as the means and 90% posterior uncertainty intervals.

Results

Across traits, height, SLA, and LNC strongly related to chilling, forcing and photoperiod treatments (β_{chill_k}, β_{force_k}, and β_{photo_k}, Fig 2 a-f & j-l), but the direction of these relationships only showed consistent trends for LNC (Fig. 2 j-l). As we predicted, height was related to chilling (β_{chill_k}) and photoperiod (β_{photo_k}), with taller species having larger responses to cues (-0.5 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). As illustrated for one characteristically acquisitive species, *Alnus incana*, and one characteristically conservative species, *Quercus rubra* (Fig S3), the cue relationships with height led to generally later budburst ($\mu_{k,g}$; Fig. 3). In contrast, seed mass had the smallest responses, with no relationship between seed mass and any cue (Fig. 2 g-i, Fig 3 d-f, & Table S3).

Of our leaf traits, we found that species SLA related to photoperiod (β_{photo_k}, -0.2 mm^2/mg per standardized photoperiod; 90% UI: -0.4, 0.0, Fig. 2 f, Table S4), but did not strongly predict responses to chilling (β_{chill_k}) or forcing treatments (β_{force_k}, Fig. 2 d and e). Thus, species with more acquisitive growth strategies (thin leaves and a lower investment in leaf mass that leads to large SLA values), had larger responses to photoperiod, contrary to our predictions (Fig. 2 f). For LNC, we found that species that produce leaves with high nitrogen content, which relates generally to high photosynthetic rates and acquisitive growth, show smaller responses to cues (Fig. 2 j-l). These findings are in line with our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g per standardized chilling; 90% UI: 0.3, 1.2, Table S5), but we also found high LNC species to be less responsive to photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0, 0.6) and to forcing (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig 2 j-l & Fig S3 d-f).

Across our models, we found species-level variation across traits (σ^2_{trait}) were comparable to or greater than variation across studies (σ^2_{study}, Fig 4). The magnitude of study-level variation (σ^2_{study}) that we found, however, suggests that models using large trait databases that fail to separate out study from species-level variation (σ^2_{trait}) may poorly estimate species traits. Variation across studies was greatest for height (with σ^2_{study} of 7.5 m compared to 5.9 m for σ^2_{trait}, Fig 4a). For seed mass and LNC study-level variation was less than that of the species-level variation, with estimates of 1 mg for study-level variation versus 1.6 for species-level variation in seed mass and estimates of 3.6 mg g^{-1} for study-level variation and 5.1 mg g^{-1} for the species-level variation in LNC (Fig 4c and d). At the lowest end, study-level variation in SLA was approximately half the value of the species-level variation (3.3 mm^2 mg^{-1} versus 7.8 mm^2 mg^{-1} for σ^2_{study} and σ^2_{trait}, respectively, Fig 4b).

Discussion

We found species traits influenced the timing of budburst in response to the three primary cues of spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or later phenology following well-established gradients in growth strategies predicted by functional trait frameworks[5,13,47,48,53]: early species tended to have traits associated with fast and acquisitive strategies while later species had traits associated with conservative, slower strategies. We found the largest budburst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and height all showing large responses across our three cues. In contrast, our one reproductive trait—seed mass—showed a smaller response. Our results provide a major step forward in integrating phenology into broader trait syndromes that shape species growth strategies, and support previous findings from more local scales that found strong relationships between height and species phenology[39,40,42]. Our findings also suggest other traits—such as seed mass—show no relationship with phenology in our more global analysis.

Effects of phenology-trait relationships on community assembly

Our findings suggest the changing pressures across the early growing season may affect the temporal assembly of communities. Strong abiotic pressures alongside weak competition early in the season were associated with early-budbursting species with acquisitive traits (shorter heights and low LNC) that allow faster return on resource investments [5,17,47]. These traits should allow early species to more easily replace tissue if lost to frost or other abiotic disturbances, and benefit from greater light availability in the open canopy of many temperate forests in the early spring. In contrast, later-budbursting species had traits associated with greater competitive abilities and slower growth Fig. 2, [5,17,47], which may help them compete for soil and light resources when most other species are already growing. These traits can be linked to other ecological processes and species characteristics, such as species successional position, as illustrated by the differences between early and late successional species (e.g., *Alnus incana* and *Quercus rubra*; Fig 2).

The traits with cue responses that deviated from our expectations also offer novel insights into the tradeoffs between traits and environmental cues. All of our traits are associated with numerous aspects of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our predictions, we found large responses to forcing for short trees, which could prevent frost damage or xylem cavitation under a late spring frost [10,30] and influence annual cambial meristem growth [26]. Similarly, the lack of a response to chilling or forcing by high SLA individuals could be driven by other trait attributes and environmental cues—selecting for species relative growth rates or leaf longevity—and not photosynthetic potential [35,47]. These findings highlight the complexity of determining the drivers of species trait profiles, and further our understanding of how traits affect community dynamics under variable environments.

Phenology-trait relationships under future climates

Incorporating phenology within broader trait syndromes could aid forecasting of species and community responses to climate change. While decades of research have documented phenological shifts with anthropogenic climate change, increasing research suggests a potential connection between phenological responses to warming and performance with warming, where species that shift their phenology more also perform better [8,28].
Our results suggest this phenology-performance relationship could be driven in part by a suite of traits that covary with phenological cues to determine how responsive species are to warming. Species with smaller responses to all cues, especially chilling and photoperiod, would tend to advance more with warming, our results suggest these species may also grow more quickly. These results could further aid in predicting the potential for invasion, as communities with similar phenologies and suites of traits, appear more susceptible to fast growing, phenologically more responsive invasive species [1,38,49].

Our analytical approach and results may be especially useful to help forecast changes in forest dynamics. Identifying the trait syndromes of forest communities over spring season can aid predictions about how climate change will alter species growth and productivity. For example, our results suggest that, by favoring more phenologically responsive species (i.e., with small chilling and photoperiod responses), warming may also favor species with acquisitive growth strategies. In contrast, conservative species, which appear less phenologically responsive to changes in temperature (due to larger chilling and photoperiod responses) could therefore face greater abiotic and biotic stress [19].
Our results could further help identify which species are most likely to be negatively impacted under future climates, and develop better strategies for climate change mitigation and conservation. Species that fail to advance phenologically with warming might experience more competition [1,4], as species that begin growth increasingly earlier with warming have more time to deplete resources. In addition to altering the timing and interactions between species within a season, species trait syndromes have the

potential to redefine the environmental conditions under which growth occurs, and as a result, shape community assembly, and productivity of diverse ecological communities. By identifying the species most vulnerable to climate change impacts, we can develop more effective management practices that prevent the loss of ecosystem services and community diversity.

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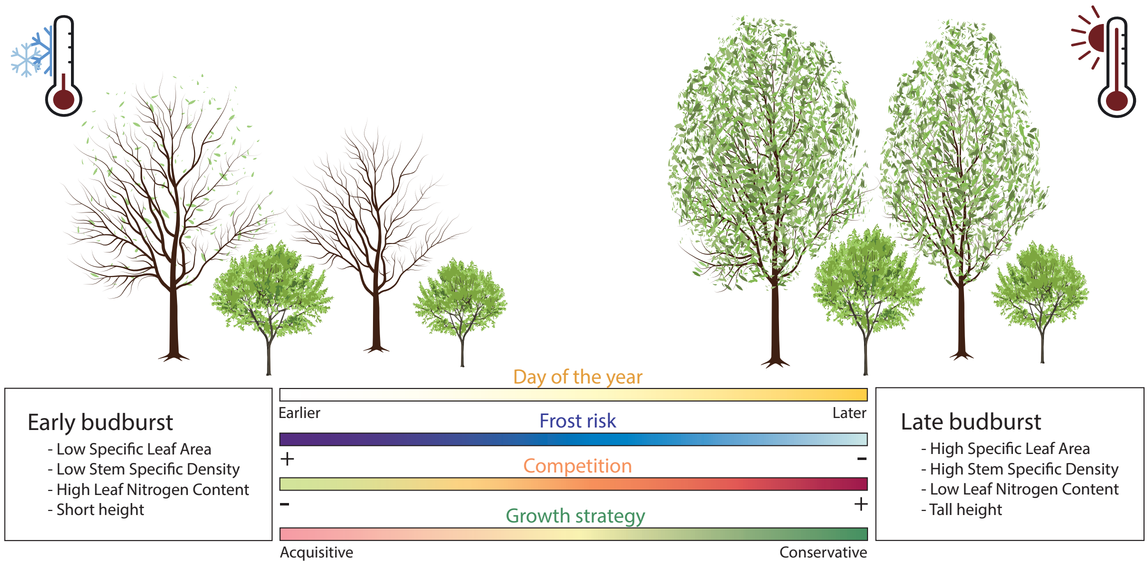

Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost but reduced competition. In contrast, we expected later-budbursting species would have traits associated with conservative growth, as they experience greater competition but a more climatically benign environment.

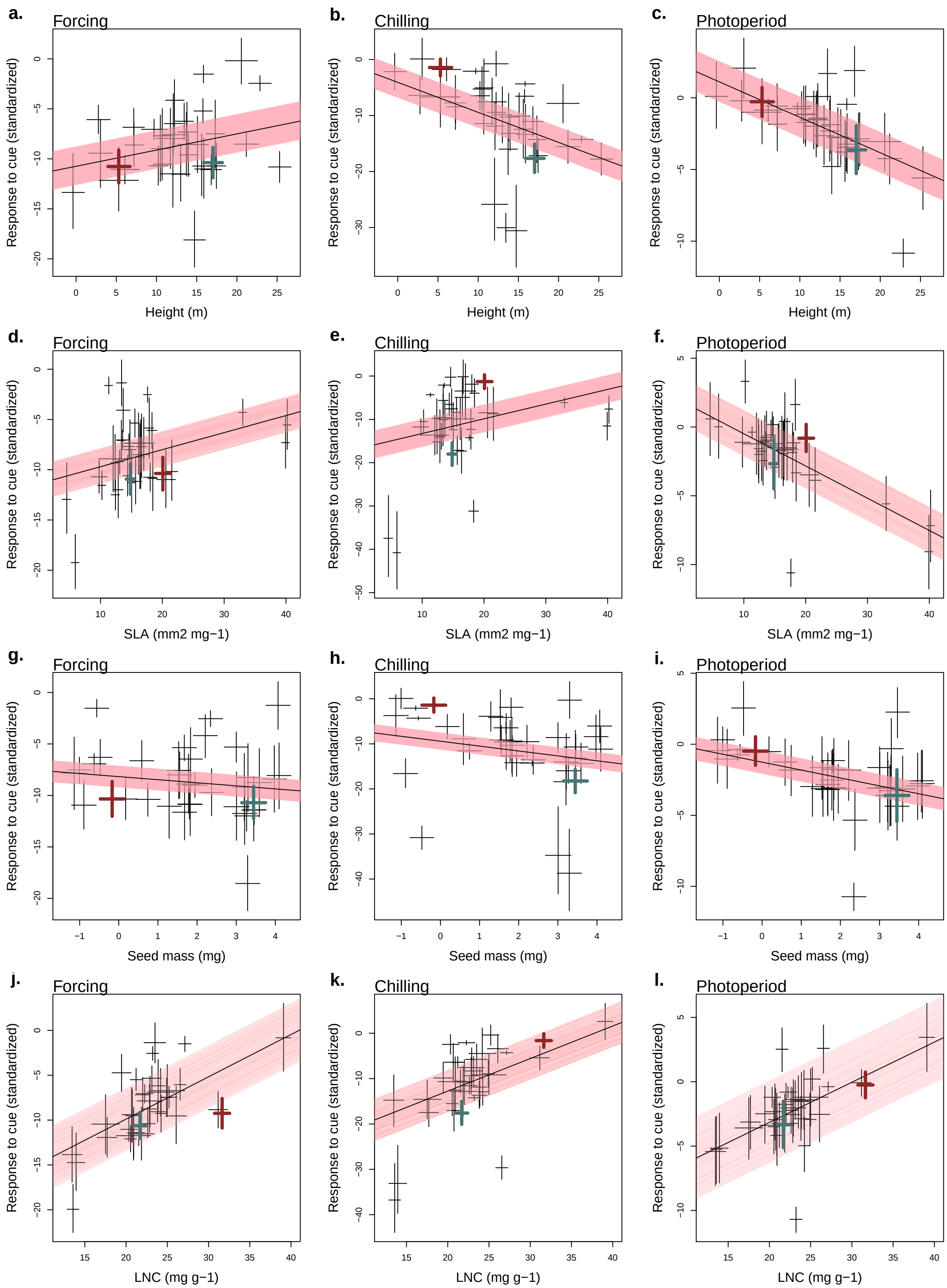

Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the black line depicting the mean linear relationship between estimated trait effects and the slope of the cue response and the pink band the 50% uncertainty interval. Each set of crossed lines represents one species (with each line spanning the 50% uncertainty interval), with the species depicted in Fig 3 colored in each panel, with the acquisitive species (*Alnus incana*) shown in red, and the conservative species (*Quercus rubra*) shown in blue.

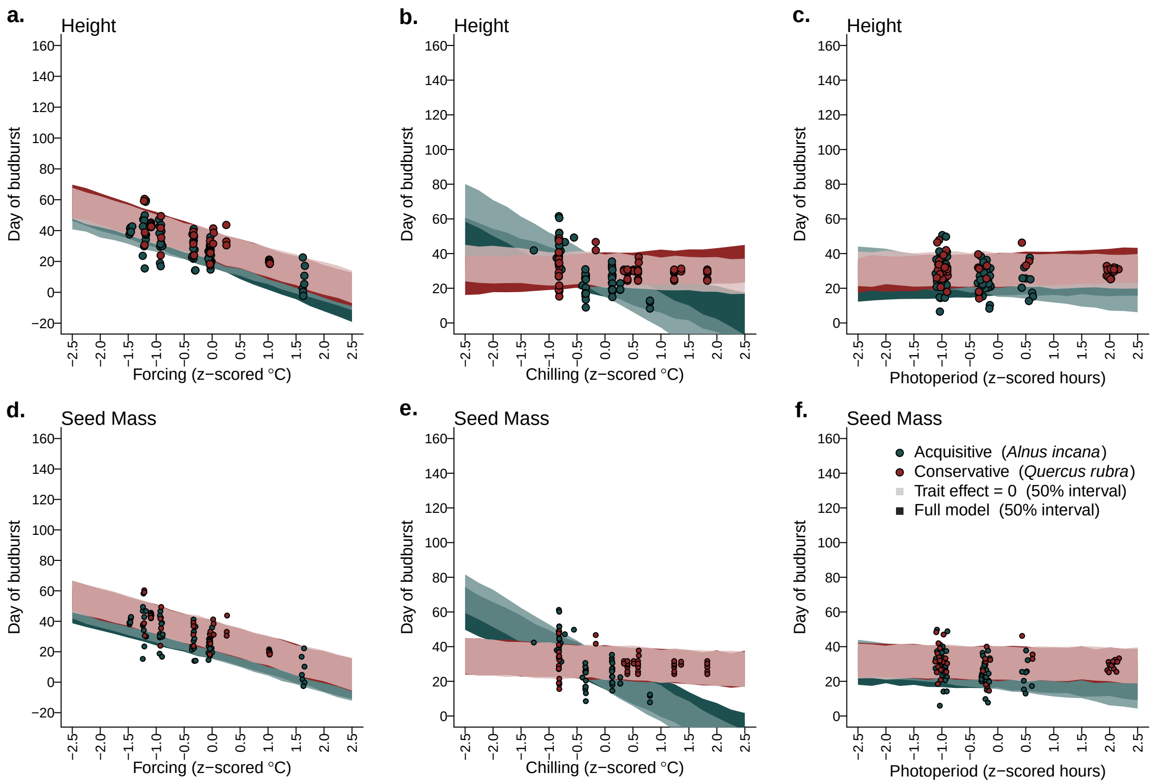

Figure 3: We expected species with traits associated with acquisitive (e.g, smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with height (**a-c**) and seed mass (**d-f**) for an acquistive species, *Alnus incana* shown in red, and a conservative species, *Quercus rubra*, shown in blue. **a,** The effect of height on budburst timing was smaller in response to forcing cues, but larger in response to both **b,** chilling and **c,** photoperiod. In contrast, seed mass had a negligible effect on **d,** forcing and **f,** photoperiod responses, **e,** but a greater response to chilling. Band represent the 50% uncertainty intervals of the model estimates. The coloured bands represent the 50% uncertainty intervals of the model estimates and points individual trait measurements.

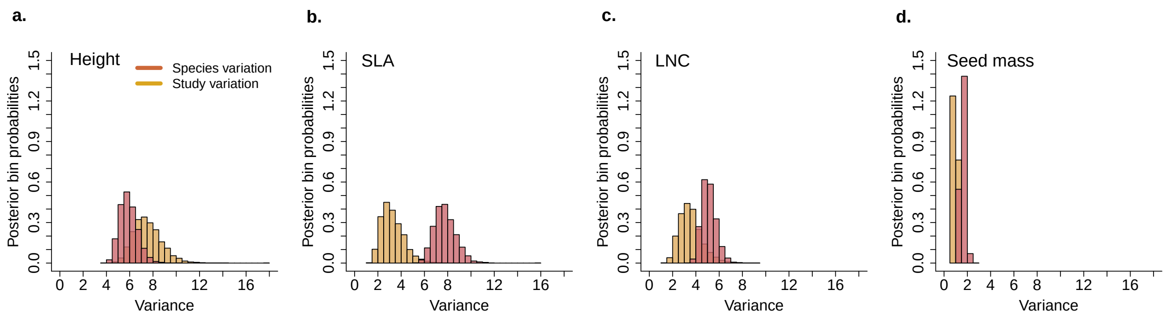

Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation, with only a. the height model estimating greater study-level variation than species-level, while our b. specific leaf area, c. leaf nitrogen content, and d. seed mass models all estimated higher species-level variation. Shown here are the posterior densities for the species-level variation, shown in red, and study-level variation, shown in yellow. For comparison, we show all x-axes spanning the minimum to maximum variances across all four traits. The histograms depict the full distribution of the study and species-level variance, where each bin is normalized by the total count of the posterior estimate.