Woody plant phenological responses are strongly associated with key functional traits

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Summary

Species phenologies—the timing of recurring life history events—can vary substantially with environmental variation. While climate change has triggered shifts in phenology and changed proximate drivers like temperature, the ultimate drivers of species-level variation are still poorly understood. In temperate forests, phenological variation across species may be driven by trade-offs between early season conditions, when the risk of tissue loss is high but resources abundant, and the more benign late season conditions, when competition is greater. This idea fits within fundamental theories of plant growth strategies and infers suites of traits that may co-vary with phenologies. But testing the role of phenology within a functional trait framework is challenging given its variability across environments. Here, we use a meta-analysis of controlled environment experiments to overcome this challenge and pair it with plant trait data from major databases. We found height, specific leaf area (SLA), and leaf nitrogen content (LNC) to have strong relationships with cue responses and budburst, but not always in the direction predicted. The conservative phenotype of tall trees with low LNC both showed the strongest responses to chilling and photoperiod and impacts on phenology. Cues, however, varied in their relationship to SLA, with low SLA species responding to forcing as predicted, but not photoperiod. Our findings demonstrate important relationships between phenological cues and broader trait phenotypes, showing that leafout phenology generally fits within a functional trait framework of acquisitive to conservative growth strategies. By better understanding these broader trait relationships, we can predict the ultimate drivers shaping species phenotypes and their influence on community dynamics.

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

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 (Cleland et al., 2007; Beard et al., 2019; Gu et al., 2022). As climate change has caused spring growth to advance in many systems (Menzel et al., 2006; Vitasse et al., 2021), there is growing concern over how these changes may impact communities and ecosystems.

Predicting these changes requires understanding the drivers of phenology both at a proximate scale—the environmental triggers of phenology, such as temperature and daylength—and at a more ultimate scale, of how timing may assemble species within a community (Ovaskainen et al., 2013; Wolkovich and Donahue, 2021). At the proximate level, changing environmental conditions across the winter and spring cause species to start growth at different times. This has been especially well documented for the start of growth in woody plants each year (Laube et al., 2014; Flynn and Wolkovich, 2018), with similar trends observed for spring phenological events across taxa, including in the timing of egg laying in birds (Crick et al., 1997; D'Alba et al., 2010) and the advance of spawning in amphibians (Tryjanowski et al., 2003; Kusano and Inoue, 2008). But this work has provided limited insights into the drivers of species differences (Laube et al., 2014; Chuine et al., 2016; Flynn and Wolkovich, 2018).

At the ultimate level, our predictions for why phenologies vary generally stem from our understanding of how selective pressures change as the early season progresses. Species that start growth early often risk high tissue loss—due to frost damage (Sakai and Larcher, 1987; Augspurger, 2009) or high herbivore apparency (Wainwright et al., 2012)—but benefit from higher resource availability (Rathcke and Lacey, 1985; Hufkens et al., 2012). In contrast, later species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008; Wolkovich and Ettinger, 2014).

Differences in the timing of selective pressures within the growing season could shape a number of species attributes. Species with earlier growth may produce cheaper tissues that can be more easily replaced if damaged (Reich et al., 1999). But later species would benefit from investing in tissues that infer greater resource acquisition and retention (Gorné et al., 2020). These 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 (Wolkovich and Ettinger, 2014).

In plants, several well studied traits have been identified as species-level proxies for varying growth strategies and responses to biotic interactions (McGill et al., 2006). These leaf and wood traits follow gradients in their trait values, having associations that range from acquisitive (fast) growth strategies to more conservative (slow) growth strategies (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Díaz et al., 2016). Collectively, these trait relationships led to the development of the leaf economic spectrum and the wood economic spectrum (Wright et al., 2004; Chave et al., 2009).

These functional trait spectra—or frameworks—have been built into decades of research linking functional traits with how species respond to abiotic and biotic factors and community assembly (Kraft and Ackerly, 2010; Paine et al., 2011; Hille Ris Lambers et al., 2012; Luo et al., 2019), but have limitations. These frameworks often fail to predict how variable traits are (Violle et al., 2012), a reason sometimes given for why phenology is excluded from studies of functional traits. However, we argue that including phenology—and its high variability—alongside other functional traits could advance the functional trait framework and help explain why species phenologies differ.

Spring phenology in temperate forests may provide the best opportunity to integrate phenology into functional trait research, especially considering the strong gradients in selective environments that occur early versus later in the spring. As in other systems, early season species trade-off high access to resources (greater soil resources and light availability) with risks of tissue loss and damage, while late season species experience a highly competitive but less risky environment. Based on these trade-offs, we predict that shrub and woody understory species, many of which budburst before canopy closure (Donnelly and Yu, 2019), would have traits associated with acquisitive growth; they thus would 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)). Canopy species that budburst later—when competition for soil resources is greatest—would have traits associated with conservative growth; being taller with denser wood (Laughlin et al., 2010), with leaf traits suited for more variable light (low SLA and LNC). Seed size may similarly be predicted from this acquisitive to conservative continuum, as acquisitive species produce smaller seeds that germinate quickly and conservative species produce larger, better provisioned, seeds.

Testing these predictions requires a reliable way to define early to late phenology, as phenology varies strongly across sites and years. The underlying cues that predict gradients in phenology, however, do not vary strongly across space and time (Chuine and Cour, 1999; Harrington and Gould, 2015; Flynn and Wolkovich, 2018). Early species generally have weak (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 stronger (larger) responses to chilling and/or photoperiod, and likely higher forcing as well (Laube et al., 2014; Flynn and Wolkovich, 2018).

To test these predictions of associations between budburst responses to environmental cues and common functional traits, we merged available data from trait databases (BIEN and TRY) with budburst data from the OSPREE database of controlled environment studies. We focus on woody species, initially considering six traits—SLA, leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC. We further removed SSD and LMDC from our focal traits, as they correlated strongly with height and SLA respectively (see supplementary material).

To better understand the relationships between phenology and other traits, we combined this novel and encompassing trait-phenology dataset with a hierarchical Bayesian joint model. This analytical approach allows us to predict phenological responses to cues based on species-level trait values, while allowing additional variation due to species. This approach thus takes a step towards predicting variation via species traits instead of species identity. When traits explain a significant portion of the variation, species will explain only a small amount, which would allow us to use trait values to predict species growth strategies and phenological responses, while providing new insights into the effects of traits on phenological cue.

Methods

For our analysis we used phenological data from the OSPREE database (Ettinger et al., 2020). The OSPREE database contains phenological data for woody, deciduous species from experiments of phenological cues. We updated the database since its initial publication, for details on the methods used see Morales-Castilla et al. (in prep).

Trait data was obtained from TRY and BIEN—two large trait databases compiling plant trait data across many individuals, species, and studies. 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. (in prep), which represents well studied species with good phenology and phylogenetic data. Using the BIEN R package (Maitner et al., 2018), we downloaded trait data for the 94 available species for 13 traits. The TRY database included 96 of our focal species with ten functional traits (Kattge et al., 2020). 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. 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 (Table S1). Duplicated data in both the TRY and BIEN datasets were also removed ($n = 434905$).

For our analysis, we aimed to only include species for which we had a complete trait profile, subsetting the phenology and trait data to include only species for which we had at least one measurement for each trait. We used a PCA to understand trait correlations and adjusted which traits we included. A PCA of our six initial traits identified high correlations between SLA and leaf dry matter content (LDMC), and between height and stem specific density (SSD) (see Supplementary material). In this analysis, the 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 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 was 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 (discussed below). These species were measured on average 19 times more frequently than other species in our dataset and therefore we randomly sampled 3000 height measurements for each of these species.

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 allowed us to jointly estimate species trait ef-

fects and responses to phenological cues in one model, carrying through all uncertainty across varying datasets and approaches (e.g. comparing across the *in situ* observational trait data in the TRY and BIEN databases and the experimental plant phenology data of the OSPREE database). As phenological cues are the most proximate drivers of variation in budburst, and appear to represent different strategies along a continuum from acquisitive to conservative, our model allows traits to influence each cue separately (Fig. 3).

The joint model includes a hierarchical linear model to partition variation for individual observations (i) of a given trait value ($y_{\text{trait}[i]}$) to the effects of species (*sp id*), study (*study id*), and residual variation (σ_{trait}, also called 'measurement error').

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

It estimates a separate value for each species ($\alpha_{\text{sp[sp id]}}$), and study ($\alpha_{\text{study[study id]}}$), 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 ($\alpha_{\text{trait sp[sp id]}}$) were then used as predictors of species-level estimates of each phenological cue ($\beta_{\text{force[sp]}}$, $\beta_{\text{chill[sp]}}$, $\beta_{\text{photo[sp]}}$)

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

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 ($\alpha_{\text{chill}[sp]}$, $\alpha_{\text{force}[sp]}$, $\alpha_{\text{photo}[sp]}$); 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 ($\alpha_{\text{pheno[sp]}}$) and observations ($\sigma_{\text{pheno}}$):

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

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

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

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 (Stan Development Team, 2018), 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.

Results

Our approach used models that jointly estimated species traits and phenological cues to understand the possible 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, our analysis partitioned the trait variation due to species from the study-level effects. Then using the species-level estimates of traits (i.e. species-level estimates with effects of study removed), we examined how traits predicted phenological cues and budburst, while allowing for residual variation in cues to be explained by a species effect.

Across our models, we found species-level variation across traits was comparable with or greater than variation across study. 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 variation (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 may poorly estimate species' traits.

We 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 other 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, and photoperiod), with a consistent direction of responses across cues for only LNC and not height or SLA (Fig. 3 a-f and j-l). Seed mass had the weakest responses, with no considerable relationship between seed mass and cues across the three cues (Fig. 3 g-i).

Height was not related to forcing, but was related to chilling and photoperiod. As we predicted, taller species had larger responses to chilling (-0.5 m per standardized chilling; 90% uncertainty interval (UI): -1, -0.1) and photoperiod (-0.2 m per standardized photoperiod; 90% UI: -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 or forcing (Fig. 2 b and d). But, SLA did relate to photoperiod (-0.2 mm^2/mg per standardized photoperiod; 90% UI: -0.4, 0.0). 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.

For LNC, we found that species that produce leaves with high nitrogen content, which relates generally 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% UI: 0.3, 1.2), with similar responses to photoperiod

250 (0.3 mg/g per standardized photoperiod; 90% UI: 0, 0.6) and to forcing cues (0.5 mg/g per standard-
251 ized forcing; 90% UI: 0.1, 0.9).
252

Discussion

254 Species traits influenced the timing of budburst in response to three primary cues for spring phenology
255 (chilling, forcing and photoperiod). Whether these trait effects led to earlier or later phenology was
256 correlated with well known gradients in traits, from acquisitive to conservative growth strategies. We
257 found the greatest budburst responses for traits related to resource acquisition and structure, with
258 SLA, LNC, and height all depicting strong responses across our three cues. In contrast, our one re-
259 productive trait—seed mass—showed a weak response. Despite finding these general trends in trait
260 relationships to phenology, we also found considerable variation across studies, often at a magnitude
261 comparable to the differences observed across species.
262

263 Our study is one of the first to jointly model budburst cues and timing with other trait relationships.
264 Using this approach we identified trends in phenological cues based on species-level trait variation,
265 while accounting for the high degree of uncertainty that arises when combining datasets of diverse
266 communities. While data limitations meant that we could only include a small number of species, our
267 dataset represents the most comprehensive trait syndrome available, making it an important first step
268 to identify general trends that scale across populations and species. Our study addresses the complex
269 interactions between traits and cues shaping species temporal niche, and contributes to a more holistic
270 approach to better forecast future changes in species temporal niche and phenotypes.
271

272 Gradients in phenology generally followed similar gradients in traits we associate with fast growing,
273 acquisitive species to conservative, slower growth strategies. Phenologically earlier species had traits
274 that inferred faster return on resource investments (Grime, 1977; Westoby, 1998; Chave et al., 2009).
275 In contrast, phenologically late species filled different trait space (Fig. 3), exhibiting a phenotype
276 that infers greater competitive abilities and slower growth (Grime, 1977; Westoby, 1998; Chave et al.,
277 2009). Our findings suggest the assembly of communities results from varying selective pressures, such
278 as strong abiotic filters early in the growing season, and greater biotic pressures later in the season.
279 By including phenology in the trait framework, we can identify the interactions across traits and cues
280 and tease apart the underlying mechanisms shaping species' temporal niche across communities.
281

Effects of phenology-trait relationships on community assembly

283 In our study of temperature forest communities, the relationships between budburst phenology and
284 other plant traits provided insights into the mechanisms that shape species phenotypes. Earlier bud-
285 bursting species had traits, such as shorter heights and low LNC, that allow them to grow quickly
286 and benefit from greater light availability in the open canopy of many early-spring temperate forests.
287 This phenotype can be linked to other ecological processes and species characteristics, such as species
288 successional position, as illustrated by the differences between early successional species, like *Alnus*
289 *incana*, and later successional species, like *Quercus ilex* (Fig 3). Our results may also be useful to help
290 predict communities' potential for invasion, as communities with similar phenologies and general trait
291 syndromes, appear more susceptible to fast growing, non-native species (Wolkovich and Cleland, 2011;
292 Alexander and Levine, 2019; Schuster et al., 2021). In identifying the trait syndromes of native forest
293 communities and the interactions between traits and environmental cues, we can better predict and
294 mitigate the challenges forest communities face with climate change.
295

296 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 strong forcing cues for short trees, which could prevent frost damage or xylem cavitation under a false spring (Clements et al., 1972; Marquis et al., 2020) and influence annual cambial meristem growth (Lenz et al., 2016). Similarly, the lack of chilling or forcing responses 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 (Westoby, 1998; Reich, 2014). These findings highlight the complexity of determining the drivers of species trait profiles, offering novel insights into how traits affect community dynamics under variable environments.

Phenology-trait relationships under future climates

Incorporating phenology within broader trait syndromes is necessary to accurately predict species responses to climate change. Recent phenological shifts are well documented, but there remains a high degree of unexplained variation across species and populations (Vitasse et al., 2009; Wolkovich and Ettinger, 2014; Zohner and Renner, 2014; Vitasse et al., 2018). Our findings demonstrate that the same environmental cues driving phenological traits also relate to leaf and structural traits and thus suggest that warming that favors species with certain phenological cues, can favor specific trait syndromes.

In temperate forests, warming may favor species with weak chilling and photoperiod requirements, as these requirements may allow phenology to shift more with warming. Our results suggest that these low cue requirements co-vary with acquisitive growth strategies. Thus, future forests may be dominated by species with lower chill and photoperiod cues and with traits that allow them to grow faster and rapidly acquire resources. In contrast, conservative species with high chilling and photoperiod requirements, could face greater abiotic stressors. Rising winter temperatures could result in insufficient chilling, while strong photoperiod cues could limit species ability to also advance in response to warmer spring conditions (Guy, 2014). Species that are less able to advance phenologically might experience more competition (Carter et al., 2018; Alexander and Levine, 2019), as priority effects allow species that begin growth earlier in the season to deplete resources. Growing under warmer summer conditions could also result in greater drought stress (Frelich and Reich, 2010). In addition to altering the distribution of species temporal niches within a season, species trait syndromes have the potential to define the environmental conditions under which growth occurs.

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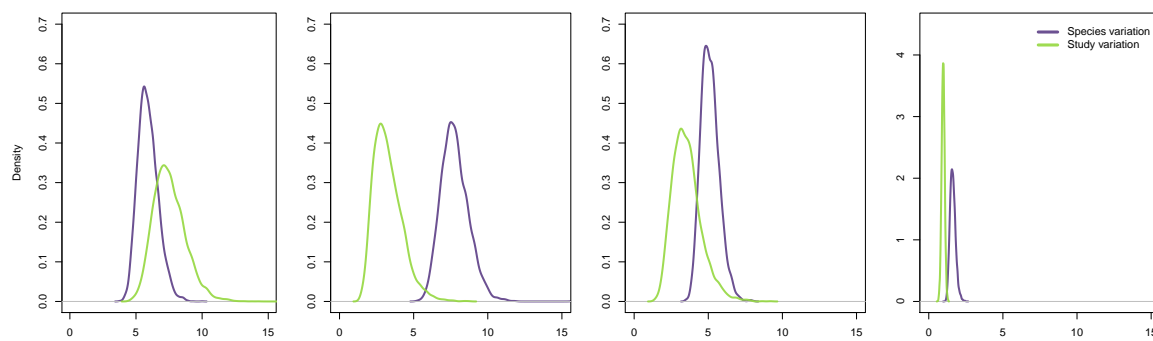
Figure 1: Comparison of the posterior densities for the species-level variation and study-level variation of a. height, b. SLA, c. LNC, and d. seed mass.
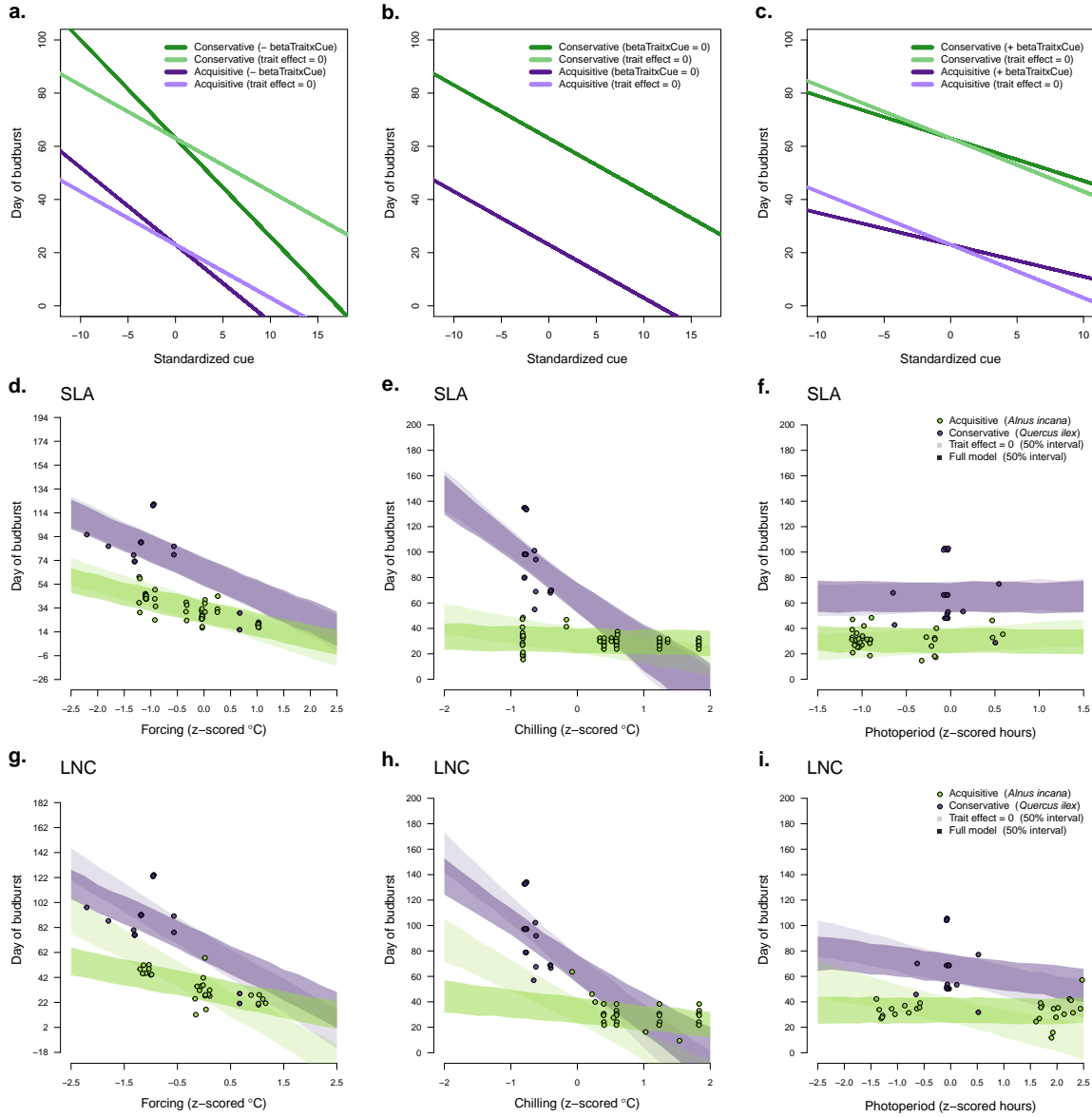
Figure 2: Functional traits may contribute to the species responses to forcing, chilling, or photoperiod cues in several ways. a) If traits are also responding to the environmental cue and lead to stronger phenological responses (larger in magnitude) then budburst will be earlier with increasing chilling, forcing and photoperiod. b) But if traits have no effect on the timing of budburst, then phenological responses will be equivalent to the cue only model estimates. c) Traits that have a opposing relationship to cues will produce weaker phenological responses (smaller in magnitude) and produce 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 cues and for LNC in response to photoperiod cues (panel d, e, g, h, and i). Only in response to photoperiod does the effect of SLA lead to stronger phenological responses and slightly earlier budburst with longer photoperiods. Species with conservative traits are shown in purple and species with acquisitive growth shown in green. Bands represent the 50% uncertainty intervals of the model estimates.
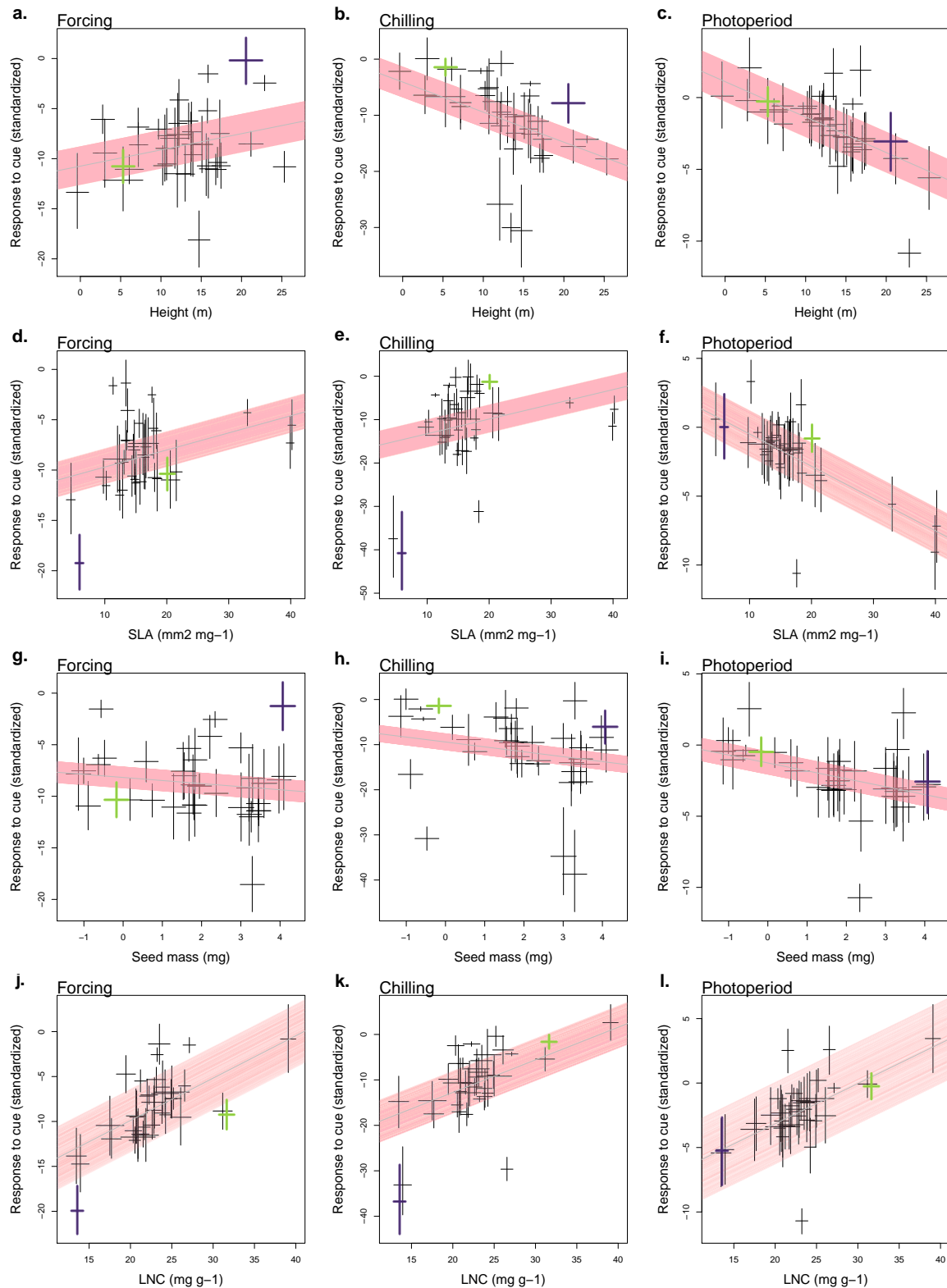
Figure 3: Estimated trait values for height (a-c), SLA (d-f), log10 Seed mass (g-i), and LNC (j-l), correlated against species-level cue responses to standardized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using our joint trait-phenology 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. Each set of crossed lines represents one species, with the species depicted in Fig 2 colored 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.