

¹ Budburst timing within a functional trait framework

²

³ Running title: Budburst responses associated with traits

⁴ **Summary**

⁵ 1. Phenology, **the timing of recurring life history events**, can vary substantially in different environments and for different species. While climate change has shifted phenology by altering its proximate drivers, **such as temperature**, changes in the ultimate drivers that select for species-level variation remain poorly explained. Theory suggests that species-level variation in phenology can result from shifting environmental pressures that favour different strategies across the spring growing season: from the early season, where higher abiotic risks and greater availability of nutrients and light favour cheaper leaves and acquisitive growth strategies, to later when a more benign environment and lower levels of light and nutrients favour conservative growth strategies. From this framework we can predict suites of traits that may co-vary with species phenologies, but the high variability in traits, **and especially phenology**, across environments, have made testing the role of phenology within a trait framework challenging.

¹⁶ 2. Using a modelling framework that accommodates this variability, we used phenological data from a database of controlled environment experiments and tree trait data from two trait databases to test the relationships between traits and three cues for tree budburst: spring temperatures (forcing), winter temperatures (chilling), and daylength (photoperiod).

²⁰ 3. We found mixed support for our predictions for how traits relate to budburst timing and cues. Species with cues indicative of earlier budburst, like low experimental chilling and photoperiod, were shorter with higher leaf nitrogen content, which are traits related to acquisitive strategies. However seed mass, our one reproductive trait, showed no relationships to cues, and other traits (e.g., specific leaf area) showed relationships in the opposite direction to our predictions.

²⁵ 4. Synthesis: Our findings show how spring leafout phenology partially fits within a functional trait framework of acquisitive to conservative growth strategies, and can lead to better predictions of how communities may shift in their growth strategies alongside changing phenology with future warming.

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²⁹ Key Words: Leafout, spring phenology, traits, trees, climate change, forest communities

³⁰ Introduction

³¹ The timing of life history events, phenology, can shape both ecosystem services and community dynam-
³² ics. Spring phenology, for example, defines the start and overall length of the growing season—shaping
³³ forest carbon storage and species interactions (Beard *et al.*, 2019; Cleland *et al.*, 2007; Gu *et al.*, 2022).
³⁴ Shifts in phenology with climate change across systems (Menzel *et al.*, 2006; Vitasse *et al.*, 2021) have
³⁵ thus led to growing concerns over their possible impacts.

³⁶

³⁷ Predicting these changes requires understanding the drivers of phenology both at a proximate scale
³⁸ (the environmental triggers that determine phenology each year) and at an ultimate scale, where
³⁹ long-term environmental pressures may select for different phenologies across species, causing certain
⁴⁰ species to be early or late relative to other species each year (Ovaskainen *et al.*, 2013; Wolkovich &
⁴¹ Donahue, 2021). At the proximate level, environmental conditions, including temperature or photoper-
⁴² iod, throughout the winter and spring cause species to start growth at different times. Groups of
⁴³ species may have more similar responses because they are from similar functional groups, successional
⁴⁴ stages (Laube *et al.*, 2014) or growth forms (Flynn & Wolkovich, 2018) that cause them to have similar
⁴⁵ growth strategies. But current work provides limited insights into the drivers of these differences across
⁴⁶ species and how they can be used to predict future changes in community dynamics (Chuine *et al.*,
⁴⁷ 2016; Flynn & Wolkovich, 2018; Laube *et al.*, 2014).

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⁴⁹ At the ultimate level, plant phenologies may vary due to changing pressures across the growing season
⁵⁰ that select for different growth strategies. Species that start growth early often risk high tissue loss due
⁵¹ to frost damage (Augspurger, 2009; Sakai & Larcher, 1987) or high herbivore apprenancy (Wainwright
⁵² *et al.*, 2012), but benefit from higher resource availability (Hufkens *et al.*, 2012; Rathcke & Lacey,
⁵³ 1985). In contrast, later active species face greater biotic pressures, especially from high competition
⁵⁴ for resources (Lopez *et al.*, 2008; Wolkovich & Ettinger, 2014). Such differences could shape physical
⁵⁵ and phenological traits related to species growth strategies and fitness (Viole *et al.*, 2007). Species
⁵⁶ leaf and wood traits can reflect trade-offs between the construction costs and longevity of tissue (Reich
⁵⁷ *et al.*, 1997; Wright *et al.*, 2004), with cheaper-to-construct tissue being associated with faster growth
⁵⁸ rates (Westoby & Wright, 2006; Wright *et al.*, 2004). Previous studies have highlighted associations
⁵⁹ between trade-offs in phenology with structural and leaf traits in both woody (Wang *et al.*, 2021;
⁶⁰ Wolkovich & Ettinger, 2014) and herbaceous species (Sporbert *et al.*, 2022) (Fig 1), and hypothesized
⁶¹ that phenology may fit within the acquisitive (fast) to more conservative (slow) growth strategies as-

62 sociated with existing trait frameworks (Chave *et al.*, 2009; Wright *et al.*, 2004).

63

64 Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation
65 of the leaf and wood economic spectra (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby &
66 Wright, 2006; Wright *et al.*, 2004), but they make limited predictions of trait variability (Viole *et al.*,
67 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving
68 the relationships between broader trait syndromes and phenology largely unknown. Understanding
69 these relationships, however, can improve forecasts of community dynamics and responses to climate
70 change. Most studies have examined the relationship between traits and phenology for a single or
71 limited number of sites, as reviewed by Wolkovich & Cleland (2014); Wolkovich & Donahue (2021),
72 though recent studies have explored these relationships for herbaceous species (Rauschkolb *et al.*, 2024;
73 Sporbert *et al.*, 2022)). At these spatial scales the problem of proximate drivers causing phenological
74 variation across species can be more easily ignored depending on the system. But habitat conditions
75 can still create considerable intraspecific variation, which for some traits has been shown to be consid-
76 erable or even exceed interspecific trait variation (Albert *et al.*, 2011; Siefert *et al.*, 2015; Zuleta *et al.*,
77 2022). Adding phenology to broader trait frameworks therefore becomes more complex as high levels
78 of variation occur across large spatial and temporal ranges.

79

80 Recent climate change has highlighted how variable plant phenology is when observed over time and
81 space across different species (Rudolf, 2019; Vitasse, 2013; Yu *et al.*, 2010), with many studies docu-
82 menting how quickly phenology can shift with warming (Fitter & Fitter, 2002; Menzel *et al.*, 2006).
83 But experiments conducted under controlled environments have shown that it is possible to consis-
84 tently define early to late phenology from the known underlying cues (Chuine & Cour, 1999; Flynn &
85 Wolkovich, 2018; Harrington & Gould, 2015). This work has found early species to generally require
86 only small amounts of forcing (**accumulated warm temperatures usually in the spring**), chilling (**cool**
87 **temperatures usually accumulated in the fall and winter**), and shorter photoperiod to leaf out. Thus
88 under experimental conditions, we observe relatively small responses to each of these cues. In contrast,
89 later species require more chilling, warmer forcing temperatures, and longer photoperiods to budburst,
90 resulting in larger responses to cues in controlled environments (Flynn & Wolkovich, 2018; Laube *et al.*,
91 2014). The consistency of these relationships allows us to estimate early to later active species across
92 plant communities and diverse species assemblages.

93

94 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-
95 nology into functional trait research. In addition to how well we understand the environmental cues
96 that trigger early versus late leafout, in many forests we see strong gradients in frost risk or nutri-

ent availability from the start to the end of the spring growing season that are likely to shape other traits (Fig 1). We might predict some variability in how traits relate to different growth strategies as a result of different selective pressures. This variability could lead to differences across groups of species (Horbach *et al.*, 2023; Wang *et al.*, 2021), such as the differences in traits that facilitate frost tolerance versus avoidance (Lenz *et al.*, 2013; Sakai & Larcher, 1987) or in herbivory (Coley *et al.*, 1985). Broadly we predict acquisitive species to be shorter, with leaf traits favorable to the low light conditions of the understory later in the growing season—that is, they should produce leaves with high specific leaf area (SLA) and leaf nitrogen content (LNC) (Díaz *et al.*, 2016; Reich *et al.*, 1997; Wright *et al.*, 2004) (Fig 1). We would predict such species to exhibit early phenology, budbursting even with low chilling and cool spring conditions (low forcing) when photoperiods are short. Canopy species that budburst later via larger cue responses and when competition for soil resources is greater, would then have traits associated with conservative growth —taller with denser wood (Chave *et al.*, 2009; Laughlin *et al.*, 2010) and leaf traits suited for the higher light conditions of the canopy (low SLA and low LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative continuum, as acquisitive species produce smaller seeds and the taller and more conservative species produce larger, better provisioned, seeds (Díaz *et al.*, 2016) Fig 1).

To test these predictions between budburst responses to environmental cues and common functional traits (height, SLA, seed mass, and LNC), we merged available data from global databases of plant traits—BIEN (Maitner *et al.*, 2018) and TRY (Kattge *et al.*, 2020)—with global budburst data from the OSPREE database of controlled environment studies (Ettinger *et al.*, 2020). We developed a hierarchical Bayesian joint model that predicts phenological responses to forcing, chilling and photoperiod treatments based on species-level trait values, while allowing additional variation due to study. This approach takes a step towards predicting variation via species traits instead of species identity. When traits explain a significant portion of the variation, species identity will explain only a small amount and thereby help forecast species phenological responses based on trait values alone.

Methods

We merged three major databases for our analysis. We gathered phenological data from the OSPREE database (Ettinger *et al.*, 2020), which contains data from experiments of dormant plant tissue from woody plants growing either in the field or in controlled environments. From OSPREE, we used the available budburst data for temperate tree species from studies that each manipulated forcing, chilling and photoperiod. We originally constructed the OSPREE database by performing a systematic review

130 of the literature, and searched both ISI Web of Science and Google Scholar using the following two
131 search terms:

132

- 133 1. TOPIC = (budburst OR leafout) AND (photoperiod or daylength) AND temperature*
134 2. TOPIC = (budburst OR leafout) AND dorman*

135

136 We then scraped the data from all articles reporting experiments that manipulated both photoperiod
137 and/or temperature cues of woody species budburst, leafout, or flowering phenology, and for which
138 there was a quantifiable response to each cue. We updated this database in July 2019 reviewing all
139 new articles found using the previous search terms. Additional details on the methods used to as-
140 semble, clean, and update this database are discussed by Ettinger *et al.* (2020) and Morales-Castilla
141 *et al.* (2024). For the purpose of this study, we obtained a subset of the budburst data from OSPREE
142 database and initially aimed to use data for the subset of 234 species used in Morales-Castilla *et al.*
143 (2024).

144

145 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020; Maitner
146 *et al.*, 2018), both of which are large trait databases that include plant trait observations across many
147 individuals, species, and studies (Table S1) and are available through slightly different mechanisms.
148 BIEN is accessible via the BIEN R package (here we used v. 1.2.5, Maitner *et al.*, 2018), and TRY is
149 requested. **We obtained data from the BIEN databases on 5 December 2018 and the TRY data on 10**
150 **April 2019.** We initially searched for trait data on the subset of 234 OSPREE species used in Morales-
151 Castilla *et al.* (2024). From BIEN, this resulted in 94 of the 234 species available in the database, for
152 which there were 13 unique traits. From the TRY database we received data for 10 unique traits for
153 96 of the 234 requested species (Kattge *et al.*, 2020). As we were interested in the trait-phenology
154 relationships of adult trees we subset the available data to **remove any observations denoted as being**
155 **from juvenile trees individuals or with heights less than 2m, which we assume removes any individuals**
156 **that were saplings when measured (Natural Resources Canada, 2020).** We further removed all data
157 from manipulative experiments or from plants growing in non-natural habitats. We then grouped
158 trait values where appropriate, for example pooling trait values for specific leaf area (SLA) with those
159 denoted as ‘SLA with petioles’, and ‘SLA without petioles’ in our analysis (see Table S1). We also
160 removed data that was duplicated in both the TRY and BIEN datasets ($n = 434,905$). For a full
161 depiction of our data cleaning process and decisions see Fig. S2.

162

163 For our analysis, we only included species for which we had a complete trait profile (i.e., all traits
164 measured for all species). For this profile, **we initially considered six commonly measured traits: SLA,**

leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC. There were 26 species that had at least one trait measurement for each of these traits. We then used a principle component analysis (PCA) to identify which (if any) of our six traits were strongly correlated. The first principal component explained 32% of variation while the second explained 24.2% of the variation, with high correlations between SLA and LDMC, and between height and SSD (Fig. S3). By excluding the trait from each of these highly correlated trait pairs with the least amount of data (specifically LDMC and SSD) we were able to increase the number of species in our dataset from the 26 species with complete data for six traits, to 37 species with complete data for four traits. The data for these 37 species were from 24 unique studies (sample sizes: height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n = 7656$). Our dataset of tree height included 13 species that were measured over 19 times more frequently than most other species. We therefore subsampled the height measurements of these 13 most frequently measured trees to reduce their influence on our height model, randomly sampling 3000 height measurements for each individual species while including all height data for the remaining, less frequently measured, 24 species. This subsampling was not required for any of the other traits included in our study.

Joint model of trait and phenology

To understand connections between phenology and species traits, we developed a Bayesian joint model that allowed us to relate each trait (height, SLA, LNC, and seed mass) to species budburst cues. We consider this a ‘joint’ model because it involves two sub-models, one that models trait observations and a second that uses shared latent processes to model how a given trait relates to the cues that shape the phenological observations. In particular, we assume that trait values are the result of multiple sources of variation, including species (α_{species}) and study-level variation (α_{study}), that combine into one observed trait value (trait sub-model). This trait value (α_{trait}) has a separate interaction with the three cues (β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$) that determines phenology and specifically the day of year of budburst (phenology sub-model). Below we describe the two sub-models, noting which parameters are shared across sub-models and which are independent.

Trait sub-model

Our trait sub-model describes the processes that shape a given trait observations for 1 to n species across each of the 1 to m studies in our trait dataset. We use hierarchical modeling to partition trait values by the error across all observations not otherwise explained by the model (σ_m^2 , often considered measurement error), species identity ($\alpha_{\text{species}_i}$), and study (α_{study_j}). In particular, we assume that a trait observation for species i from study j ($Y_{\text{trait}_{i,j}}$) has the following normal distribution:

$$Y_{\text{trait}_{i,j}} \sim \text{Normal}(\mu_{i,j}, \sigma_m^2) \quad (1)$$

197 with

$$\mu_{i,j} = \alpha_{\text{grand trait}} + \alpha_{\text{species}_i} + \alpha_{\text{study}_j} \quad (2)$$

198 where $\alpha_{\text{species}_i}$ and α_{study_j} are elements of the normal random vectors:

$$\boldsymbol{\alpha}_{\text{species}} = \begin{bmatrix} \alpha_{\text{species}_1} \\ \alpha_{\text{species}_2} \\ \vdots \\ \alpha_{\text{species}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{species}} \sim \text{Normal}(0, \sigma_{\text{species}}^2) \quad (3)$$

$$\boldsymbol{\alpha}_{\text{study}} = \begin{bmatrix} \alpha_{\text{study}_1} \\ \alpha_{\text{study}_2} \\ \vdots \\ \alpha_{\text{study}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \text{Normal}(0, \sigma_{\text{study}}^2) \quad (4)$$

199 Mathematically, the latent parameter or overall mean trait value ($\alpha_{\text{grand trait}}$) represents a trait value
200 that is independent of the other parameters in the model, namely the parameter for species ($\alpha_{\text{species},i}$)
201 and study-level ($\alpha_{\text{study},j}$) offsets from that overall mean trait value. The σ_m^2 parameter is the mea-
202 surement error for the observed trait values, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and study-level
203 variances in trait values. Of these parameters, the $\boldsymbol{\alpha}_{\text{trait}}$ is shared by the phenology sub-model.

204 Phenology sub-model

205 Our phenology sub-model describes the processes that determine the relationships between traits and
206 environmental cues and their effects on phenological observations for 1 to n species, specifically the
207 timing (day of year) of budburst from the updated OSPREE dataset. The observations of budburst
208 for species k under g treatment levels of each cue (c_g, f_g, p_g , for chilling, forcing and photoperiod
209 treatments respectively, which we z -scored to allow direct comparison between cues) is represented by
210 parameter $Y_{\text{pheno}_{k,g}}$, and assumed to follow a normal distribution:

$$Y_{\text{pheno}_{k,g}} \sim \text{Normal}(\mu_{k,g}, \sigma_d^2) \quad (5)$$

211 with

$$\mu_{k,g} = \alpha_{\text{pheno}_k} + \beta_{\text{chilling}_k} \cdot c_g + \beta_{\text{forcing}_k} \cdot f_g + \beta_{\text{photoperiod}_k} \cdot p_g \quad (6)$$

²¹² and

$$\beta_{\text{chilling}_k} = \alpha_{\text{chilling}_k} + \beta_{\text{trait.chilling}} \cdot \alpha_{\text{trait}_k} \quad (7)$$

$$\beta_{\text{forcing}_k} = \alpha_{\text{forcing}_k} + \beta_{\text{trait.forcing}} \cdot \alpha_{\text{trait}_k}$$

$$\beta_{\text{photoperiod}_k} = \alpha_{\text{photoperiod}_k} + \beta_{\text{trait.photoperiod}} \cdot \alpha_{\text{trait}_k}$$

²¹³ where α_{pheno_k} , $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$ are elements of the normal random vectors:

$$\boldsymbol{\alpha}_{\text{pheno}} = \begin{bmatrix} \alpha_{\text{pheno}_1} \\ \alpha_{\text{pheno}_2} \\ \vdots \\ \alpha_{\text{pheno}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \text{Normal}(0, \sigma_{\text{pheno}}^2) \quad (8)$$

$$\boldsymbol{\alpha}_{\text{chilling}} = \begin{bmatrix} \alpha_{\text{chilling}_1} \\ \alpha_{\text{chilling}_2} \\ \vdots \\ \alpha_{\text{chilling}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{chilling}} \sim \text{Normal}(0, \sigma_{\text{chilling}}^2) \quad (9)$$

$$\boldsymbol{\alpha}_{\text{forcing}} = \begin{bmatrix} \alpha_{\text{forcing}_1} \\ \alpha_{\text{forcing}_2} \\ \vdots \\ \alpha_{\text{forcing}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{forcing}} \sim \text{Normal}(0, \sigma_{\text{forcing}}^2) \quad (10)$$

$$\boldsymbol{\alpha}_{\text{photoperiod}} = \begin{bmatrix} \alpha_{\text{photoperiod}_1} \\ \alpha_{\text{photoperiod}_2} \\ \vdots \\ \alpha_{\text{photoperiod}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{photoperiod}} \sim \text{Normal}(0, \sigma_{\text{photoperiod}}^2) \quad (11)$$

(12)

²¹⁴ The model partitions day of budburst for species (k) as a combination of the overall mean day of
²¹⁵ budburst without the influence of chilling, forcing, or photoperiod treatments ($\alpha_{\text{pheno},k}$, normally dis-
²¹⁶ tributed with a mean of μ_{pheno} and variance σ_{pheno}^2) combined with the effects of treatments both
²¹⁷ dependent and independent of trait values. The parameters $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$
²¹⁸ represent the trait-independent responses of species k to chilling, forcing, and photoperiod treat-
²¹⁹ ments respectively, each with an associated mean (μ_{chilling} , μ_{forcing} , $\mu_{\text{photoperiod}}$) and variance ($\sigma_{\text{chilling}}^2$,
²²⁰ $\sigma_{\text{forcing}}^2$, $\sigma_{\text{photoperiod}}^2$) across species. The shared parameter between the trait and phenology sub-model,
²²¹ α_{trait_k} , represents the effect of the species trait value on its responses to chilling ($\beta_{\text{trait.chilling}}$), forcing
²²² ($\beta_{\text{trait.forcing}}$), and photoperiod ($\beta_{\text{trait.photoperiod}}$). Finally, our model provides an estimate of σ_d^2 , which

223 is the variance arising from measurement error for the observed day of budburst.

224

225 The model was coded in the Stan (Stan Development Team, 2024), which is a probabilistic program-
226 ming language for building Bayesian models. We used the rstan package (Stan Development Team,
227 2018) to interface with and run the Stan code in R version 3.3.6 (R Development Core Team, 2017).
228 For our model, we chose weakly informative priors, and validated them using a series of prior predic-
229 tive checks. The model was fit with 1,000 iterations per chain across 4 chains (4,000 total sampling
230 iterations), and all models met basic diagnostic checks, including no divergences, high effective sample
231 size (n_{eff}), and \hat{R} close to 1, fitting the data well (Fig S4). In our discussion of the results we
232 present our model estimates as the means and 90% posterior uncertainty intervals (UI), with the 50%
233 UI depicted in the figures and both the 90% and 50% UI included in the supplementary tables to allow
234 the strength of relationships to be assess and compared. We consider parameters with UI that overlap
235 to be similar to each other and those that include zero in the 90% UI to have small effects.

236 Results

237 Across traits, height, SLA, and LNC were related to one or more environmental cue ($\beta_{chilling_k}$, $\beta_{forcing_k}$,
238 or $\beta_{photoperiod_k}$, Fig 2 a-f & j-l), with only LNC showing a relationship with all three cues (Fig. 2 j-l).
239 As we predicted, height was negatively related to chilling ($\beta_{chilling_k}$) and photoperiod ($\beta_{photoperiod_k}$),
240 with taller species having larger responses to high chilling and longer photoperiod conditions (-0.5 m
241 per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized pho-
242 toperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). These large responses in the timing of budburst (as
243 estimated by $\mu_{k,g}$), reflect taller tree species' requirement for more chilling and longer photoperiods
244 to budburst. conditions that are often only met later in the growing season, while shorter species will
245 budburst under the lower chilling and photoperiod conditions that occur earlier in the spring . In
246 contrast, seed mass had a negligible relationship with budburst and all three cues (Fig. 2 g-i & Table
247 S4).

248

249 Of the studied leaf traits, we found that SLA related to photoperiod ($\beta_{photoperiod_k}$, -0.2 mm²/mg per
250 standardized photoperiod; 90% UI: -0.5, 0.0, Table S3), but with larger responses to longer photoperi-
251 ods for high SLA species (Fig. 2 f). We did not find strong responses to chilling ($\beta_{chilling_k}$) or forcing
252 treatments ($\beta_{forcing_k}$, Fig. 2 d & e) however. The relationship between LNC and budburst cues, were
253 in line with our predictions, with high LNC species being less responsive to chilling (0.7 mg/g per
254 standardized chilling; 90% UI: 0.2, 1.2, Table S5), forcing (0.5 mg/g per standardized forcing; 90%
255 UI: 0.1, 0.8), and photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6, Fig 2 j-l).

256 This suggests that species that produce leaves with high nitrogen content, which relates generally to
257 high photosynthetic rates and acquisitive growth, are likely to budburst under early spring conditions
258 based on the relationships between this trait and environmental cues.

259

260 We found that the species-level variance across traits were comparable to, or greater than, variance
261 across studies (using our model that partitions the measurement error in the trait values from variance
262 from species and study-level effects (Fig 3). For height, variance across studies (σ_{study}^2) was greater (7.5
263 m; 90% UI: 5.7, 9.8), than the variance caused by species ($\sigma_{\text{species}}^2$, 6 m; 90% UI: 4.9, 7.3, Fig 3a). For
264 seed mass and LNC, study-level variance was less than that of the species-level variance, with variance
265 in seed mass observations of 1 mg (90% UI: 0.8, 1.1) and 1.6 mg (90% UI: 0.8, 1.1) for study-level and
266 species-level variance respectively and for LNC 3.6 mg g⁻¹ (90% UI: 2.2, 5.3) for study-level variance
267 and 5.1 mg g⁻¹ for the species-level variance (90% UI: 2.2, 5.3, Fig 3c and d). The difference between
268 species and study-level variance was greatest for SLA, with the estimate of 3.3 mm² mg⁻¹ (90% UI: 2,
269 5.1) for study-level variance being approximately half that of the estimated species-level variance of
270 7.8 mm² mg⁻¹ (90% UI: 6.4, 9.4, Fig 3b).

271

272 Discussion

273 We found several species traits influenced the timing of budburst in response to one or more of the
274 three primary cues of spring phenology. In general, early species that budburst under low levels of
275 forcing and chilling, and shorter photoperiod (Flynn & Wolkovich, 2018; Laube *et al.*, 2014), exhibited
276 relationships with several traits associated with fast and acquisitive growth strategies. Later bud-
277 bursting species, which require higher forcing and chilling, and longer photoperiods to initiate growth
278 (Flynn & Wolkovich, 2018; Laube *et al.*, 2014), however, exhibited traits indicative of conservative,
279 slower growth strategies. Specifically, the trait effects of height and LNC on the timing of budburst did
280 follow these well-established gradients in growth strategies predicted by functional trait frameworks
281 (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004).
282 But in the case of SLA, its relationship to phenological cues was opposite of our predictions. Species
283 with high SLA—as a result of having the larger, thin leaves, with low investment in leaf mass that
284 are indicative of acquisitive growth strategies—exhibited larger responses to photoperiod. Seed mass,
285 which was our one reproductive trait, showed the smallest response to all three cues. Our results are
286 in line with previous studies conducted at more local scales that found large relationships between
287 height and species phenology (Osada & Hiura, 2019; Seiwa, 1999), as well as findings from large-scale
288 research which found no relationship between phenology and seed mass in woody plants (Bolmgren &

289 D. Cowan, 2008; Ettinger *et al.*, 2018).

290

291 In addition to identifying trait-phenology relationships shaping the timing of spring budburst, our
292 results provide further insights into the use of data from large databases to estimate ecological pro-
293 cesses. By partitioning the different sources of variation that contribute to observed trait values, we
294 found study-level variance made a considerable contribution to the overall variance. Such study-level
295 variance is likely the result of several factors, **including differences across sites**, observer error, and
296 differences in methodologies, that are present in any dataset that pools data from diverse sources. **We**
297 **found a particularly strong effect in our height data, as the variance due to study differences exceeded**
298 **the estimated species-level variance. This suggests that models using large trait databases that fail to**
299 **separate out study from species-level variance may poorly estimate species traits, especially for species**
300 **observed in a single study, and therefore may need to account for this variance to make accurate pre-**
301 **dictions.**

302

303 Effects of phenology-trait relationships on community assembly

304 Our findings can be used to infer how changing pressures across the early growing season may affect the
305 temporal assembly of communities. Species with small cue requirements, **as exemplified by their small**
306 **responses to experimental cues and earlier budburst**, exhibit traits indicative of acquisitive growth
307 strategies that allow faster return on resource investments, like shorter heights and high LNC (Chave
308 *et al.*, 2009; Grime, 1977; Westoby, 1998). **In deciduous forests**, these traits would allow early species
309 to benefit from greater light availability in the open forest canopy in the early spring and to withstand
310 the low light conditions later in the season. In contrast, later-budbursting species had traits associated
311 with slower, more conservative, growth (Chave *et al.*, 2009; Grime, 1977; Westoby, 1998), which may
312 help them compete for the more limited soil and light resources later in the growing season. Similar
313 trait-phenology relationships have also been linked to other ecological processes and species character-
314 istics that define community structure and diversity, such as species successional position (Laube *et al.*,
315 2014), leading to the differences we observed for height and LNC in our example comparing *Alnus in-*
316 *cana* (a pioneer species) and *Quercus rubra* (a later successional species; Fig 2). **While we were able to**
317 **leverage previous work that identified the cues of budburst timing in woody species, further research is**
318 **needed to understand the primary drivers of other phenological events and plant communities, such as**
319 **in savannas or tropical forests, which may be shaped by cues other than light or seasonal temperatures.**

320

321 The trait by cue relationships that deviated from our expectations also offer novel insights into the

322 potential trade-offs between traits and environmental cues. All of our traits are associated with multiple
323 aspects of growth and function (Maynard *et al.*, 2022), and may be adaptive for reasons other than
324 those we predicted. This is the case for tree height, which is related to mechanical strength and water
325 transport (Chave *et al.*, 2009), and SLA which plays a role in light acquisition, water use, and herbivore
326 resistance (Poorter *et al.*, 2009). Since we only found a responses to chilling and photoperiod with tree
327 height, the reliance on these cues could prevent frost damage or xylem cavitation under a late spring
328 frost (Clements *et al.*, 1972; Marquis *et al.*, 2020) and influence annual cambial meristem growth (Lenz
329 *et al.*, 2016). Similarly, the lack of a relationship between SLA and temperature was surprising, given
330 that SLA can also mitigate the effects of temperature and frost risk. Differences in leaf area will also
331 cause the thickness of the leaf boundary layer to change, altering the rate of heat transfer and the risk
332 of frost damage in the spring (Lusk *et al.*, 2018). Variation in traits like SLA also reflects differences
333 in species relative growth rates or leaf longevity, and not just photosynthetic potential (Reich, 2014;
334 Westoby, 1998). Our findings thus provide novel insight into the other physiological constraints or
335 trade-offs between commonly measured traits and leaf development and highlight the complexity and
336 challenges in determining the drivers of species trait profiles.

337 Future outlook and applications

338 Incorporating phenology within broader trait syndromes could aid in forecasting species and commu-
339 nity responses to climate change. Decades of research have documented phenological advances with
340 anthropogenic climate change (Fitter & Fitter, 2002; Menzel *et al.*, 2006), however, increasing research
341 suggests a potential benefit, as plant species that shift their phenology with warming also perform
342 better (Cleland *et al.*, 2012). Our results suggest phenology-performance relationships could be driven
343 in part by a suite of traits that covary with cues to determine how responsive species are to warming.
344 Species with small cue responses are likely to have acquisitive traits, such as short heights and high
345 LNC, that allow them to grow quickly, with faster resource accumulation and possibly greater carbon
346 sequestration over a longer growing season. However, if winter temperaures continue to rise, there is
347 strong evidence that species phenology is likely to be effected by changes in chilling cues (Ettinger
348 *et al.*, 2020; Guy, 2014). In years with less extreme winter temperatures, we may observe faster accu-
349 mulation of chilling and earlier budburst as a result (Guy, 2014). But the strong relationships between
350 photoperiod and other traits we observed suggest the rate of advances in the start of the spring grow-
351 ing season may ultimately be limited by other trait-cue relationships. Understanding these complex
352 trait-phenology relationships provides insight into how climate change will alter species coexistence
353 and create novel species assemblages across communities (Rudolf, 2019; Wolkovich & Donahue, 2021).

354

355 By identifying key trait-cue relationships that shape spring growth, we can also predict how cur-
356 rent species assemblages are likely to change, potentially altering species interactions, such as plant-
357 pollinator interactions and species invasions. By applying the approach used here to other phenological
358 events, such as flowering or fruiting time, we can use existing trait data to predict how changes in
359 climate cues are likely to alter species interactions and pollination. Changes in temperature are al-
360 tering flowering phenology in woody plants, with longer flowering duration and overlap across species
361 (Pareja-Bonilla *et al.*, 2025). Applying our modelling approach to flowering traits and phenology would
362 allow us to better predict the loss of pollinator services and impacts that changes in flowering timing
363 will have on the reproductive success of native plant communities.

364

365 Finally, the insights we can gain from incorporating phenology into the existing trait frameworks can
366 be applied to restoration ecology and the management of invasive species. Invasive plants tend to have
367 earlier phenologies (Alexander & Levine, 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019) and are
368 more likely to have traits that facilitate fast growth (Fridley *et al.*, 2022). By identifying the trait-cue
369 relationships that shape budburst, we can use existing trait data from invasive species to better predict
370 whether they are likely to out compete native species by growing earlier in the season and competing
371 with native species for soil nutrients or light resources. This could lead to more effective management
372 practices and successful restoration initiatives that protect native plant communities under future
373 climate conditions.

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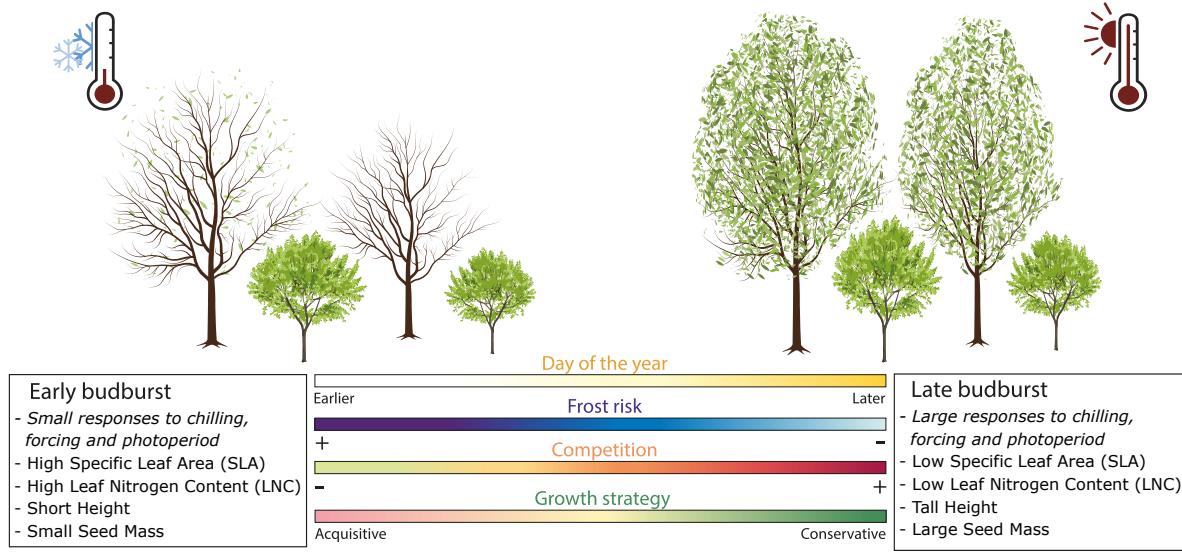


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies (Chave *et al.*, 2009; Westoby & Wright, 2006; Wright *et al.*, 2004), which may also include phenology (Sporbert *et al.*, 2022). Drawing on previous research in plants, we predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater abiotic and biotic risk but reduced competition. In contrast, we expected later-budbursting species would have traits associated with conservative growth, as they experience greater competition but a more climatically benign environment. Previous studies looking at different phenological events, such as flowering, or suites of non-woody species, have found varying relationships between traits and phenology, highlighting the complexity that may shape species timings.

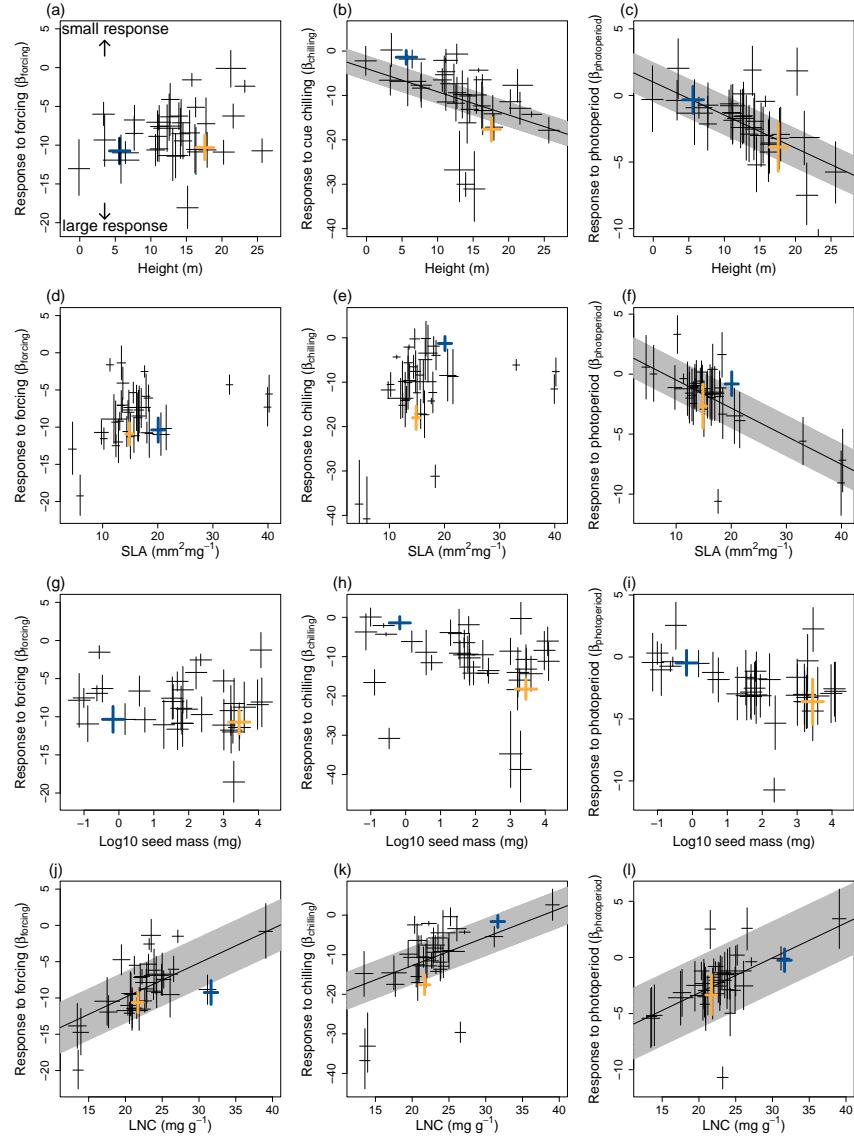


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the solid black lines depicting large linear relationships between estimated trait effects and the slopes of the cue responses (either β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$ for each trait) and the gray band the 50% uncertainty interval. As illustrated by the arrows in panel a, species with small cue responses have more positive values, while species large responses to cues have more negative values, advancing more in their budburst as cues change. Each set of crossed lines represents one species (with each line spanning the 50% uncertainty interval), depicting how well our model fits the data across all species. To illustrate the relationship between traits and the three phenological cues, we highlight two example species that differ greatly in their architecture and life history. *Alnus incana*, shown in blue, is a shorter, shrubby tree species with a growth strategy characteristic of an acquisitive species and *Quercus rubra*, shown in yellow, a taller and characteristically conservative species.²²

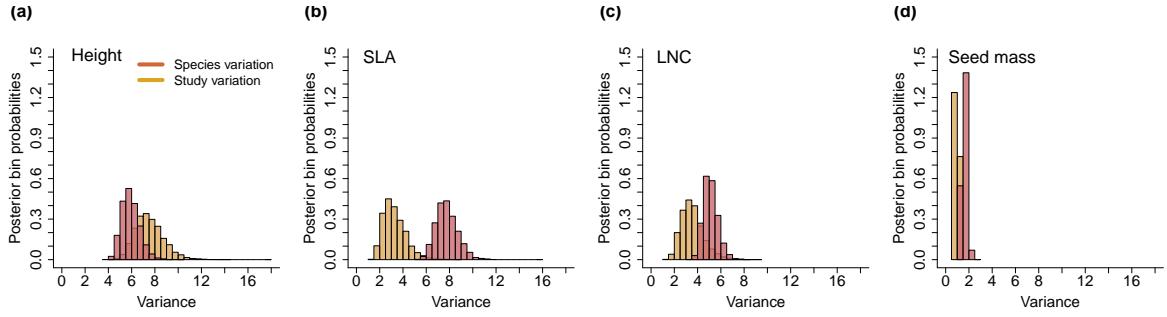


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only (a) the height model estimating greater study-level variation than species-level, while our (b) specific leaf area, (c) leaf nitrogen content, and (d) seed mass models all estimated higher species-level variation. Shown here are the posterior densities for the species-level variation, shown in red, and study-level variation, shown in yellow. For comparison, we show all x-axes spanning the minimum to maximum variances across all four traits. The histograms depict the full distribution of the study and species-level variance, where each bin is normalized by the total count of the posterior estimate.