Woody plant phenological responses are strongly associated with key functional traits

Deirdre Loughnan[1], Faith A M Jones[1], Geoffrey Legault[1], Mira Garner[2],
Darwin Sodhi[3], Daniel Buonaiuto[4], Catherine Chamberlain[5], Ignacio Morales Castilla [6],
Ailene Ettinger[7], and E M Wolkovich[1]

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

[2] Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

[3] Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts,
USA;

[4] XXXX

[5] XXXX

[6] Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

[7] XXXX

Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca

1

1 Summary

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

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 bread 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. 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.

3   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.

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 added an additional 12 papers that met our selection criteria. For
additional information on the construction of the OSPREE database and methods of cue estimates,
see (Ettinger2020). 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 received from the TRY databases for 96 of our species (Table
S1 - table of requested traits for each database). Additional trait Data was obtained from the BIEN
database using the BIEN R package (Maitner2017). All trait data were requested or downloaded in
December 2018. We only included trait data from adult individuals with a minimum height of 1.42 m
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 simply 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, whichr 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 the SLA and LDMC leaf traits, 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 we could include in our analysis as we had had at least one trait measurement for 37 species

104 (height n = 47781, seed mass n = 281, LNC n = 3853, SLA n = 7656). Given the abundance of height
105 data and overrepresentation of height measurements for six of our focal species, we randomly sampled
106 3000 height measurements for each of these species to include in our analysis (n = 27318). This was
107 done to reduce the effect of trait values from these frequently measured species from overwhelming
108 the partial pooling effect in our model. In addition we excluded the single seed mass observation from
109 the HE Marx dataset from BIEN, as it was difficult to include include the study-level effect in our model.
110

Joint model of trait and phenology

112 Our models jointly estimated species traits and the phenological cues to understand connections be-
113 tween phenology (specifically days to budburst) and other plant traits.... Because we drew on large
114 trait databases for our analyses we partitioned trait variation due to species versus study-level effects.
115 We then used the species-level estimates of traits (ie., estimates of species with study removed) to
116 examine how traits predicted phenological cues, which in turn predict budburst, while allowing for
117 residual variation in cues to be explained by a species effect)
118 This model is a departure from current efforts in several ways: first, while these steps would normally
119 be done separately, our models allow use to jointly estimate species trait effects and responses to
120 phenological cues. This allows separating out the trait versus residual species effect; second, we focus
121 on phenological cues as predictors for day of budburst and thus allow traits to influence each cue (cite
122 slopes (current Fig 3)).

123 1. To study the direct link between traits and cue responses, we developed a joint hierarchical
124   Bayesian model that consists of both a trait model and a phenology model.

125 2. Each trait was modeled indiviudally because of differences in study number and the number of
126   individual trait measurements.

127 3. The first part of the joint model is a hierarchical intercept only model where $Y_{i,j}$ is the observed
128   trait value of species i from study j.

129 4. The observed trait value is composed of $\alpha_{\text{trait},i}$, the "grand" species trait value across all in-
130   dividuals of a species independent of environment, and the study-level variation, $\alpha_{\text{study},j}$ that
131   represents study-level differences in environment or observation methods, and random error.

132 This results in the following sub-model for each trait:

$$Y_{i,j} \sim normal(\mu_{i,j}, \sigma_{\text{trait}}) \tag{1}$$

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

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

with:

$$\boldsymbol{\alpha}_{\text{trait}} = \{\alpha_{\text{trait},1}, \ldots, \alpha_{\text{trait},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{trait}} \sim normal(\mu_{\alpha_{\text{trait}}}, \sigma_{\alpha_{\text{trait}}}) \tag{3}$$
$$\boldsymbol{\alpha}_{\text{study}} = \{\alpha_{\text{study},1}, \ldots, \alpha_{\text{study},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim normal(0, \sigma_{\alpha_{\text{study}}})$$

134 Parameters $\mu_{\alpha_{\text{trait}}}$ and $\sigma_{\alpha_{\text{trait}}}$ represent the mean trait value across all species and the standard devi-
135 ation in trait values between species, respectively.
136

137 1. The "grand" trait values of species that are independent of study, $\alpha_{\text{trait},i}$, links the trait model
138   to the phenology part of the joint model.

139   2. The strucutre of the phenology model is similar to that of (Ettinger2020), except species' re-
140   sponses to forcing ($\beta_{\text{force},i}$), chilling ($\beta_{\text{chill},i}$), and photoperiod ($\beta_{\text{photo},i}$) are the species-specific
141   response independent of a species trait value (e.g., $\alpha_{\text{force},i}$) combined with the effect of its trait
142   value (e.g., $\beta_{\text{trait.force}}$) multiplied by $\alpha_{\text{trait},i}$.

143   3. Here $Z_{i,k}$ is the day of budburst for species i experiencing forcing (F_k), chilling (C_k), and pho-
144   toperiod (P_k).

145   4. Each cue was z-scored to account for differences in the scale of predictors across studies (Gel-
146   man2006), as well as differences in the natural units for the cues

147   The phenology part of the joint model can thus be written as:

$$Z_{i,k} \sim normal(\mu_{i,k}, \sigma_{\text{pheno}}) \tag{4}$$

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

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

with:

$$\beta_{\text{force},i} = \alpha_{\text{force},i} + \beta_{\text{trait.force}} \times \alpha_{\text{trait},i} \tag{6}$$
$$\beta_{\text{chill},i} = \alpha_{\text{chill},i} + \beta_{\text{trait.chill}} \times \alpha_{\text{trait},i}$$
$$\beta_{\text{photo},i} = \alpha_{\text{photo},i} + \beta_{\text{trait.photo}} \times \alpha_{\text{trait},i}$$

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

$$\boldsymbol{\alpha}_{\text{pheno}} = \{\alpha_{\text{pheno},1}, \ldots, \alpha_{\text{pheno},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim normal(\mu_{\alpha_{\text{pheno}}}, \sigma_{\alpha_{\text{pheno}}}) \tag{7}$$
$$\boldsymbol{\alpha}_{\text{force}} = \{\alpha_{\text{force},1}, \ldots, \alpha_{\text{force},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{force}} \sim normal(\mu_{\alpha_{\text{force}}}, \sigma_{\alpha_{\text{force}}})$$
$$\boldsymbol{\alpha}_{\text{chill}} = \{\alpha_{\text{chill},1}, \ldots, \alpha_{\text{chill},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chill}} \sim normal(\mu_{\alpha_{\text{chill}}}, \sigma_{\alpha_{\text{chill}}})$$
$$\boldsymbol{\alpha}_{\text{photo}} = \{\alpha_{\text{photo},1}, \ldots, \alpha_{\text{photo},n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photo}} \sim normal(\mu_{\alpha_{\text{photo}}}, \sigma_{\alpha_{\text{photo}}})$$

149   Parameters had weakly informative prior distributions (generally normal or half-normal distributions)
150   that we obtained using our prior knowledge of functional trait diversity in deciduous species and cue
151   responses. Priors were also validated using a series of prior predictive checks. The joint model was
152   coded in the Stan programming language (Stan citation) and fit to the trait and phenology data (see
153   above) using the rstan package (version, citation). Model fits were deemed valid based on *Stan's*
154   diagnostic metrics, including no divergences across 1000 iterations, high effective sample size (n_eff),
155   and scale reduction factor $\hat{R}$ close to 1 across 4 chains.
156   Finally, we used a phylogenetic generalized least-squares regression model (PGLS) to test the rela-
157   tionship between day of budburst and each trait. This analysis allowed us to test for phylogenetic
158   non-independence in the phenology-trait relationship (Freckleton2002). We obtained a rooted phylo-
159   genetic tree by pruning the tree developed by (Smith2018a) and performed the PGLS analysis using
160   the mean trait values and mean posterior estimates of the cue responses from our joint model. The
161   PGLS was run using the "Caper" package in R (Orme2013).
162

5   Results

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

165   (a) Our models jointly estimated species traits and the phenological cues to understand con-
166   nections between phenology—specifically days to budburst—and other plant traits.

167   (b) Because we drew on large trait databases, which combine data across many studies, for our
168   analyses we partitioned trait variation due to species versus study-level effects. We then
169   used the species-level estimates of traits (ie., estimates of species with study removed) to
170   examine how traits predicted phenological cues, which in turn predicted budburst, while
171   allowing for residual variation in cues to be explained by a species effect.

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

173   (a) Across our models, we found study-level variation across traits that was often comparable
174   with or greater than variation across species.

175   (b) Variation across studies was greatest for height (7.5 m compared to 5.9 m species-level
176   variation, Fig. 1).

177   (c) For seed mass and LNC study-level variation was less than that of the species-level variation
178   (seed mass study-level variation: 1 mg; versus species-level variation: 1.6 mg; LNC study-
179   level variation 3.6 mg g^{-1} versus species-level variation: 5.1 mg g^{-1}) (Fig. 1).

180   (d) At the lowest end, study-level variation in SLA was approximately half the value of the
181   species-level variations (and 3.3 mm^2 mg^{-1} versus 7.8 mm^2 mg^{-1}, respectively).

182   (e) The magnitude of study-level variation here suggests models using large trait databases that
183   fail to separate out study from species-level variation will misestimate species' traits.

184 3. Very short paragraph reminding audience of the model and connecting figure on cue-trait rela-
185   tionships.

186   (a) We next combined these species-level trait estimates with data on forcing, chilling and
187   photoperiod values from a large meta-analysis of experiments to test if traits (height, SLA,
188   seed mass, LNC) related to phenological cues and species budburst dates (Fig. 2).

189   (b) For some traits we found much of the variation in phenological cues across species could be
190   explained by trait variation (see panel a-f and j-l in Fig 3), while for others traits were weak
191   predictors (see g-i in Fig 3).

192 4. Discuss how height, SLA, and LNC were partially in line with predictions

193   (a) Across traits, height, SLA, and LNC strongly predicted responses to different cue-levels
194   (forcing, chilling, photoperiod), with the direction of responses were consistent across cues
195   for LNC and not height or SLA (Fig. 3 a-f and j-l).

196   (b) Taller species had small responses to forcing (0.2 m per standardized forcing; 90% uncer-
197   tainty interval: -0.1, 0.5).

198   (c) However, as we predicted, taller species had larger responses to chilling (-0.5 m per stan-
199   dardized chilling; 90% uncertainty interval interval: -1, -0.1)) and photoperiod (-0.3 m per
200   standardized photoperiod; 90% uncertainty interval: -0.6, 0), both of which are cues that
201   would generally lead to later budburst and fit within an overall conservative growth strategy.

202   (d) Species' SLA did not strongly predict responses to chilling (SexprslaBCSpMean mm^2/mg
203   per standardized chilling; 90% uncertainty interval: -0.1, 0.7, Fig. 2 b).

204   (e) However, SLA did relate strongly to photoperiod ((SexprslaBPSpMean mm^2/mg per stan-
205   dardized photoperiod; -0.4, 0). Thus, species with more acquisitive growth strategies (thin
206   leaves and a lower investment in leaf mass that leads to high SLA values), had larger re-
207   sponses to photoperiod cues, contrary to our predictions.

208   (f) As we predicted, species with high SLA values (acquisitive strategy) had a smaller response
209   to forcing cues ((0.2 mm^2/mg per standardized forcing; 90% uncertainty interval: -0.1, 0.4),
210   with low SLA species being more responsive to forcing (Fig. 3 d).

(g) 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: 0.2, 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).

5. ...But Seed mass

(a) Of our four traits, seed mass had the weakest responses across the three cues (Fig. 3 g-i).

(b) 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, 0.8)) or photoperiod or chilling (-1.1 mg per standardized chilling; -2.8, 0.7). -0.6 mg per standardized photoperiod; -1.6, 0.4).
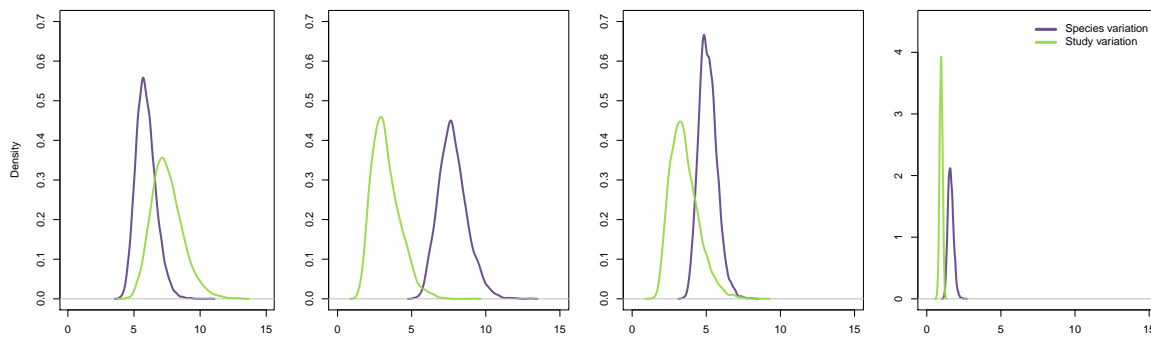

Figure 1: Comparison of the posterior densities for the species-level variation and study-level variation of a. height, b. SLA, c. LNC, and d. seed mass.
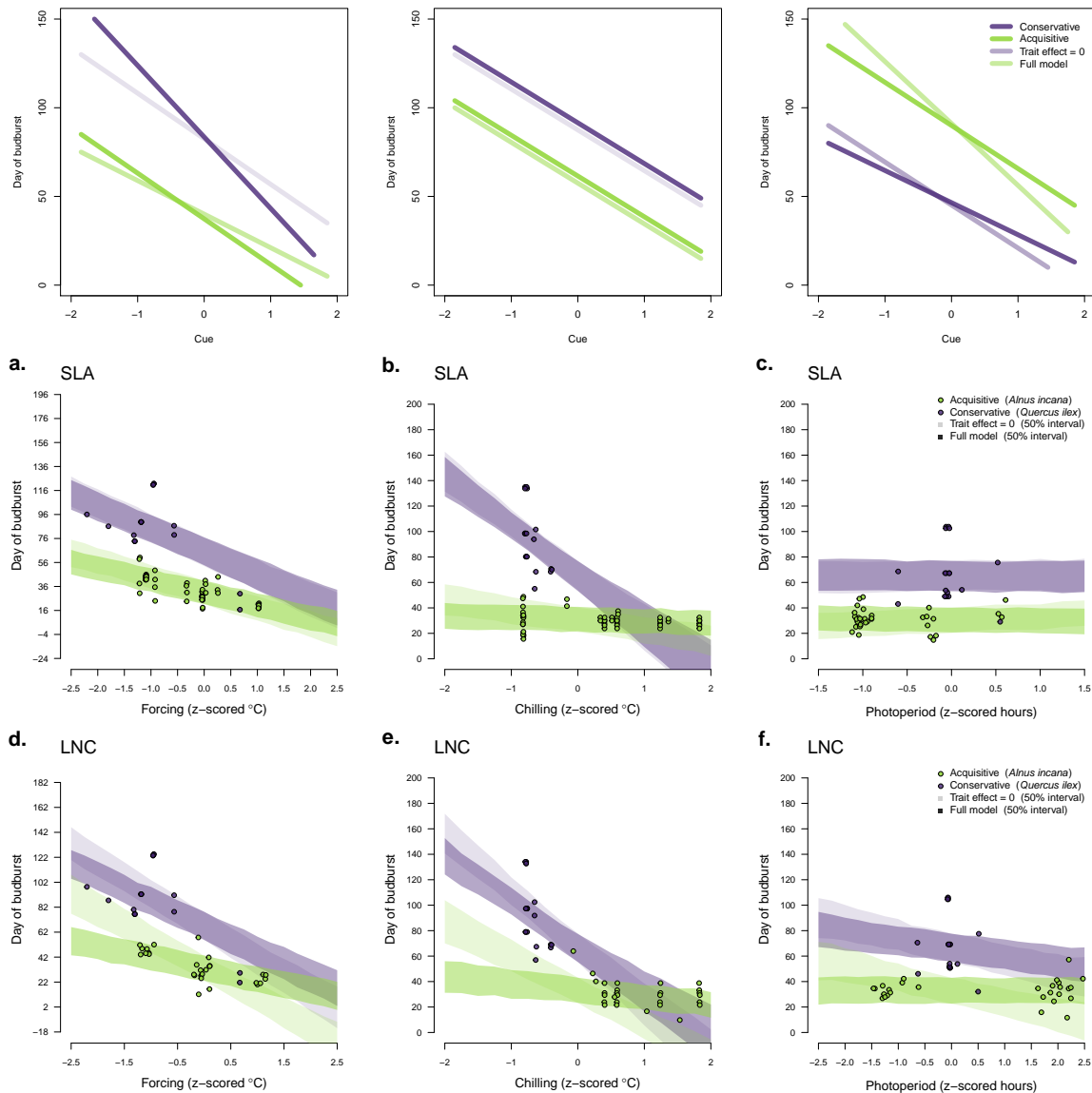
6   Discussion

Figure 2: 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 trati 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 epresent the 50% uncertainty interval for the posterior cue estimates for the full model) versus without (lighter bands represent the 50% uncertainty interval 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.
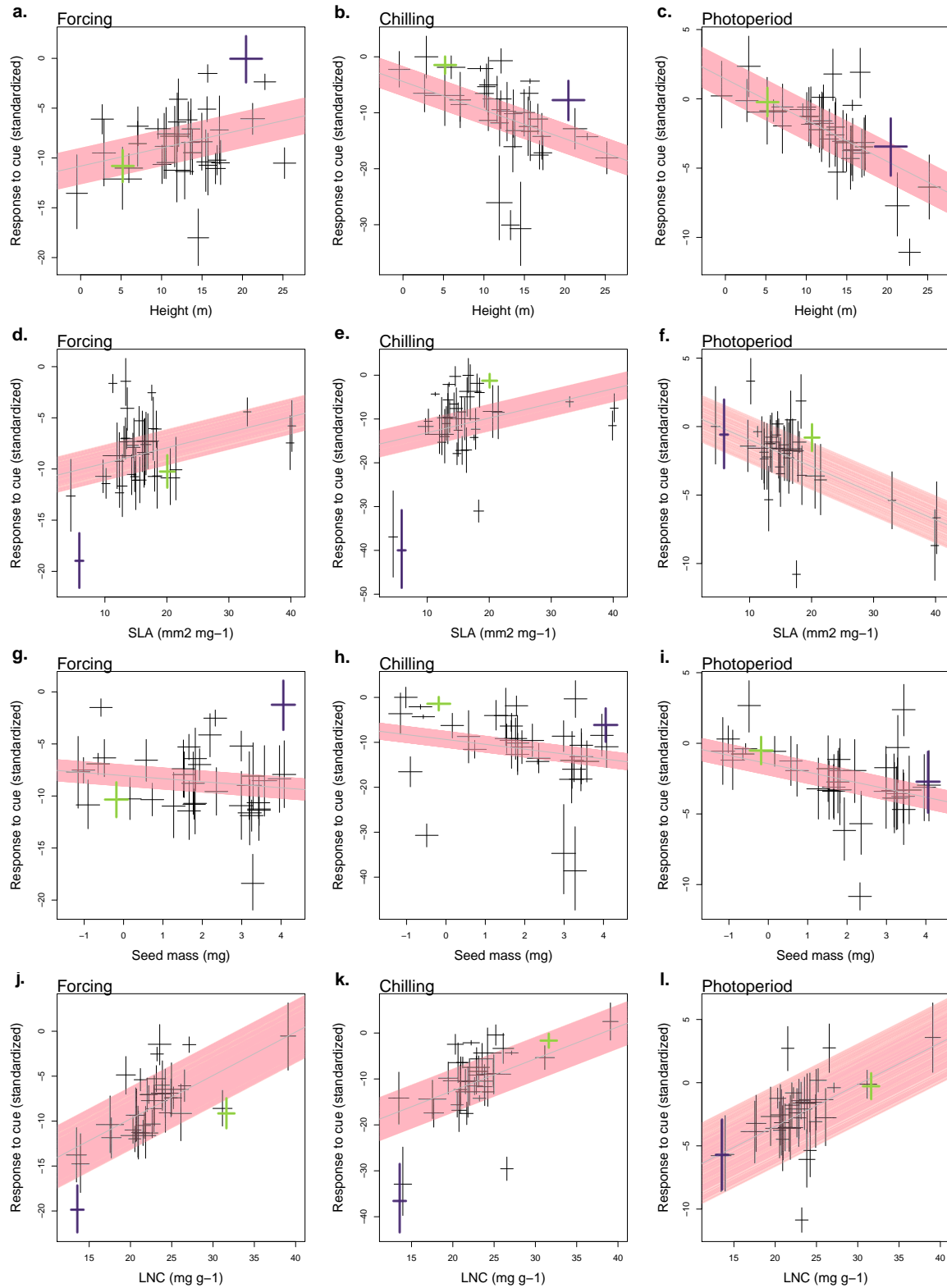
Figure 3: Estimated trait values for height (a-c), SLA (d-f), log10 Seed mass (g-i), and LNC (j-l), correlated against species-level cue responses to standarsized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using our joint trait-phenology 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.