

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

3 Deirdre Loughnan¹, Faith A M Jones¹, Geoffrey Legault¹, Mira Garner²,
Darwin Sodhi³, Daniel Buonaiuto⁴, Catherine Chamberlain⁵, Ignacio Morales Castilla ⁶,
Ailene Ettinger⁷, and E M Wolkovich¹

4 November 18, 2022

5 ¹ Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, 2424
6 Main Mall Vancouver, BC Canada V6T 1Z4.

7
8 ² Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;
9

10
11 ³ Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts,
12 USA;

13
14 ⁴ XXXX

15
16 ⁵ XXXX

17
18 ⁶ Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

19
20 ⁷ XXXX

21
22 Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca
23

Summary

Key Words: Budburst phenology, functional traits, Trees, climate change

Introduction

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

(a) To predict species invasive potential, several studies have measured quantifiable functional traits and drawn links between traits, resource use, and growth strategies ().

(b) Traits that promote earlier growth in the spring can lead to priority effects, with the earlier growth of one species inferring greater resource availability and a competitive advantage on later developing species ().

(c) However, the same traits we associate with native plants' abilities to track changes in climate may also allow invasive species greater fitness and adaptive advantage to invasive species ().

(d) Understanding the links between species' traits, climate factors, and species' temporal niche will provide insight into likely responses of species fitness and community dynamics in response to climate change and plant invasions.

2. Through decades of work, generalizable trends between easy to measure plant traits and differences in growth and competitive strategies have been drawn for diverse and globally distributed species.

(a) This work has produced several schemes, included the leaf economic spectrum and wood economic spectrum, with well defined axes along which most species fall (??).

i. Acquisitive vs Conservative: One of the cornerstone axes of variation along which plant growth and strategies can be defined is from acquisitive to conservative growth.

ii. Species that are able to efficiently acquire resources, with relatively higher growth rate experience tradeoffs with higher growth potential coming at the cost of being less competitive. These traits can confer competitive advantages to invasive species for example.

iii. Species with slower growth are better able to withstand lower resource availability, but invest more in tissue longevity and their ability to withstand competitive landscapes.

(b) Previous work has focused, however, on traits associated with species abiotic and biotic niches, few studies have explored the relationship of species temporal niche within the broader functional trait framework ().

Some text for intro and methods...

A major goal of trait ecology has been to predict species-level characteristics by their traits alone. If successful, we would then 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.

1 Predictions

1. We predict that species that have traits associated with acquisitive growth, including shorter heights, high specific leaf area (SLA), high leaf nitrogen content per mass (LNC), and lower seed mass, will have smaller responses to chilling, photoperiod and forcing cues.
2. In contrast, species with conservative growth and higher competitive abilities, such as low SLA, low LNC, greater heights and heavier seeds, will be more responsive to all three cues.

2 Methods - pre-outline methods

Our analysis combine 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. We updated OSPREE since its initial publication, using the original search terms:

- (budburst OR leaf-out) AND (photoperiod OR daylength) AND temperature* (yielded additional 623 publications since previous OSPREE publication)
- (budburst OR leaf-out) AND dormant* (yielded additional 270 publications since previous OSPREE publication).

In updating the database, we added an additional 12 papers that met selection criteria for inclusion in OSPREE see Ettinger2020 for more details).

Trait data was obtained from TRY and BIEN - two large trait databases compiling plant trait data across many individuals, species, and studies that we obtained on XX date, and thus were last updated... XX

We began by searching for all available trait data for the 234 woody species with budburst data in the OSPREE database. The TRY database included 96 of these species for ten functional traits (Table S1 - table of requested traits for each database). Using the BIEN R package (Maitner2017), we downloaded trait data for 94 species for 13 traits. All trait data were requested or downloaded in December 2018. Only trait data from adult individuals with a minimum height of 1.42 m was included in our analyses and we removed all data from experiments or from plants growing in non-natural habitats. Traits were also grouped where appropriate, for example, with traits denoted as SLA, SLA with petioles, and SLA without petioles all categorized as simply SLA in our analysis (see Table S1). Duplicated data in both the TRY and BIEN datasets were also removed ($n = 434905$). Finally, we subsetted the data to include only species for which we had a complete dataset for each species and trait, which 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% of variation while the second explained 24.2% of the variation (Fig. ??). Due to strong association between specific leaf area (SLA) and leaf dry matter content (LDMC), and between stem specific density (SSD) and height, we 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 with at least one trait measurement per trait to 37 species with data from 24 studies (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. This was done to reduce the effect of trait values from these frequently measured species from overwhelming the partial pooling effect in our model. In addition we excluded the single seed mass observation from the HE Marx dataset from BIEN, as it was difficult to include include the study-level effect in our model.

Joint model of trait and phenology

To understand connections between phenology and other species traits, we built a joint model for each trait (height, SLA, LNC, and seed mass) with the major phenological cues (forcing, chilling, and photoperiod) to predict day of year of budburst. This approach allowed us to jointly estimate species trait effects and responses to phenological cues in one model, carrying through all uncertainty across varying datasets and approaches (e.g., TRY and BIEN observational databases of traits and the database of experiments in plant phenology, OSPREE). As phenological cues are the most proximate drivers of variation in budburst (cite Ettinger2020), and appear to represent different strategies along a continuum from acquisitive to conservative, our model allow traits to influence each cue separately (cite slopes (current Fig 3)).

The joint model includes a hierarchical linear model to partition variation in observed trait values ($y_{\text{trait}[i]}$) to the effects of species, study, and residual variation (σ_{trait} , sometimes called ‘measurement error’).

$$\begin{aligned}\mu_{\text{trait}} &= \alpha_{\text{grand trait}} + \alpha_{\text{sp}[\text{sp}]} + \alpha_{\text{study}[\text{study id}]} \\ \alpha_{\text{trait sp}[\text{sp}]} &\sim \text{normal}(0, \sigma_{\alpha_{\text{trait sp}}}) \\ \alpha_{\text{study}[\text{study id}]} &\sim \text{normal}(0, \sigma_{\alpha_{\text{study}}}) \\ y_{\text{trait}[i]} &\sim \text{normal}(\mu_{\text{trait}}, \sigma_{\text{trait}})\end{aligned}\tag{1}$$

It estimates a separate value for each species ($\alpha_{\text{sp}[\text{sp}]}$), and study ($\alpha_{\text{study}[\text{study id}]}$), while partially pooling across species and studies to yield overall estimates of variance across each ($\sigma_{\alpha_{\text{sp}}}$ and $\sigma_{\alpha_{\text{study}}}$, respectively). This partial pooling (often called ‘random effects’) controls for variation in sample size and variability to yield more accurate estimates for each species.

These species-level estimates of traits ($\alpha_{\text{trait sp}[\text{sp id}]}$) were then used a predictors of species-level estimates of each phenological cue ($\beta_{\text{force}[\text{sp}]}$, $\beta_{\text{chill}[\text{sp}]}$, $\beta_{\text{photo}[\text{sp}]}$)

$$\begin{aligned}\beta_{\text{chill}[\text{sp}]} &= \alpha_{\text{chill}[\text{sp}]} + \beta_{\text{trait.chill}} \times \alpha_{\text{trait sp}[\text{sp}]} \\ \beta_{\text{force}[\text{sp}]} &= \alpha_{\text{force}[\text{sp}]} + \beta_{\text{trait.force}} \times \alpha_{\text{trait sp}[\text{sp}]} \\ \beta_{\text{photo}[\text{sp}]} &= \alpha_{\text{photo}[\text{sp}]} + \beta_{\text{trait.photo}} \times \alpha_{\text{trait sp}[\text{sp}]} \end{aligned}\tag{2}$$

This model allows an overall effect of each trait—estimated across species—on each phenological cue ($\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$), while also allowing for species-level variation in cues that is not explained by traits ($\alpha_{\text{chill}[\text{sp}]}$, $\alpha_{\text{force}[\text{sp}]}$, $\alpha_{\text{photo}[\text{sp}]}$; this importantly means that variation across species is not forced onto the trait effect). Thus the model tests the power of traits to predict species-level differences.

Days to budburst ($y_{\text{pheno}[i]}$) is then predicted by the phenological cues and variation across experiments in chilling, forcing and photoperiod levels (C_i , F_i , P_i , respectively, which we z-scored to allow direct comparison of cues), with residual variation allowed across species ($\alpha_{\text{pheno}[\text{sp}]}$) and observations (σ_{pheno}):

$$\begin{aligned}\mu_{\text{pheno}} &= \alpha_{\text{pheno}[\text{sp}]} + \beta_{\text{chill}[\text{sp}]} \times C_i + \beta_{\text{force}[\text{sp}]} \times F_i + \beta_{\text{photo}[\text{sp}]} \times P_i \\ y_{\text{pheno}[i]} &\sim \text{normal}(\mu_{\text{pheno}}, \sigma_{\text{pheno}})\end{aligned}\tag{3}$$

The model includes partial pooling for residual variation in days to budburst across species and variation in each phenological cue not attributed to the trait:

$$\begin{aligned}\alpha_{\text{pheno}} &\sim \text{normal}(\mu_{\alpha_{\text{pheno}}}, \sigma_{\alpha_{\text{pheno}}}) \\ \alpha_{\text{force}} &\sim \text{normal}(\mu_{\alpha_{\text{force}}}, \sigma_{\alpha_{\text{force}}}) \\ \alpha_{\text{chill}} &\sim \text{normal}(\mu_{\alpha_{\text{chill}}}, \sigma_{\alpha_{\text{chill}}}) \\ \alpha_{\text{photo}} &\sim \text{normal}(\mu_{\alpha_{\text{photo}}}, \sigma_{\alpha_{\text{photo}}})\end{aligned}\tag{4}$$

We chose weakly informative priors, and validated them using a series of prior predictive checks. The model was coded in the Stan programming language (Stan citation), fit using the rstan package (version, citation) with 1,000 iterations per chain across 4 chain (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.

3 Results

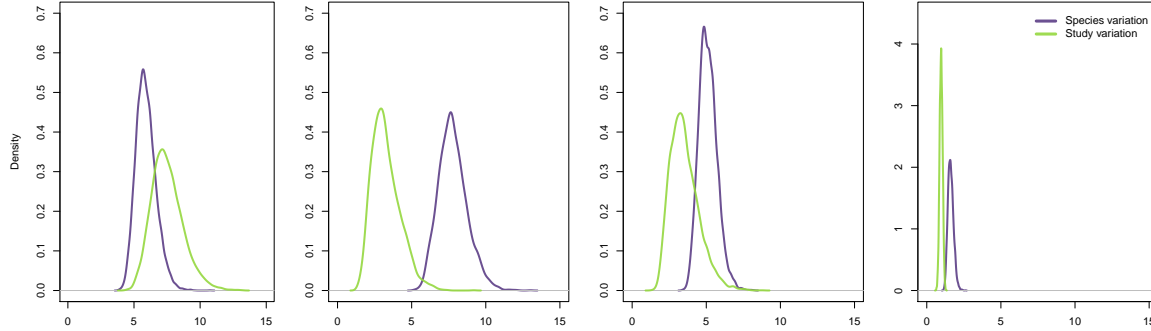


Figure 1: Comparison of the posterior densities for the species-level variation and study-level variation of a. height, b. SLA, c. LNC, and d. seed mass.

Our approach used models that jointly estimated species traits and phenological cues to understand the connections between phenology, with a focus on days to budburst, and other plant traits. Since our trait data was from large trait databases, which combine data across many studies, we analysis partitioned the trait variation due to species from the study-level effects. Then using the species-level estimates of traits (ie. species-level estimates with study removed), we examine how traits predicted phenological cues, which in turn predicted budburst, while allowing for residual variation in cues to be explained by a species effect.

Across our models, we found study-level variation across traits to be comparable with or greater than variation across species. Variation across studies was greatest for height (7.5 m compared to 5.9 m species-level variation, Fig. ??). For seed mass and LNC study-level variation was less than that of the species-level variation (seed mass study-level variation: 1 mg; versus species-level variation: 1.6 mg; LNC study-level variation 3.6 mg g⁻¹ versus species-level variation: 5.1 mg g⁻¹) (Fig. ??). At the lowest end, study-level variation in SLA was approximately half the value of the species-level variations (and 3.3 mm² mg⁻¹ versus 7.8 mm² mg⁻¹, respectively). The magnitude of study-level variation we observed suggests that models using large trait databases that fail to separate out study from species-level variation will misestimate species' traits.

We next combined the species-level trait estimates with data on forcing, chilling and photoperiod values from the OSPREE database of phenological experiments in order to test if traits (height, SLA, seed mass, LNC) related to phenological cues and species budburst dates (Fig. ??). 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 ??), while others traits were weak predictors (see g-i in Fig ??).

Across traits, height, SLA, and LNC strongly predicted responses to different cue-levels (forcing, chilling, photoperiod), with a consistent direction of responses across cues for only LNC and not height

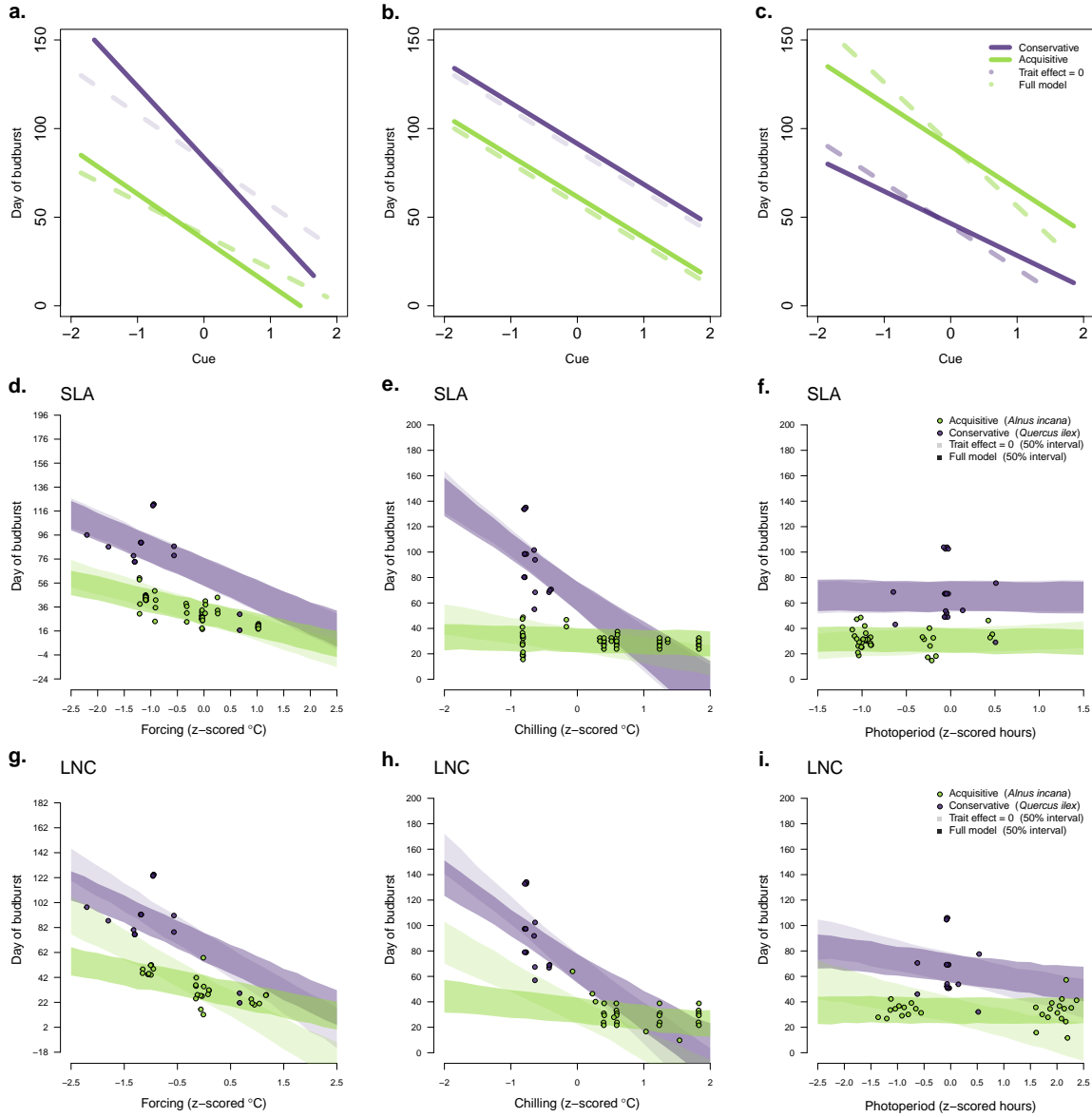


Figure 2: We predict a) some traits associated with conservative (e.g. high SLA and LNC) and acquisitive growth (small heights and large seeds) will lead to advances in day of budburst (earlier day of budburst) due to stronger responses to environmental cues (z-scored cue value), while b) other traits may have no relationship (as for the relationship between SLA and photoperiod in panel f) or c) traits may have the opposite relationship with growth strategies, with traits associated with conservative growth having earlier budburst than species with traits associated with acquisitive strategies, while they may also lead to delays in day of budburst (later day of budburst) caused by stronger responses to environmental cues (z-scored cue value). This delay in day of budburst due to trait effects was found for both SLA and LNC in response to forcing and chilling and the effect of LNC on species responses to photoperiod cues (panel d, e, g, h, and i). Species with conservative traits are shown in purple and species with acquisitive growth shown in green. Dark bands represent the 50% interval of the full model, while opaque bands represent the 50% interval of the model with out trait effects.

or SLA (Fig. ?? a-f and j-l). Taller species had small responses to forcing (0.2 m per standardized forcing; 90% uncertainty interval: -0.1, 0.5). But 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.

Species' SLA did not strongly predict responses to chilling ($\text{SexprslaBCSpMean mm}^2/\text{mg}$ per standardized chilling; 90% uncertainty interval: -0.1, 0.7, Fig. ?? b). However, SLA did relate strongly to photoperiod ($\text{SexprslaBPSpMean mm}^2/\text{mg}$ per standardized photoperiod; -0.4, 0). Thus, species with more acquisitive growth strategies (thin leaves and a lower investment in leaf mass that leads to high SLA values), had larger responses to photoperiod cues, contrary to our predictions. In line with our predictions, species with high SLA values (acquisitive strategy) had a smaller response to forcing cues (0.2 mm^2/mg per standardized forcing; 90% uncertainty interval: -0.1, 0.4), with low SLA species being more responsive to forcing (Fig. ?? d).

For LNC, we found that species that produce leaves with high nitrogen content, which relate to high photosynthetic rates and acquisitive growth, were less responsive to cues (Fig. ?? j-i)). 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% uncertainty interval: 0.2, 1.2), with similar responses to photoperiod (0.3 mg/g per standardized photoperiod; 90% uncertainty interval: 0, 0.7) and to forcing cues (0.5 mg/g per standardized forcing; 90% uncertainty interval: 0.1, 0.8).

Of our four traits, seed mass had the weakest responses across the three cues (Fig. ?? g-i). While the direction of the species responses were in line with our predictions, we did not find a considerable relationship between seed mass and cue responses for forcing (-0.3 mg per standardized forcing; -1.4, 0.8) or photoperiod or chilling (-1.1 mg per standardized chilling; -2.8, 0.7). -0.6 mg per standardized photoperiod; -1.6, 0.4).

4 Discussion

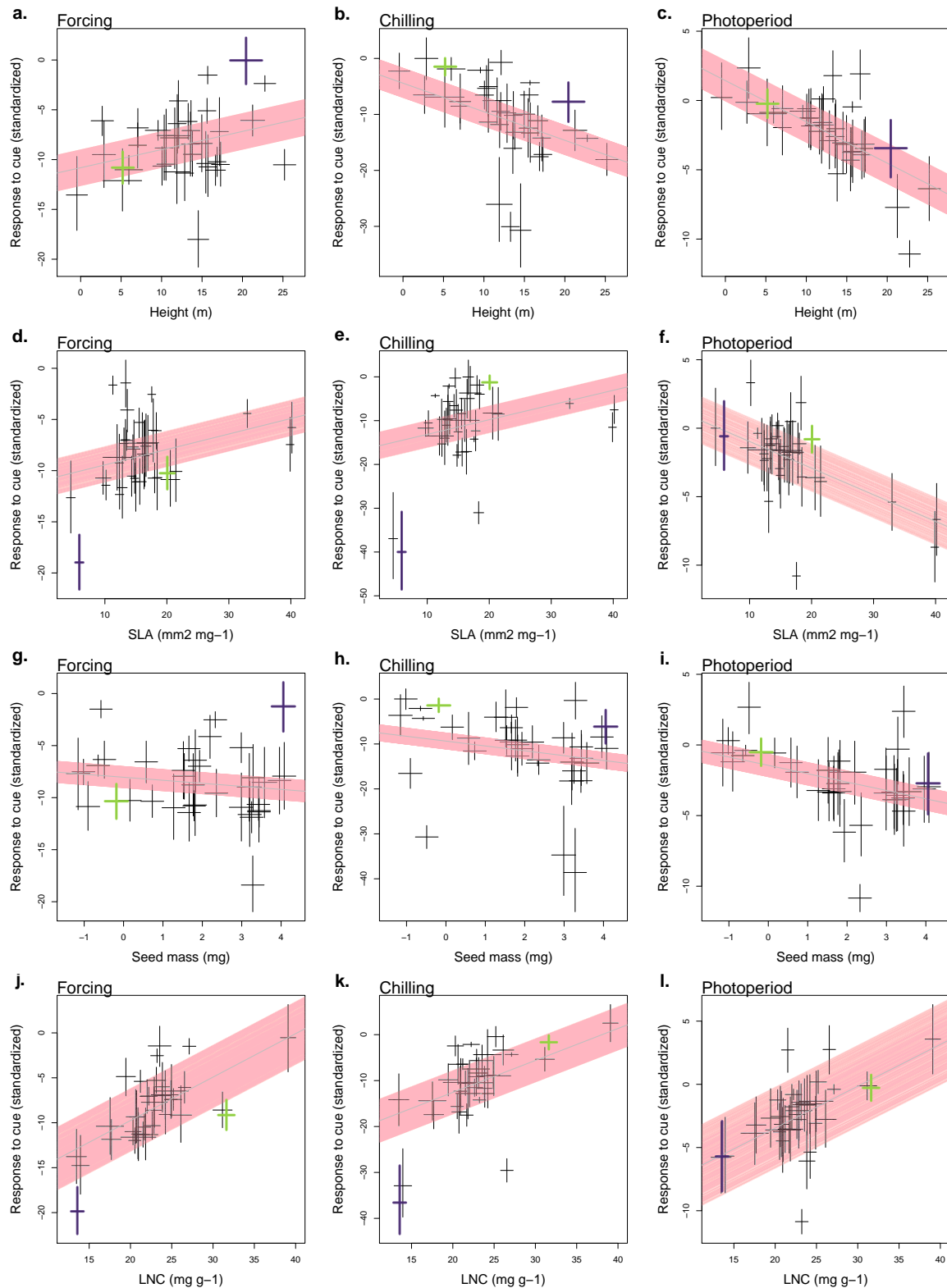


Figure 3: Estimated trait values for height (a-c), SLA (d-f), log10 Seed mass (g-i), and LNC (j-l), correlated against species-level cue responses to standardized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using our joint trait-phenology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