

1 Woody plant phenological responses are strongly associated
2 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 more abundant, and conditions later in the season, when the environment is benign but competition greater. This idea fits within fundamental theories of plant growth strategies and infers a suite of traits that may co-vary with phenologies. But testing the role of phenology within a functional trait framework is challenging given how variable it is across different 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 we predicted. Chilling and photoperiod were both related to height and LNC, with the conservative phenotype of tall trees with low LNC showing the strongest impacts on phenology. Cues varied in their relationship to SLA, with low SLA species responding to forcing as predicted, but not photoperiod. Our results show that leafout phenology generally fits within a functional trait framework of acquisitive to conservative growth strategies. Our findings are some of the first to demonstrate the relationships between phenological cues and broader trait phenotypes, allowing us to better predict the ultimate drivers shaping species phenotypes and 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^{1–3}. As climate change advances spring in many systems^{4,5} there is growing concern over how these advances 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^{6,7}. 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^{8,9}, with similar trends observed for spring phenological events across taxa, including in the timing of egg laying in birds^{10,11} and the advancing of spawning in amphibians^{12,13}. But this work has provided limited insights into the drivers of species differences^{8,9,14}.

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^{15,16} or high herbivore apparency¹⁷—but benefit from higher resource availability^{18,19}. In contrast, later species face greater biotic pressures, especially from high competition for resources^{20,21}.

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 damaged²². But later species would benefit from investing in tissues that infer greater resource acquisition and retention²³. 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 traits²¹.

In plants, several well studied traits have been identified as species-level proxies for varying growth strategies and responses to species interactions²⁴. 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^{25–28}. Collectively, these trait relationships led to the development of the leaf economic spectrum and the wood economic spectrum^{27,29}.

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^{30–33}, but have limitations. These frameworks often fail to predict how variable traits are³⁴, 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 current 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 closure³⁵, 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 wood³⁶, 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^{9,37,38}. 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^{8,9}.

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 nine traits—SLA, leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC. We further removed SSD and LDMC 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 database³⁹. 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 see⁴⁰.

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 in⁴⁰, which represents well studied species with good phenology and phylogenetic data. Using the BIEN R package⁴¹, we downloaded trait data for 94 species for 13 traits. The TRY database included 96 of our focal species with ten functional traits (Table 1). 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 specific leaf area and leaf dry matter content, and between height and stem specific density (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 leaf dry matter content and stem specific density) 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 $n = 7656$). To reduce the influence of 13 tree species in our mixed-effects models (discussed below), which were measured on average 19 times more frequently than other species in our dataset 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 effects 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’).

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

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

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

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

179 This model allows an overall effect of each trait—estimated across species—on each phenological cue
180 ($\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$), while also allowing for species-level variation in cues that is not
181 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
182 is not forced onto the trait effect. Thus the model tests the power of traits to predict species-level
183 differences.

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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:

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

185 We chose weakly informative priors, and validated them using a series of prior predictive checks. The
186 model was coded in the Stan programming language, fit using the rstan package⁴², with 1,000 iterations
187 per chain across 4 chain (4,000 total sampling iterations), and all models met basic diagnostic checks,
188 including no divergences, high effective sample size (n_{eff}), and \hat{R} close to 1.

189 Results

190 Our approach used models that jointly estimated species traits and phenological cues to understand the
191 possible connections between phenology, with a focus on days to budburst and other plant traits. Since
192 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 (ie. 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 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 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, photoperiod), with a consistent direction of responses across cues for only LNC and not height or SLA (Fig. 3 a-f and j-l).

Height was not related to forcing (0.2 m per standardized forcing; 90% uncertainty interval: -0.2, 0.5), 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: -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 mm²/mg per standardized chilling; 90% uncertainty interval: -0.1, 0.7, Fig. 2 b). However, SLA did relate strongly to photoperiod (-0.2 mm²/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 mm²/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 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% 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 without 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).

Discussion

Species traits influenced the timing of budburst date in response to its three primary cues. Whether these trait effects led to earlier or later budburst phenology was correlated with well known gradients in traits, from acquisitive to conservative growth strategies. We found the greatest budburst responses for traits related to resource acquisition and structure, with SLA, LNC, and height all depicting strong responses across our three cues. In contrast, our one reproductive trait—seed mass—showed a weak response. Despite finding these general trends in trait relationships to phenology, we also found considerable variation across studies, often at a magnitude comparable to the differences observed across species.

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

Effects of traits and phenology correlations for community assembly

Gradients in budburst phenology generally followed similar gradients in traits we associate with fast growing, acquisitive species to conservative, slower growth strategies. Early budbursting species had trait phenotypes that infer greater photosynthetic potential and faster return on resource investments^{25,29,43}. This phenotype allows species to grow quickly and benefit from greater light availability in the springs open canopy, which is likely beneficial for early, shorter species, like *Alnus* (Fig. 3). Late budbursting species filled different trait space (Fig. 3), exhibiting traits that infer greater competitive abilities and slower growth^{25,29,43}. This more conservative phenotype is likely beneficial for canopy species, such as *Quercus* (Fig. 3). Our findings suggest the assembly of forest communities results from varying selective pressures, such as strong abiotic filters early in the growing season, and greater biotic pressures later in the season. By including phenology in the trait framework, we can identify the interactions across traits and cues and tease apart the underlying mechanisms shaping species' temporal niche across communities.

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 plant 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^{44,45} and influence annual cambial meristem growth⁴⁶. Similarly, the strong forcing response of high SLA individuals' could be driven by other trait attributes—such as relative growth rates or selection for shorter leaf longevity—and not photosynthetic potential^{25,47}. 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^{21,48–50}. Our findings demonstrate that

the same environmental cues driving phenological traits also relate to leaf and structural traits and thus suggests potentially that warming that favors species with certain phenological cues, also favors certain trait syndromes.

In temperate forests, warming temperatures could favour species with acquisitive growth strategies, as they are less limited by chilling and photoperiod requirements and possess traits that infer faster growth and resource acquisition. In contrast, conservative species could face greater abiotic stressors. Rising winter temperatures could result in insufficient chilling, while strong photoperiod cues could limit their ability to also adapt to earlier spring conditions⁵¹. Species that are less able to advance phenologically might experience more competition^{52,53}, while growing under warmer summer conditions could result in greater drought stress⁵⁴. In addition to altering the distribution of species temporal niche within a season, species trait syndromes have the potential to reshape species assemblages and community dynamics.

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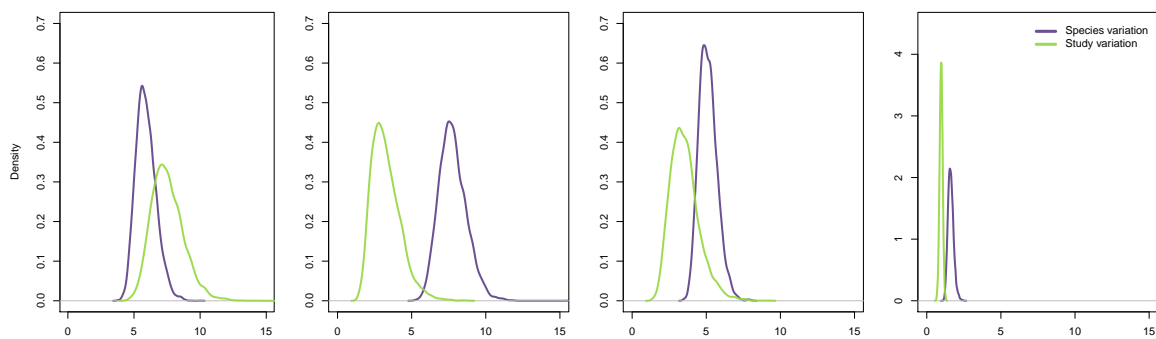


Figure 1: Comparison of the posterior densities for the species-level variation and study-level variation of a. height, b. SLA, c. LNC, and d. seed mass.

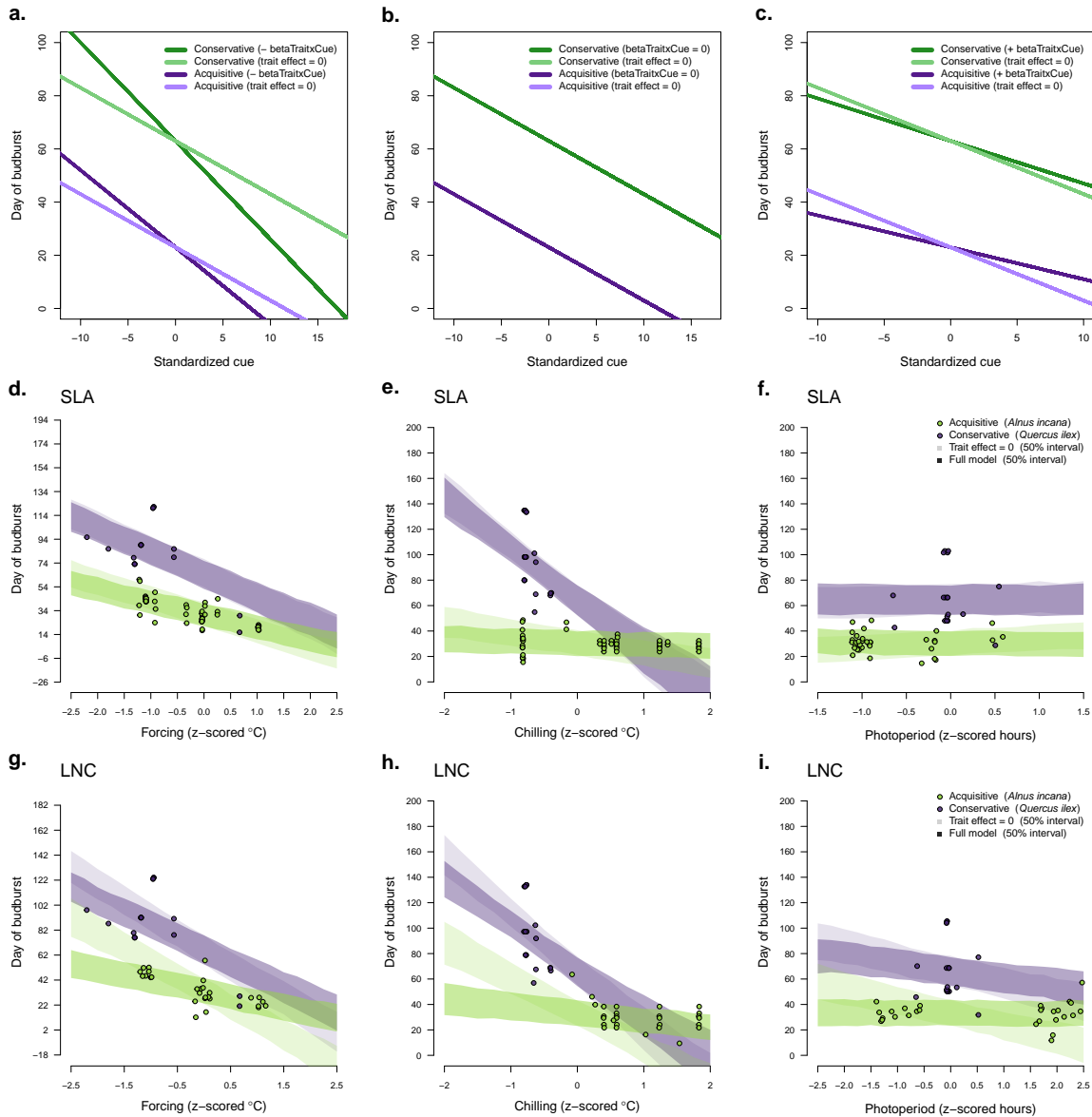


Figure 2: Functional traits may contribute to the species responses to forcing, chilling, or photoperiod cues in several ways. a) If traits are also responding to the environmental cue and lead to stronger phenological responses (larger in magnitude) then budburst will be earlier with increasing chilling, 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.

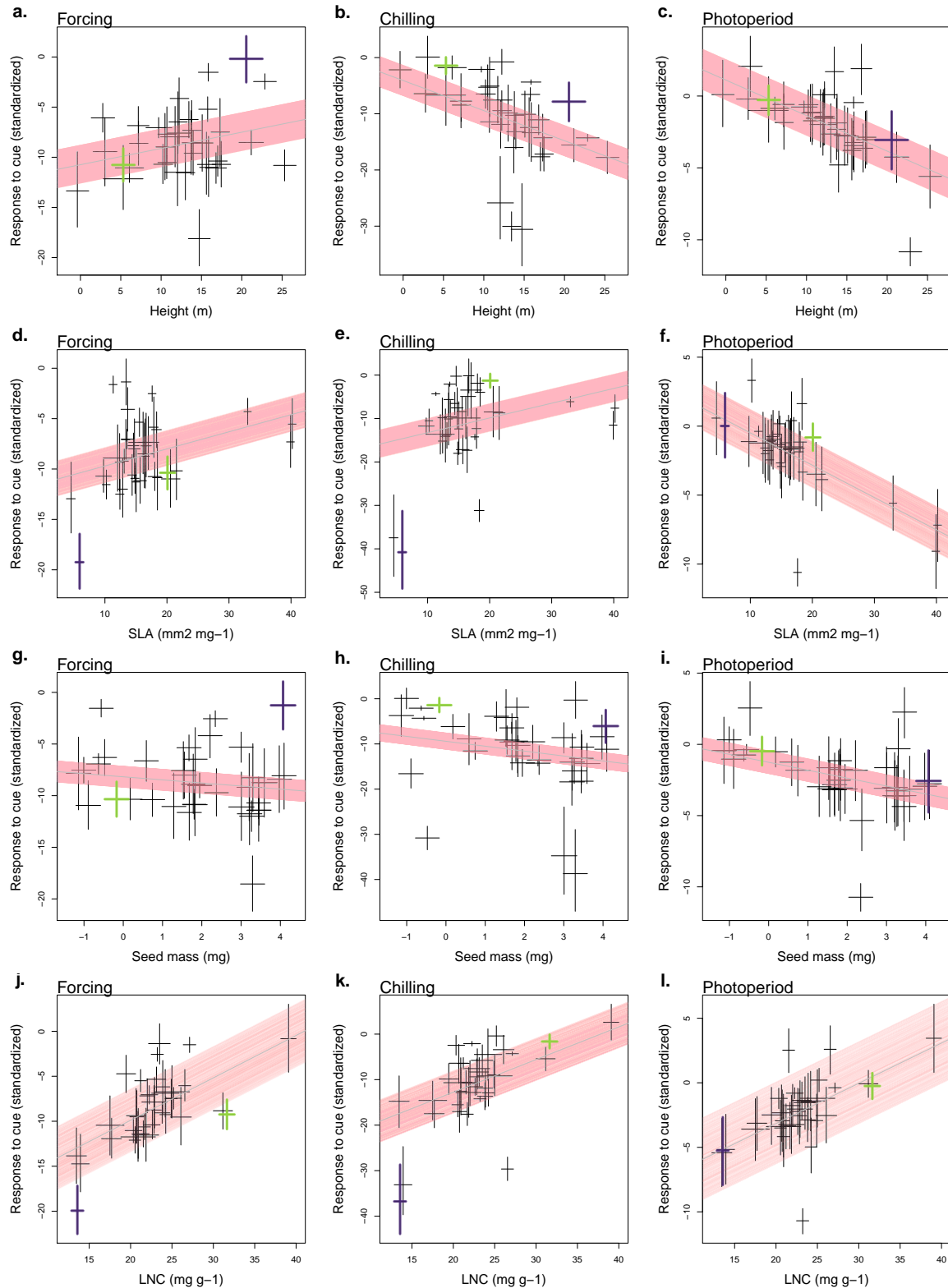


Figure 3: Estimated trait values for height (a-c), SLA (d-f), log10 Seed mass (g-i), and LNC (j-l), correlated against species-level cue responses to standardized forcing (a, d, g & j), chilling (b, e, h & k), and photoperiod cues (c, f, i & l). Parameters were estimated using our joint trait-phenology 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.