

1 Woody plant phenological responses are strongly associated
2 with key functional traits

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1 Summary

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2 Introduction

Invasive plants are shaping plant communities worldwide, filling vacant niches and displacing native plants through the novel community landscapes and changes in resource availability.

1. many studies have tried to predict species invasive potential based on functional traits and the links between traits, resource use, and growth strategies
2. the same traits we associate with native plants tracking changes in climate may also allow invasive species greater fitness and adaptive advantage to invasive species
3. traits that promote earlier growth in the spring = priority effects and less competitive temporal niche
4. understanding the links between species traits', climate, and temporal niche will provide greater insight into likely responses of species fitness and community dynamics in response to climate change
1. Functional traits: decades of work associating easy to measure traits related to growth and competition
2. drawing broad generalizable trends independent of species
 - (a) Early vs late - expect species like many invasive, with fast growth strategies, all along fast axes = high sea, high photosynthesis (LNC), small seeds
3. Phenology is similarity a well studied traits not included in broader framework
4. invasives fill empty niche early in the growing season
5. studies of woody plants - focus on how app are responding to changes in climate and the effect of key abiotic cues on growth and phenology
6. In woody plants there are 3 key cues - chilling, forcing, photoperiod
7. We assume these cues would relate to broader growth strategies
 - (a) Particularly tradeoff in resource investment and chilling
 - (b) Forcing vs risk frost
 - (c) Photoperiod and photosynthetic potential
8. Relate cues to traits
9. Predictions, limitations of previous work
10. Our aims

Some text for intro and methods...

A major goal of trait ecology has been to predict species-level characteristics by their traits alone; to do this, we need to be able to replace species distinctions in models with species' traits. To that aim, our models are designed to attribute phenological variation (days to budburst) to species' trait values, while allowing for residual variation explained by species (partially-pooled). When traits explain a

significant portion of variation, species will explain only a small amount, and suggest we may be able to predict species for which we only have trait values.

While phenology in observational data is often considered highly variable, it is actually highly predictable in experiments where the major cues (forcing, chilling, photoperiod) are known and thus we focus on cues here.

3 Predictions

1. Chilling Species with high chilling requirements will have traits associated with greater protection from harsh conditions and higher competitive abilities, but requiring longer periods to accumulate chilling and days to budburst.

- (a) SLA should positively correlate with increasing chill requirements since leaves with large SLA are less frost tolerant
- (b) Height should positively correlate since there will be more competition for light
- (c) Seed mass may negatively correlate, as later species have less time for seed development

2. Forcing Species with low forcing requirements will express traits related to frost tolerance and high productivity through faster resource acquisition.

- (a) Leaves should have smaller SLA because smaller, thicker leaves are more frost tolerant •
- (b) Shorter in height, as there is less competition for light prior to canopy closure
- (c) Seed mass may be greater as there is more time for seed development
- (d) LNC will be greater and is a proxy for photosynthetic rates

3. Photoperiod Species with high photoperiod requirements will budburst later and should have traits associated with greater competitive abilities.

- (a) SLA should positively correlate with increasing photoperiod requirements
- (b) Height should positively correlate since there will be more competition for light
- (c) LNC will be lower in later budbursting species

4 Methods - pre-outline methods

For our analysis, we combined phenological data from the OSPREE database (Ettinger2020) with functional trait data from the TRY (Kattge2020) and BIEN (Enquist2016) trait databases.

The OSPREE database contains phenological data for woody, deciduous species from experiments of phenological cues. First published in 2019, this database has since been updated, and now includes the review of an additional 623 and 270 new publications from each of the following search terms:

- (budburst OR leaf-out) AND (photoperiod OR daylength) AND temperature*
- (budburst OR leaf-out) AND dorman*.

From this subsequent review, we an additional 12 papers met our selection criteria. For additional information on the construction of the OSPREE database and methods of cue estimates, see (OSPREE). Our analysis used all available budburst data for our 37 focal species, with the data originating from 28 unique studies.

Both TRY and BIEN are large databases compiling plant trait data across many individuals, species, and studies. We initially collected all available trait data for the 234 species for which there is budburst data in the OSPREE database.

Trait data for ten functional trait was recieved from the TRY databases for 96 of our species (Table S1 - table of requested traits for each database). Additional trait Data was also obtained from the BIEN database using the BIEN R package (Maitner2017). All trait data were requested or downloaded in December 2018. For our analysis, we only included trait data from adult individuals with a minimum height of 1.42 m and we removed all data from experiments or growing in non-natural habitats. Traits were also grouped where appropriate, for example, with separate entries for SLA values with petioles, without petioles, and for which no petiole presence was specified were all categorized as simply SLA in our analysis (see Table S1). Duplicated data across the datasets were also removed ($n = 434905$). Finally, we subsetting the data to include only species for which we had a complete dataset for each species and trait. This resulted in a dataset of only 26 species and six functional traits. After performing a PCA, we further refined our trait selection, and only included traits that did not show strong correlations. In this analysis, the principle component explained 32.2% of variation while the second explained 23.4% of the variation (Fig. S1). Due to strong association between the SLA and LDMC leaf traits, and similarly between stem specific density (SSD) and height, we further reduced the number of traits in our analysis to include only height, seed mass, LNC, and SLA. By including only these four traits, we were able to increase the number of species we could include in our analysis as we had had at least one trait measurement for 37 species (height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n = 7656$). Given the abundance of height data and overrepresentation of height measurements for six of our focal species, we randomly sampled 3000 height measurements for each of these species to include in our analysis ($n = 27318$). This reduces the effect of trait values from these frequently measured species from overwhelming the partial pooling effect in our model. In addition we excluded seed mass data from the HE Marx dataset from BIEN, as it consisted of only one value, making it challenging to include the study level effect in our model.

Joint model of trait and phenology

To understand the implications of linking traits directly to cue responses, we developed a joint hierarchical Bayesian model. Our model is composed of two sub-models, a trait model and a phenology model, that are co-estimated and linked by a shared parameter. Since each trait varied in the number of studies in which it is included as well as the number of individuals for which it is measured, we chose to model each trait separately. The first part of the joint model is a hierarchical intercept only model where the response variable $Y_{i,j}$ is the observed trait value of species i from study j , and is assumed to be normally distributed. We further assume that the observed trait value is composed of a “grand” species trait value $\alpha_{\text{trait},i}$ that is shared across all individuals of a species and that is independent of environment, a hierarchical grouping term on the intercept for study, $\alpha_{\text{study},j}$, to account for study-level differences in environment or observation methods, and random error. This results in the following sub-model for each trait:

$$Y_{i,j} \sim \mathcal{N}(\mu_{i,j}, \sigma_{\text{trait}}) \quad (1)$$

where σ_{trait} represents random error in the trait value (i.e., independent of study or species) and:

$$\mu_{i,j} = \alpha_{\text{trait},i} + \alpha_{\text{study},j} \quad (2)$$

with:

$$\begin{aligned} \boldsymbol{\alpha}_{\text{trait}} &= \{\alpha_{\text{trait},1}, \dots, \alpha_{\text{trait},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{trait}} \sim \mathcal{N}(\mu_{\boldsymbol{\alpha}_{\text{trait}}}, \sigma_{\boldsymbol{\alpha}_{\text{trait}}}) \\ \boldsymbol{\alpha}_{\text{study}} &= \{\alpha_{\text{study},1}, \dots, \alpha_{\text{study},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \mathcal{N}(0, \sigma_{\boldsymbol{\alpha}_{\text{study}}}) \end{aligned} \quad (3)$$

Parameters $\mu_{\alpha_{\text{trait}}}$ and $\sigma_{\alpha_{\text{trait}}}$ represent the mean trait value across all species and the standard deviation in trait values between species, respectively. The mean effect of study is assumed to be centered at 0 with standard deviation $\sigma_{\alpha_{\text{study}}}$.

The second part of the joint model is a hierarchical linear model where the normally distributed response variable $Z_{i,k}$ is the day of budburst for species i experiencing forcing (F_k), chilling (C_k), and photoperiod (P_k). This sub-model is linked to the trait sub-model via the shared parameters $\alpha_{\text{trait},i}$, representing the “grand” trait values of species that are independent of study. The overall structure of the phenology sub-model is similar to that of (Ettinger2020), except species’ responses to forcing ($\beta_{\text{force},i}$), chilling ($\beta_{\text{chill},i}$), and photoperiod ($\beta_{\text{photo},i}$) are treated not as single parameters but as a combination of parameters, a species-specific response that is independent of its trait value (e.g., $\alpha_{\text{force},i}$) and an effect of its trait value (e.g., $\beta_{\text{trait,force}}$) that is multiplied by $\alpha_{\text{trait},i}$ and does not differ between species. In other words, species responses to cues interact with their “grand” trait values, and we assume this interaction is independent of species identity. The phenology sub-model can thus be written as:

$$Z_{i,k} \sim \mathcal{N}(\mu_{i,k}, \sigma_{\text{pheno}}) \quad (4)$$

where σ_{pheno} represents random error in budburst day and:

$$\mu_{i,k} = \alpha_{\text{pheno},i} + \beta_{\text{force},i} \times F_k + \beta_{\text{chill},i} \times C_k + \beta_{\text{photo},i} \times P_k \quad (5)$$

with:

$$\begin{aligned} \beta_{\text{force},i} &= \alpha_{\text{force},i} + \beta_{\text{trait,force}} \times \alpha_{\text{trait},i} \\ \beta_{\text{chill},i} &= \alpha_{\text{chill},i} + \beta_{\text{trait,chill}} \times \alpha_{\text{trait},i} \\ \beta_{\text{photo},i} &= \alpha_{\text{photo},i} + \beta_{\text{trait,photo}} \times \alpha_{\text{trait},i} \end{aligned} \quad (6)$$

and all species-specific parameters are, as in the trait sub-model, given hierarchical structure whereby:

$$\begin{aligned} \alpha_{\text{pheno}} &= \{\alpha_{\text{pheno},1}, \dots, \alpha_{\text{pheno},n}\}^T \text{ such that } \alpha_{\text{pheno}} \sim \mathcal{N}(\mu_{\alpha_{\text{pheno}}}, \sigma_{\alpha_{\text{pheno}}}) \\ \alpha_{\text{force}} &= \{\alpha_{\text{force},1}, \dots, \alpha_{\text{force},n}\}^T \text{ such that } \alpha_{\text{force}} \sim \mathcal{N}(\mu_{\alpha_{\text{force}}}, \sigma_{\alpha_{\text{force}}}) \\ \alpha_{\text{chill}} &= \{\alpha_{\text{chill},1}, \dots, \alpha_{\text{chill},n}\}^T \text{ such that } \alpha_{\text{chill}} \sim \mathcal{N}(\mu_{\alpha_{\text{chill}}}, \sigma_{\alpha_{\text{chill}}}) \\ \alpha_{\text{photo}} &= \{\alpha_{\text{photo},1}, \dots, \alpha_{\text{photo},n}\}^T \text{ such that } \alpha_{\text{photo}} \sim \mathcal{N}(\mu_{\alpha_{\text{photo}}}, \sigma_{\alpha_{\text{photo}}}) \end{aligned} \quad (7)$$

Parameters $\mu_{\alpha_{\text{pheno}}}$, $\mu_{\alpha_{\text{force}}}$, $\mu_{\alpha_{\text{chill}}}$, $\mu_{\alpha_{\text{photo}}}$ represent the mean budburst day, response to forcing, response to chilling, and response to photo period across all species, respectively. Parameters $\sigma_{\alpha_{\text{pheno}}}$, $\sigma_{\alpha_{\text{force}}}$, $\sigma_{\alpha_{\text{chill}}}$, $\sigma_{\alpha_{\text{photo}}}$ are the standard deviations between species.

Forcing, chilling, and photoperiod (F_k , C_k , P_k) were z-scored to account for differences in the scale of predictors across studies (Gelman2006), as well as differences in the natural units for the cues. We assumed parameters had weakly informative prior distributions (generally normal or half-normal distributions) that we obtained from a series of prior predictive checks where the objective was to produce a wide but also plausible range of trait and phenology values (e.g., budburst dates between days 0 – 365). The joint model was coded in the Stan programming language (Stan citation) and fit to the trait and phenology data (see above) using the rstan package (version, citation). For all traits, model fits were deemed valid based on *Stan’s* diagnostic metrics, including no divergences across 1000 iterations, high effective sample size (n_{eff}), and scale reduction factor \hat{R} close to 1 across 4 chains. We quantify 90% uncertainty interval of posterior distributions using the highest probability density index.

We selected our priors using our prior knowledge of functional trait diversity in deciduous species and cue responses. In doing so, we assume that stronger environmental cues will result in earlier budburst dates, as reflected by negative cue values. Priors of the phenology portion of our model reflect this, and are centered on negative values.

Finally, we used a phylogenetic generalized least-squares regression model (PGLS) to test the relationship between day of budburst and individual traits. This analysis allowed us to test for phylogenetic non-independence in the phenology-trait relationship (Freckleton2002). We obtained a rooted phylogenetic tree by pruning the tree developed by (Smith2018a) and performed the PGLS analysis using the mean trait values and mean posterior estimates of the cue responses from our joint model. The PGLS was run using the "Caper" package in R (Orme2013).

5 Results

1. Quick overview of models again ... (but try not to repeat ourselves from methods)

- (a) Our models jointly estimated species traits and the phenological cues to understand connections between phenology (specifically days to budburst) and other plant traits.
- (b) Because we drew on large trait databases for our analyses we partitioned trait variation due to species versus study-level effects. We then used the species-level estimates of traits (ie., estimates of species with study removed) to examine how traits predicted phenological cues, which in turn predict budburst, while allowing for residual variation in cues to be explained by a species effect.
- (c) (Move to methods): This model is a departure from current efforts in several ways: first, while these steps would normally be done separately, our models allow them to be jointly estimated at once. This allows separating out the trait versus residual species effect; second, we focus on phenological cues as predictors for day of budburst and thus allow traits to influence each cue.

2. Review of trait model part ... comparing study variation to species level variation

- (a) Across our models, we found important study-level variation across traits.
- (b) In our height model, study level variation was greater (7.5) than species level variation (5.9) (Fig. 1).
- (c) In contrast, study level variation in our SLA model was approximately half the value of the species level variations (7.8 and 3.3 respectively).
- (d) In the seed mass and LNC models it was considerably less than that of the species level variation (seed mass species level variation: 1.6 and study level variation: 1; LNC species level variation: 5.1 and study level variation 3.6) (Fig. 1).

3. Very short paragraph reminding audience of the model and connecting figure on cue-trait relationships.

- (a) We next combined these trait-level estimates (Fig. 2) with data on forcing, chilling and photoperiod values from a large meta-analysis of experiments to test if traits (height, SLA, seed mass, LNC) related to phenological cues and species budburst dates (Fig. 3).
- (b) For some traits we found much of the variation in phenological cues across species could be explained by trait variation (see panel a-f and j-l in Fig 2), while for others traits were weak predictors (see g-i in Fig 2).

4. Discuss how Height and SLA were partially in line with predictions

- (a) Across traits, height, SLA, and LNC showed the greatest responses to changes in cues level, though the direction of responses were consistent across cues for only LNC and not height or SLA (Fig. 2 a-f and j-l).

- (b) Taller species had extremely weak responses to forcing (0.2 m per standardized forcing; 90% uncertainty interval: -0.1, 0.5).
- (c) However, as we predicted, taller species had larger responses to chilling (-0.5 m per standardized chilling; 90% uncertainty interval: -1, -0.1) and photoperiod (-0.3 m per standardized photoperiod; 90% uncertainty interval: -0.6, 0, both of which are cues that would generally lead to later budburst and fit within an overall conservative growth strategy.
- (d) High SLA species, which produce thin leaves with a relatively lower investment in leaf mass, had weaker forcing cues, contrary to our predictions, resulting in delayed budburst as forcing cues increased ((0.2 mm²/mg per standardized forcing; 90% uncertainty interval: -0.1, 0.4). However, as we predicted, chilling cues were also weak (0.3 mm²/mg per standardized chilling; 90% uncertainty interval: -0.1, 0.7). Across the range of trait values, low SLA (conservative) species did generally have a greater advance in budburst in response to chilling than high SLA (acquisitive species) (2 b), again following the predicted gradient in growth strategies.
- (e) While our model did estimate stronger photoperiod cues (-0.2 mm²/mg per standardized photoperiod; -0.4, 0) as photoperiod increased, the effect on budburst dates were negligible (2), suggesting no relationship between SLA and photoperiod.
- (f) We found that species that produce leaves with high nitrogen content, which relate to high photosynthetic rates, showed weaker trait responses to all three cues, resulting in delayed budburst when trait effects were accounted for (0.5 mg/g per standardized forcing; 90% uncertainty interval: 0.1, 0.8; 0.7 mg/g per standardized chilling; 90% uncertainty interval: 0.2, 1.2; and 0.3 mg/g per standardized photoperiod; 90% uncertainty interval: 0, 0.7. These findings are partially in line with our predictions as we predicted that LNC would have a weak relationship with chilling, but contrary to our predictions, increases in forcing and photoperiod also produced weaker, delaying effects on budburst.

5. ...But Seed mass

- (a) Of our four traits, seed mass had the weakest responses across the three cues (Fig. 2 g-i).
- (b) Contrary to our predictions, we did not find a relationship between seed mass and cue responses for forcing ((-0.3 mg per standardized forcing; -1.4, 0.8)) or photoperiod and only a moderate responses to chilling (-1.1 mg per standardized chilling; -2.8, 0.7). -0.6 mg per standardized photoperiod; -1.6, 0.4).

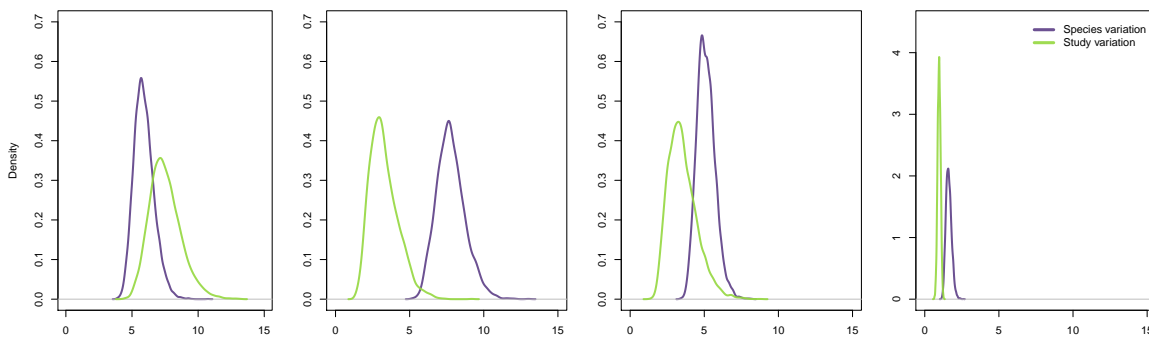


Figure 1: Comparison of the posterior densities for the species level variation and study level variation of a. height, b. SLA, c. LNC, and d. seed mass.

6 Discussion

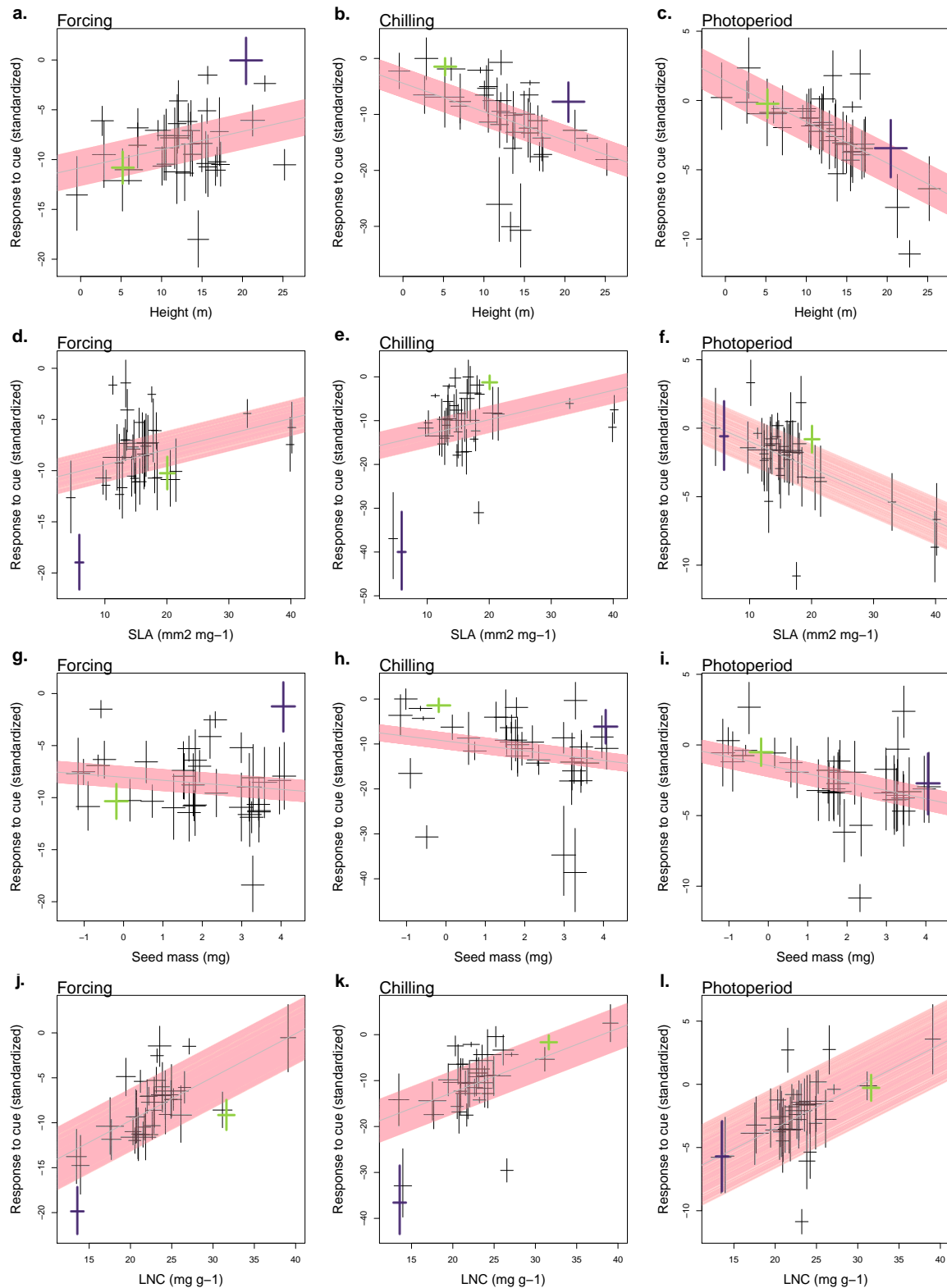


Figure 2: Estimated trait values for height (a-c), SLA (d-f), log10 Seed mass (g-i), and LNC (j-l), correlated against species level cue responses to forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using our joint trait-phenology model, with the grey line depicting the mean linear relationship between estimated trait effects and the slope of the cue response. The 50% confidence interval is depicted by the pink band. The species depicted in Fig 3 are highlighted in each panel, with the acquisitive species shown in green, and the conservative species, shown in purple.

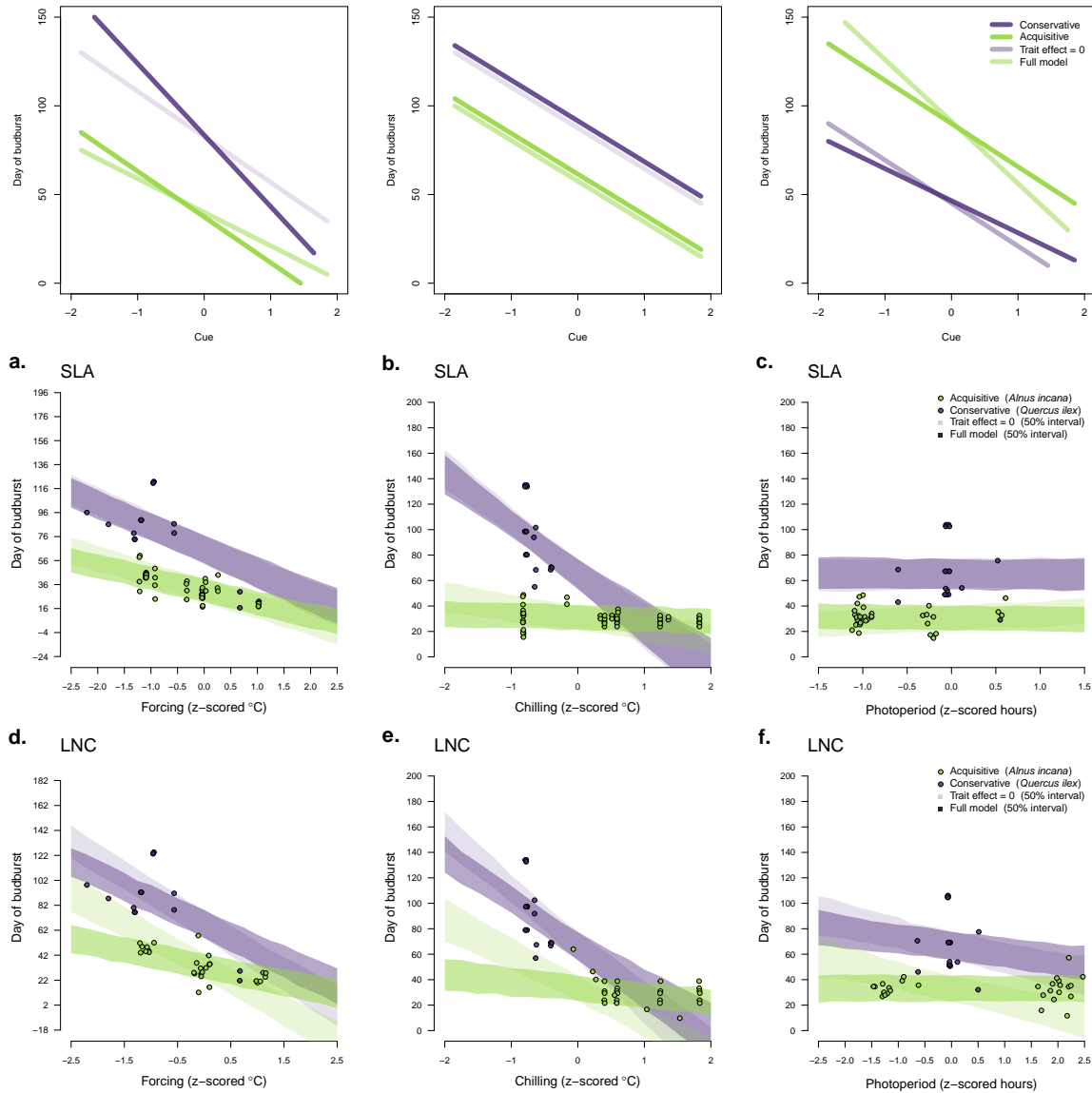


Figure 3: Comparisons of estimated cue responses of a representative species with a trait value associated with acquisitive growth strategies, shown in green, or conservative growth strategies, shown in purple. Panels a. to c. represent a conceptual framework for interpreting trait responses. a) If species with traits associated with conservative (shown in dark purple) and acquisitive growth (shown in darker green) have stronger cue responses and greater advances in budburst date with increasing environmental cues, this will produce a steeper response (or slope) of the full model in comparison to the cue only (trait effect = 0) model. Furthermore, species with acquisitive traits are predicted to budburst earlier than species with more conservative traits. b) Functional traits that have no relation to budburst phenology will result in a trait effect estimated at or close to zero and result in no difference in the slopes of the full model relative to the cue only model. c) Traits with a positive estimated effect will result in the full model having a weaker budburst response to increasing environmental cues, leading to later budburst dates than estimated using the cue only model in which trait effects are zero. Budburst dates of species with traits associated with acquisitive growth will also be later if our estimates do not support the predicted gradients in growth strategies. Some traits strongly predicted phenological responses to cues, as seen by comparing the model estimates including trait (darker bands represent the 50% uncertainty interval for the posterior cue estimates for the full model) versus without (lighter bands represent the 50% uncertainty interval for the posterior cue estimates with a trait effect of zero), which is especially obvious in the species with the higher trait values. Points represent the raw budburst data for each respective species. We show the full range of all treatment values (x axis) though most species cover only a portion of this range.

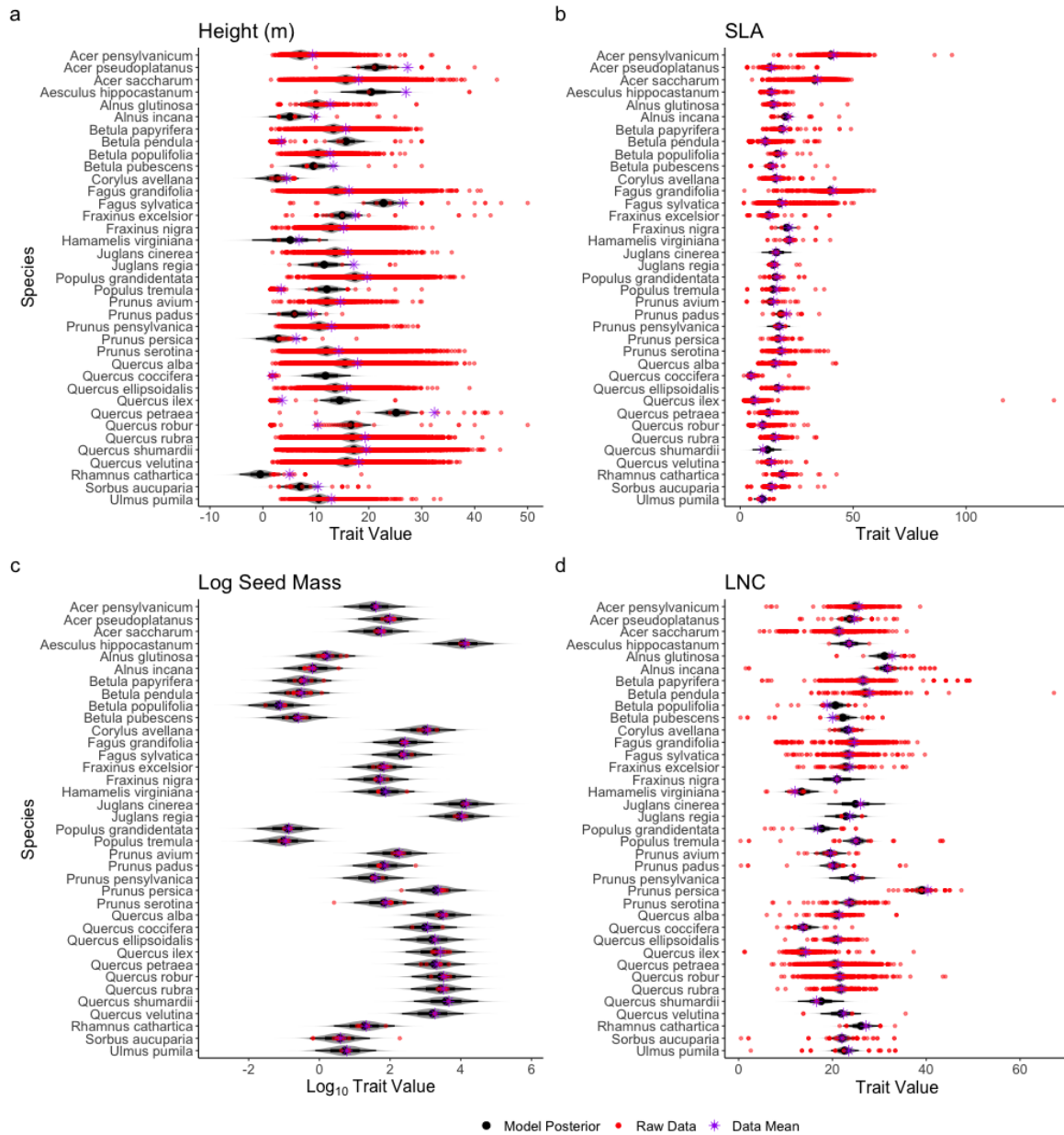


Figure 4: Comparisons of estimated model fits and raw data from joint models of trait effects on budburst phenological cues for 37 species of woody deciduous plants. Four functional traits – a. height, b. SLA, c. seed mass, and d. LNC – were modelled individually, with the calculated trait value being used to jointly model species responses to standardized chilling, forcing, and photoperiod cues. Model posteriors are shown in black, with the thicker line depicting the 66% interval and the thinner black line the 97% interval. Overall species level model posterior distributions were well aligned with the raw data, shown in red, and the species level means from the raw data, denoted as a purple star.