Woody plant phenological responses are strongly associated with key functional traits

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Summary

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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 they create.

    (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 growing species benefiting from more available light and soil nutrients ().

    (c) Many of the same traits that allow species to invade also allow native plants to track advances in spring temperatures and climate. ().

    (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, we have identified generalizable trends between easy to measure plant traits and differences in growth and competitive strategies that are applicable to 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 (Chave2009, Westoby2001).

        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 weaker competitors. These traits can incur competitive advantages to invasive species or species adapting to optimal growth conditions earlier in the year.

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

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

3. To integrate phenology into the broader trait framework we require a greater understanding of how the timing of phenological events is shaped by environmental conditions.

    (a) In woody plants there are 3 primary cues - chilling, forcing, photoperiod - that are the determinants of spring budburst.

    (b) The transition of buds from winter endodormancy to ectodormancy is governed by exposure to chilling temperatures for extended periods of time (Cook2012), while spring forcing temperatures are needed to initiate spring growth following this dormancy release. The effects of warming winter and spring temperatures, while they can lead to earlier dormancy breaking and spring growth, may be tempered by species photoperiod requirements, as daylengths remain constants.

(c) Field observations of phenology are highly variable, but under controlled cue exposure, phenological events such as budburst are highly predictable.

(d) Decades of experimental work have shown increases in all three of these cues lead to the advance of spring budburst, but responses are highly species specific, with interactions between cues having compensatory effects (Harrington2015, Flynn2018, Caffarra2011, Zohner2016).

(e) Given the importance of these cues in determining the timing of growth, other traits related to species fitness under variable resource availabilities and and competitive landscapes may also influence cue responses and the timing of phenological events.

4. A primary goal of trait ecology is to predict species-level characteristics by traits alone, but how well this can be applied to a highly variable and species specific trait such as phenology is unclear.

(a) If successful, this approach allows us to replace species distinctions in models with species' trait values. 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 growth strategies and phenological responses for which we only have trait values.

(b) Drawing on previous studies, we would expect species with high chilling requirements will budburst later in the spring and possess traits favourable under competitive conditions associated with conservative growth strategies.

(c) Conversely, species with low forcing, chilling, and photoperiod requirements that budburst earlier in the spring benefit from having traits favourable under high light conditions prior to canopy closure and faster therefore possess a trait syndrome associated with acquisitive growth strategies.

5. In this study, we test for associations between plant phenological responses to environmental cues and common functional traits.

(a) Using available trait data from trait databases and budburst data for tree species in controlled environmental studies from the Observed Spring Phenology Response in Experimental Environments (OSPREE), we explicitly test for the relative differences in functional traits and the timing of bud-burst in response to experimental forcing, chilling, and photoperiod cues.

(b) We predict that species with trait values associated with acquisitive growth, including shorter heights, high specific leaf area (SLA), high leaf nitrogen content per mass (LNC), and lower seed mass, strategies will budburst earlier than species with conservative traits, such as low SLA, low LNC, greater heights and heavier seeds (Fig. 2 a-c).

(c) We predict that species with high leaf traits such as SLA and LNC will be less responsive to forcing cues, with low chilling and photoperiod requirements (Fig. 2 d-i).

(d) Traits syndromes most associated with competitive abilities, including taller trees and larger seem masses, conversely, we predict to have stronger chilling and photoperiod cue responses (Fig. ?? a-c).

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.

1   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 dorman* (yielded additional 270 publications since previous OS-PREE 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 theses 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

159 drivers of variation in budburst (cite Ettinger2020), and appear to represent different strategies along
160 a continuum from acquisitive to conservative, our model allow traits to influence each cue separately
161 (cite slopes (current Fig 3)).
162

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').

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

163 It estimates a separate value for each species ($\alpha_{\text{sp[sp]}}$), and study ($\alpha_{\text{study[study id]}}$), while partially pool-
164 ing across species and studies to yield overall estimates of variance across each ($\sigma_{\alpha_{\text{sp}}}$ and $\sigma_{\alpha_{\text{study}}}$,
165 respectively). This partial pooling (often called 'random effects') controls for variation in sample size
166 and variability to yield more accurate estimates for each species.
167

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

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

168 This model allows an overall effect of each trait—estimated across species—on each phenological cue
169 ($\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$), while also allowing for species-level variation in cues that is not
170 explained by traits ($\alpha_{\text{chill}[sp]}$, $\alpha_{\text{force}[sp]}$, $\alpha_{\text{photo}[sp]}$; this importantly means that variation across species
171 is not forced onto the trait effect). Thus the model tests the power of traits to predict species-level
172 differences.
173

Days to budburst ($y_{\text{pheno}[i]}$) is then predicted by the phenological cues and variation across experi-
ments 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 ($\alpha_{\text{pheno[sp]}}$) and observations
(σ_{pheno}):

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

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

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

174 We chose weakly informative priors, and validated them using a series of prior predictive checks.
175 The model was coded in the Stan programming language (Stan citation), fit using the rstan package
176 (version, citation) with 1,000 iterations per chain across 4 chain (4,000 total sampling iterations), and
177 all models met basic diagnostic checks, including no divergences, high effective sample size (n_eff),
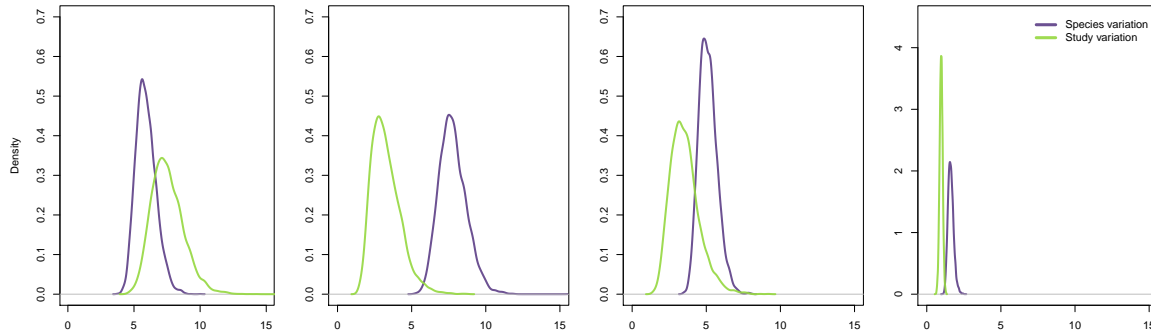178 and $\hat{R}$ close to 1.

2   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. 1). 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. 1). At the lowest end, study-level variation in SLA was approximately half the value of the species-level variations (and 3.3 mm^2 mg^{-1} versus 7.8 mm^2 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. 2). 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 3), while others traits were weak predictors (see g-i in Fig 3).

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 or SLA (Fig. 3 a-f and j-l). Taller species had small responses to forcing (0.2 m per standardized forcing; 90% uncertainty interval: -0.2, 0.5). But as we predicted, taller species had larger responses to chilling (-0.5 m per standardized chilling; 90% uncertainty interval interval: -1, -0.1)) and photoperiod (-0.2 m per standardized photoperiod; 90% uncertainty interval: -0.5, 0), both of which are cues that would generally lead to later budburst and fit within an overall conservative growth strategy.

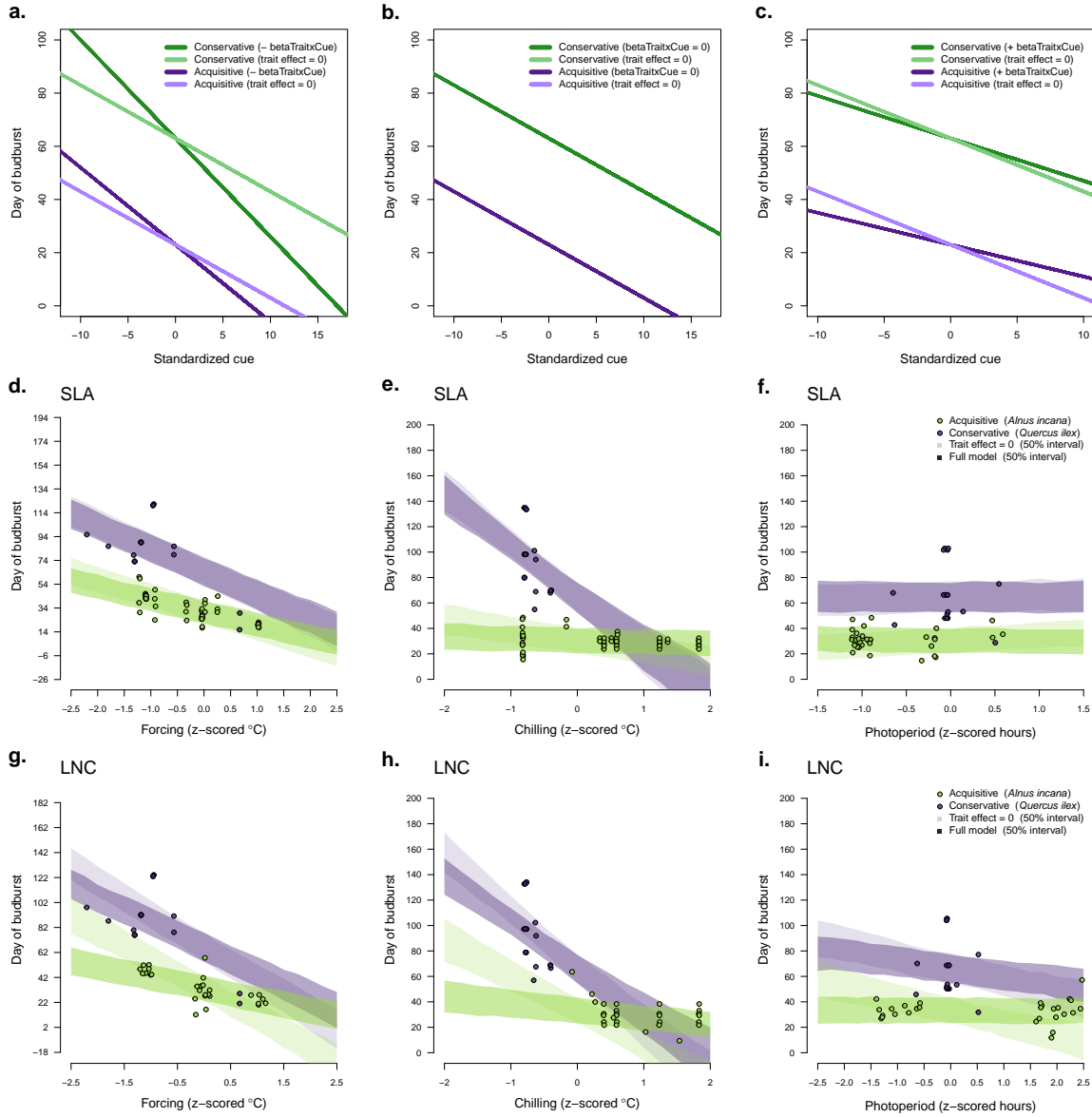Species' SLA did not strongly predict responses to chilling (0.3 mm^2/mg per standardized chilling;

Figure 2: Functional traits may contribute to the species responses to chilling, forcing, or photoperiod cues in several way. a) If traits are contribute negatively to the timing of phenological events, we expect the phenological response to be stronger and budburst earlier with increasing cue values. b) But if traits have no effects on the timing of budburst then cue responses will be zero and equivalent to the cue only trends. c) Lastly, traits that have a positive contribution to the timing of phenological events produce weaker responses with later budburst dates. A 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. Uncertainty intervals represent the 50% interval of the model estimates.

90% uncertainty interval: -0.1, 0.7, Fig. 2 b). However, SLA did relate strongly to photoperiod (-0.2 mm^2/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. 3 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. 3 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: 0.3, 1.2), with similar responses to photoperiod (0.3 mg/g per standardized photoperiod; 90% uncertainty interval: 0, 0.6) and to forcing cues (0.5 mg/g per standardized forcing; 90% uncertainty interval: 0.1, 0.9).

Of our four traits, seed mass had the weakest responses across the three cues (Fig. 3 g-i). While the direction of the species responses were in line with out predictions, we did not find a considerable relationship between seed mass and cue responses for forcing ((-0.3 mg per standardized forcing; -1.4, 0.9)) or photoperiod or chilling (-1.1 mg per standardized chilling; -2.8, 0.7). -0.6 mg per standardized photoperiod; -1.6, 0.3).
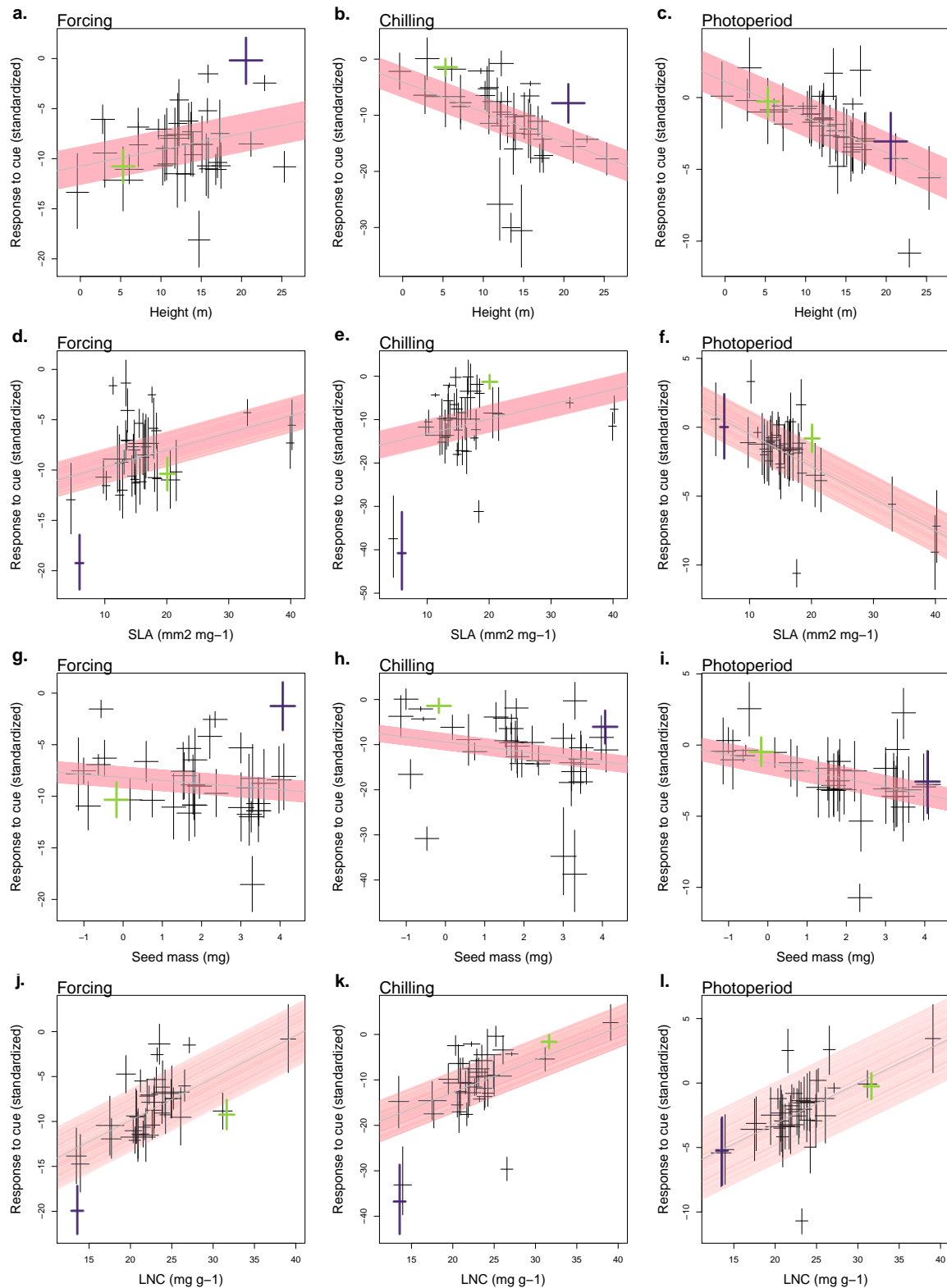
3   Discussion

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 2 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.