

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 environmental triggers, **such as temperature**, changes in the 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. This framework predicts a suite of traits that may co-vary with species phenologies, but the high variability in **phenology** across environments has made testing its role within a trait framework challenging.
- ¹⁵ 2. Using a modelling framework that accommodates this variability, with phenological data from a database of controlled environment experiments and tree trait data from two major databases we tested for relationships between traits and spring phenology in trees. Specifically, we examined the cues that drive early to late 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 phenology. Species with cues that lead to earlier budburst (**small responses to experimental chilling and photoperiod**) were shorter with **higher leaf nitrogen content**, both traits related to acquisitive strategies and thus are in line with our predictions. However our one reproductive trait of seed mass showed no relationship with phenology, and other traits (e.g., specific leaf area) showed relationships in the opposite direction to our predictions.
- ²⁶ 4. Synthesis: Our findings show how spring budburst phenology partially fits within a functional trait framework of acquisitive to conservative growth strategies. Leveraging these relationships could improve predictions of how communities shift in their growth strategies alongside changing phenology

29 with future warming.

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31 Key words: Leafout, spring phenology, traits, trees, climate change, forest communities

32 **Introduction**

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

38

39 Predicting these changes requires understanding the environmental triggers of phenology, including
40 temperature or photoperiod, that cause species to start growth at different times. Groups of species
41 may have more similar responses to these environmental triggers because they are from similar func-
42 tional groups, successional stages (Laube *et al.*, 2014) or growth forms (Flynn & Wolkovich, 2018)
43 that cause them to have similar growth strategies. But current work provides limited insights into
44 the drivers of these differences across species and how they can be used to predict future changes in
45 community dynamics (Chuine *et al.*, 2016; Flynn & Wolkovich, 2018; Laube *et al.*, 2014).

46

47 Understanding these species-level differences requires considering how long-term environmental and
48 biotic pressures may select for certain species to be early or late relative to other species each year
49 (Ovaskainen *et al.*, 2013; Wolkovich & Donahue, 2021). Species that start growth early often risk high
50 tissue loss due to frost damage (Augspurger, 2009; Sakai & Larcher, 1987) or high herbivore apparen-
51 cy (Wainwright *et al.*, 2012), but benefit from higher resource availability (Hufkens *et al.*, 2012; Rathcke
52 & Lacey, 1985). In contrast, later active species face greater biotic pressures, especially from high
53 competition for resources (Lopez *et al.*, 2008; Wolkovich & Ettinger, 2014). Such differences could
54 shape physical and phenological traits related to species growth strategies and fitness (Violle *et al.*,
55 2007). Species leaf and wood traits can reflect trade-offs between the construction costs and longevity
56 of tissue (Reich *et al.*, 1997; Wright *et al.*, 2004), with cheaper-to-construct tissue being associated
57 with faster growth rates (Westoby & Wright, 2006; Wright *et al.*, 2004). Previous studies have high-
58 lighted associations between trade-offs in phenology with structural and leaf traits in both woody
59 (Wang *et al.*, 2021; Wolkovich & Ettinger, 2014) and herbaceous species (Sporbert *et al.*, 2022), and
60 hypothesized that phenology may fit within the acquisitive (fast) to more conservative (slow) growth
61 strategies associated with existing trait frameworks (Chave *et al.*, 2009; Wright *et al.*, 2004, Fig 1).

62

63 Globally, gradients from acquisitive to conservative strategies appear common and form the foundation
64 of the leaf and wood economic spectra (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby &
65 Wright, 2006; Wright *et al.*, 2004), but they make limited predictions of trait variability (Violette *et al.*,
66 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving
67 the relationships between broader trait syndromes and phenology largely unknown. Understanding
68 these relationships, however, can improve forecasts of community dynamics and responses to climate
69 change. Most studies have examined the relationship between traits and phenology for a single or
70 limited number of sites (as reviewed by Wolkovich & Cleland, 2014; Wolkovich & Donahue, 2021),
71 though recent studies have explored these relationships across sites for herbaceous species (Rauschkolb
72 *et al.*, 2024; Sporbert *et al.*, 2022). At more local spatial scales the problem of disentangling the local
73 environmental triggers that shape traits (and vary across sites) and cause variation within or across
74 species, can be more easily ignored in some systems (but see Albert *et al.*, 2011; Siefert *et al.*, 2015;
75 Zuleta *et al.*, 2022, for discussion of systems with high trait variation within one species, site, or year).
76 Adding phenology to broader trait frameworks therefore becomes more complex as high levels of vari-
77 ation occur across larger spatial and temporal scales.

78

79 Recent climate change has highlighted how variable plant phenology is when observed over time and
80 space across different species (Rudolf, 2019; Vitasse, 2013; Yu *et al.*, 2010), with many studies docu-
81 menting how quickly phenology can shift with warming (Fitter & Fitter, 2002; Menzel *et al.*, 2006). But
82 experiments conducted under controlled environments have shown that it is possible to consistently de-
83 fine early to late phenology from the known underlying cues (Chuine & Cour, 1999; Flynn & Wolkovich,
84 2018; Harrington & Gould, 2015). This work has found that early species have small responses in ex-
85 periments to the three major cues that determine woody plant budburst: forcing (accumulated warm
86 temperatures usually in the spring), chilling (cool temperatures usually accumulated in the fall and
87 winter), and photoperiod, while later species generally have larger responses to these cues (Flynn &
88 Wolkovich, 2018; Laube *et al.*, 2014). These responses suggest early species require lower amounts of
89 forcing, chilling and shorter photoperiods to budburst, while species that budburst later require higher
90 amounts of forcing, chilling and longer photoperiods (see Flynn & Wolkovich, 2018, for further details).
91 The consistency of these relationships, alongside increasing evidence that intra-specific variation in tree
92 spring phenology is low given the same climate (Aitken & Bemmels, 2016; Zeng & Wolkovich, 2024),
93 allows us to estimate early to later active species across plant communities and diverse species assem-
94 blages.

95

96 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-

nology into functional trait research. In addition to how well we understand the environmental cues that lead to early versus late budburst, in many forests strong gradients in frost risk or nutrient availability from the start to the end of the spring growing season likely shape other traits (Fig 1). These gradients should drive differences in growth strategies of early versus late species, and thus be related to differences in traits (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). We would predict such species to exhibit early budburst phenology. Canopy species that budburst later when competition for soil resources is greater, would then have traits associated with conservative growth, being 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 taller and more conservative species produce larger, better provisioned seeds (Díaz *et al.*, 2016).

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 the OS-
142 PREE database and initially aimed to use data for the 234 species used in Morales-Castilla *et al.* (2024).

143

144 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020; Maitner
145 *et al.*, 2018), both of which are large trait databases that include plant trait observations across many
146 individuals, species and studies (Table S1) and are available through slightly different mechanisms.
147 BIEN is accessible via the BIEN R package (here we used v. 1.2.5, Maitner *et al.*, 2018), and TRY is
148 requested. **We obtained data from the BIEN databases on 5 December 2018 and the TRY data on 10**
149 **April 2019.** We initially searched for trait data on the subset of 234 OSPREE species used in Morales-
150 Castilla *et al.* (2024). From BIEN, this resulted in 94 of the 234 species available in the database, for
151 which there were 13 unique traits. From the TRY database we received data for 10 unique traits for
152 96 of the 234 requested species (Kattge *et al.*, 2020). As we were interested in the trait-phenology re-
153 lationships of adult trees we subsetted the available data to **remove any observations denoted as being**
154 **from juvenile individuals or with heights less than 2 m (following Natural Resources Canada, 2020,** we
155 **assume this removes most individuals that were saplings when measured; analyses using an alternative**
156 **cut-off of 1.37 m showed similar results).** We further removed all data from manipulative experiments
157 or from plants growing in non-natural habitats. We then grouped trait values where appropriate, for
158 example pooling trait values for specific leaf area (SLA) with those denoted as ‘SLA with petioles’,
159 and ‘SLA without petioles’ in our analysis (see Table S1). We also removed data that was duplicated
160 in both the TRY and BIEN datasets ($n = 434,905$). For a full depiction of our data cleaning process
161 and decisions see Fig. S1.

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. S2). 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 (Fig S3, 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). Species-specific trait values (α_{trait} , described below) have a separate interaction with the three cues (β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$) that determine 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

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

(3)

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

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

$$\boldsymbol{\alpha}_{\text{study}} = \begin{bmatrix} \alpha_{\text{study}_1} \\ \alpha_{\text{study}_2} \\ \vdots \\ \alpha_{\text{study}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \text{Normal}(0, \sigma_{\text{study}}^2) \quad (5)$$

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 parameters for species and
201 study-level (α_{species} and α_{study} , respectively), from that overall mean trait value. The σ_m^2 parameter
202 is the measurement error for the observed trait values, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and
203 study-level variances in trait values. Of these parameters, we combine the mean trait value ($\alpha_{\text{grand trait}}$)
204 with species-specific effects from the mean trait value (α_{species}) to form $\boldsymbol{\alpha}_{\text{trait}}$, which is shared by the
205 phenology sub-model.

206 Phenology sub-model

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

$$Y_{\text{pheno}_{k,g}} \sim \text{Normal}(\mu_{k,g}, \sigma_d^2) \quad (6)$$

²¹³ with

$$\mu_{k,g} = \alpha_{\text{pheno}_k} + \beta_{\text{chilling}_k} \cdot c_g + \beta_{\text{forcing}_k} \cdot f_g + \beta_{\text{photoperiod}_k} \cdot p_g \quad (7)$$

²¹⁴ and

$$\beta_{\text{chilling}_k} = \alpha_{\text{chilling}_k} + \beta_{\text{trait.chilling}} \cdot \alpha_{\text{trait}_k} \quad (8)$$

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

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

²¹⁵ where α_{pheno_k} , $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$ are elements of the normal random vectors:

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

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

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

$$\boldsymbol{\alpha}_{\text{photoperiod}} = \begin{bmatrix} \alpha_{\text{photoperiod}_1} \\ \alpha_{\text{photoperiod}_2} \\ \vdots \\ \alpha_{\text{photoperiod}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{photoperiod}} \sim \text{Normal}(0, \sigma_{\text{photoperiod}}^2) \quad (12)$$

(13)

²¹⁶ The model partitions day of budburst for species (k) as a combination of the overall mean day of
²¹⁷ budburst without the influence of chilling, forcing, or photoperiod treatments ($\alpha_{\text{pheno},k}$, normally dis-
²¹⁸ tributed with a mean of μ_{pheno} and variance σ_{pheno}^2) combined with the effects of treatments both de-
²¹⁹ pendingent and independent of trait values. The parameters $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$ represent
²²⁰ the trait-independent responses of species k to chilling, forcing and photoperiod treatments respectively,
²²¹ each with an associated mean (μ_{chilling} , μ_{forcing} , $\mu_{\text{photoperiod}}$) and variance ($\sigma_{\text{chilling}}^2$, $\sigma_{\text{forcing}}^2$, $\sigma_{\text{photoperiod}}^2$)

222 across species. The shared parameter between the trait and phenology sub-model, α_{trait_k} , represents
223 the effect of the species trait value on its responses to chilling ($\beta_{\text{trait.chilling}}$), forcing ($\beta_{\text{trait.forcing}}$), and
224 photoperiod ($\beta_{\text{trait.photoperiod}}$). Finally, our model provides an estimate of σ_d^2 , which is the variance
225 arising from measurement error for the observed day of budburst.

226

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

238 Results

239 Across traits, height, SLA, and LNC were related to one or more environmental cue ($\beta_{\text{chilling}_k}$, β_{forcing_k} ,
240 or $\beta_{\text{photoperiod}_k}$, Fig 2 a-f & j-l), with only LNC showing a relationship with all three cues (Fig. 2 j-l).
241 As we predicted, height was negatively related to chilling ($\beta_{\text{chilling}_k}$) and photoperiod ($\beta_{\text{photoperiod}_k}$),
242 with taller species having larger responses to high chilling and longer photoperiod conditions (-0.5 m
243 per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized pho-
244 toperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). These large responses in the timing of budburst (as
245 estimated by $\mu_{k,g}$), in response to chilling and photoperiod treatments, likely reflect that taller tree
246 species require more chilling and forcing to budburst (conditions that are often met later in the grow-
247 ing season), while shorter species budburst earlier under the lower chilling and photoperiod conditions
248 that occur earlier in the spring. In contrast, seed mass had a negligible relationship with budburst and
249 all three cues (Fig. 2 g-i & Table S3).

250

251 Of the studied leaf traits, we found that SLA related to photoperiod ($\beta_{\text{photoperiod}_k}$, -0.2 mm²/mg per
252 standardized photoperiod; 90% UI: -0.5, 0.0, Table S4), but with larger responses to longer photope-
253 riodes for high SLA species (Fig. 2 f). But we did not find strong responses to chilling ($\beta_{\text{chilling}_k}$) or
254 forcing treatments (β_{forcing_k} , Fig. 2 d & e). The relationship between LNC and budburst cues, was

in line with our predictions, with high LNC species being less responsive to chilling (0.7 mg/g per standardized chilling; 90% UI: 0.2, 1.2, Table S5), forcing (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.8), and photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6, Fig 2 j-l). This suggests that species that produce leaves with high nitrogen content, which relates generally to high photosynthetic rates and acquisitive growth, are likely to budburst under early spring conditions (based on the relationships between this trait and environmental cues).

261

We found that the species-level variance across traits were comparable to, or greater than, variance across studies (using our model that partitions the measurement error in the trait values from variance from species and study-level effects; Fig 3). For height, variance across studies (σ_{study}^2) was greater (7.5 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). But for seed mass and LNC, study-level variance was less than that of the species-level variance, with variance 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 species-level variance respectively and for LNC 3.6 mg g⁻¹ (90% UI: 2.2, 5.3) for study-level variance and 5.1 mg g⁻¹ for the species-level variance (90% UI: 2.2, 5.3, Fig 3c and d). The difference between species and study-level variance was greatest for SLA, with the estimate of 3.3 mm² mg⁻¹ (90% UI: 2, 5.1) for study-level variance being approximately half that of the estimated species-level variance of 7.8 mm² mg⁻¹ (90% UI: 6.4, 9.4, Fig 3b).

273

274 Discussion

We found several species traits influenced the timing of budburst in response to one or more of the three primary cues of spring phenology. In general, early species (those with smaller responses to chilling, forcing and photoperiod in experiments Flynn & Wolkovich, 2018; Laube *et al.*, 2014), had relationships with several traits associated with fast and acquisitive growth strategies. Later budbursting species (those with larger responses to chilling, forcing and photoperiod in experiments Flynn & Wolkovich, 2018; Laube *et al.*, 2014), however, had traits indicative of conservative, slower growth strategies. Specifically, the trait effects of height and LNC on the timing of budburst followed well-established gradients in growth strategies predicted by functional trait frameworks (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004). But in the case of SLA, its relationship to spring phenological cues was opposite of our predictions. Species with high SLA—as a result of having the larger, thin leaves, with low investment in leaf mass, and generally indicative of acquisitive growth strategies—had larger responses to photoperiod. Seed mass, which was our one reproductive trait, showed the weakest response to all three cues, suggesting no connection

288 between seed mass and spring phenology. Our results are in line with previous studies conducted
289 at more local scales that found large relationships between height and species phenology (Osada &
290 Hiura, 2019; Seiwa, 1999), as well as findings from large-scale research which found no relationship
291 between phenology and seed mass in woody plants (Bolmgren & D. Cowan, 2008; Ettinger *et al.*, 2018).

292

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

303

304 Effects of phenology-trait relationships on community assembly

305 Our findings suggest that changing pressures across the early growing season may affect the temporal
306 assembly of communities. Early-active species had traits indicative of acquisitive growth strategies
307 that allow faster return on resource investments, like shorter heights and high LNC (Chave *et al.*,
308 2009; Grime, 1977; Westoby, 1998). In deciduous forests, these traits would allow early-budbursting
309 species to benefit from greater light availability in the open forest canopy in the early spring and
310 to withstand the low light conditions later in the season. In contrast, later-budbursting species had
311 traits associated with slower, more conservative growth (Chave *et al.*, 2009; Grime, 1977; Westoby,
312 1998), which may help them compete for the more limited soil and light resources later in the grow-
313 ing season. Similar trait-phenology relationships have also been linked to other ecological processes
314 and species characteristics that define community structure and diversity, such as species successional
315 position (Laube *et al.*, 2014), leading to the differences we observed for height and LNC in our exam-
316 ple comparing *Alnus incana* (a pioneer species) and *Quercus rubra* (a later successional species; Fig 2).

317

318 While our study focuses mainly on early versus later spring phenology, our approach and findings may
319 provide insights into potential trade-offs between traits and the phenological cues that underlie early
320 versus late budburst timing. This is particularly true for the relationships that deviated from our ex-

321 pectations. Our finding that tree height (which is related to mechanical strength and water transport
322 (Chave *et al.*, 2009)) was associated with chilling and photoperiod cues (but not forcing) suggests that
323 species use of these two cues may be tied to preventing frost damage or xylem cavitation under a late
324 spring frost (Clements *et al.*, 1972; Marquis *et al.*, 2020). Similarly, the lack of a relationship between
325 SLA and temperature cues (chilling and forcing) was surprising, given that differences in leaf area can
326 also affect heat transfer, such that thicker leaves with higher SLA may have an increased risk of frost
327 damage (Lusk *et al.*, 2018). Many different traits may contribute to decreasing the risk of frost damage
328 (e.g., trichome density, cuticle type, Sakai & Larcher (1987)) and thus a composite of many traits may
329 give better insights into links between traits and frost damage. Further, well-studied traits, such as
330 SLA, often reflect multiple aspects of growth and function (Maynard *et al.*, 2022), and may be adaptive
331 for reasons other than those we predicted. Variation in SLA can also capture differences in species rela-
332 tive growth rates or leaf longevity, and not just photosynthetic potential (Reich, 2014; Westoby, 1998).

333

334 Our findings highlight the complexity and challenges in determining the drivers of species trait profiles
335 to understand how phenology fits within a functional trait framework, but expanding to more diverse
336 species and ecosystems could help. Major trait frameworks today, such as the leaf and wood economic
337 spectra, generally emerged from studies across highly different ecosystems (Chave *et al.*, 2009; Díaz
338 *et al.*, 2016), while relationships within certain habitats or regions often show much weaker relation-
339 ships (Funk & Cornwell, 2013; Messier *et al.*, 2017). Our focus on budburst timing for temperate
340 woody species leverages the largest databases of traits and phenological experiments, but it still has a
341 limited sample size of species and focuses on only one major ecosystem, which is primarily controlled
342 by temperature (Chapin *et al.*, 2011; Kattge *et al.*, 2020). Extending into other types of plant com-
343 munities controlled by other factors, such as in savannas or tropical forests, which may be shaped by
344 cues other than light or seasonal temperatures, could greatly expand how we understand the role of
345 phenology within trait syndromes.

346

347 Future outlook and applications

348 Incorporating phenology within broader trait syndromes could aid in forecasting species and commu-
349 nity responses to climate change. Decades of research have documented phenological advances with
350 anthropogenic climate change (Fitter & Fitter, 2002; Menzel *et al.*, 2006), however, increasing research
351 suggests a potential benefit to earlier phenologies, as plant species that shift their phenology with
352 warming also perform better (Cleland *et al.*, 2012). Our results suggest phenology-performance rela-
353 tionships could be driven in part by a suite of traits that covary with phenology to determine how

354 responsive species are to warming. Our results suggest that early-active species—which other studies
355 have found to also be those that advance more with warming (Fuccillo Battle *et al.*, 2022; Menzel *et al.*,
356 2020)—are likely to have acquisitive traits (such as shorter heights and high LNC) that allow them to
357 grow quickly, accumulate resources faster and possibly have greater carbon sequestration over a longer
358 growing season. How much these relationships continue in the future also depends on how warming
359 in the winter and spring continues, and the complexities of exactly how chilling and photoperiod cues
360 operate, which is an area of active debate. Studies to date suggest chilling may decrease in most places
361 with warming (Guy, 2014; Wang *et al.*, 2022) while research on photoperiod has variously suggested
362 photoperiod cues could stall responses for some later-active species (Ettinger *et al.*, 2021) or have at
363 most a relatively small effect (Ettinger *et al.*, 2021, 2020).

364

365 The insight that understanding trait-phenology relationships provides regarding how climate change
366 may alter species coexistence and create novel species assemblages across communities (Rudolf, 2019;
367 Wolkovich & Donahue, 2021) could have important implication for restoration ecology, including for
368 pollinator communities and invasive plant management. For example, applying our approach to flower
369 and fruit traits may help link plant phenology to pollinator communities, with the opportunity to better
370 predict shifts in phenology and pollination services with climate change (Leclerc *et al.*, 2024; Pareja-
371 Bonilla *et al.*, 2025). Opportunities to better manage invasive plants may come from their tendency
372 to have earlier phenologies (Alexander & Levine, 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019)
373 and traits that facilitate fast growth (Fridley *et al.*, 2022). By identifying the trait-cue relationships
374 that shape phenology, we could use existing trait data from invasive species to better predict whether
375 they are likely to out-compete native species by growing earlier in the season and drawing down soil
376 nutrients and/or light resources that later-active native species may rely on (Buonaiuto & Wolkovich,
377 2023; Dawson-Glass *et al.*, 2025; Hess *et al.*, 2019; Weidlich *et al.*, 2021). This could lead to better
378 identifying which species may be of most concern and thus lead to effective management practices that
379 protect native plant communities under future climate conditions.

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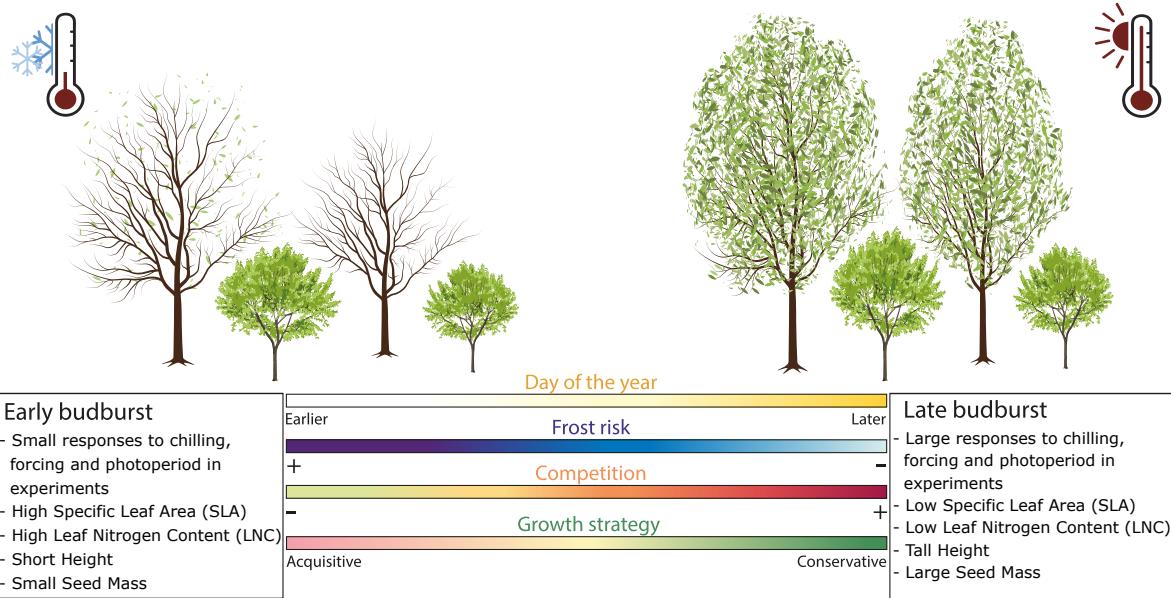


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies (Chave *et al.*, 2009; Westoby & Wright, 2006; Wright *et al.*, 2004), which may also include phenology. Drawing on previous research in plants, we predicted that early-budbursting species 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 are more likely to 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 (König *et al.*, 2018; Sun & Frelich, 2011), have found varying relationships between traits and phenology, highlighting the complexity that may shape species timings.

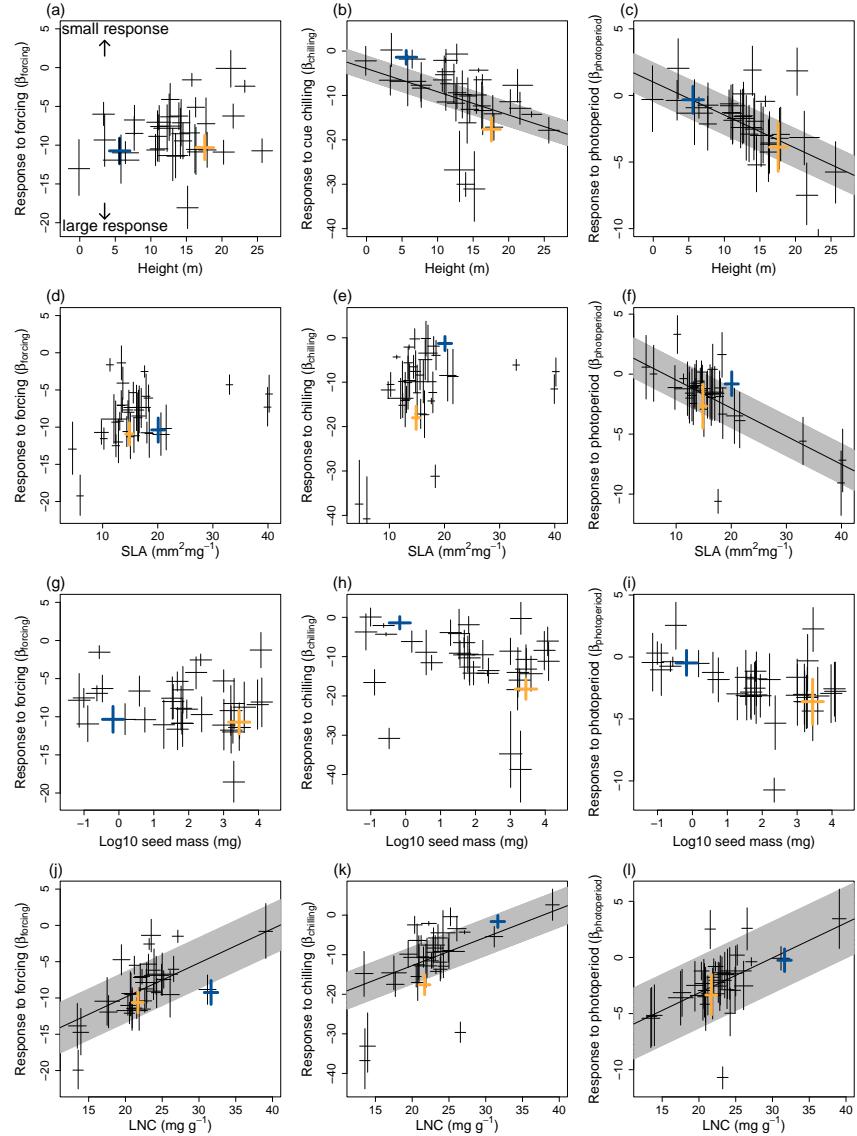


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the solid black lines showing the relationship between estimated trait effects and the responses to phenological cues (either β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$ for each trait, shown only where this relationship does not include zero within the 90% UI, and with the gray band the 50% uncertainty interval). As illustrated by the arrows in panel a, species with smaller responses to cues (chilling, forcing, photoperiod) have more positive values, while species with larger responses to cues have more negative values. 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 growth forms and life history. *Alnus incana*, shown in blue,²³ 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.

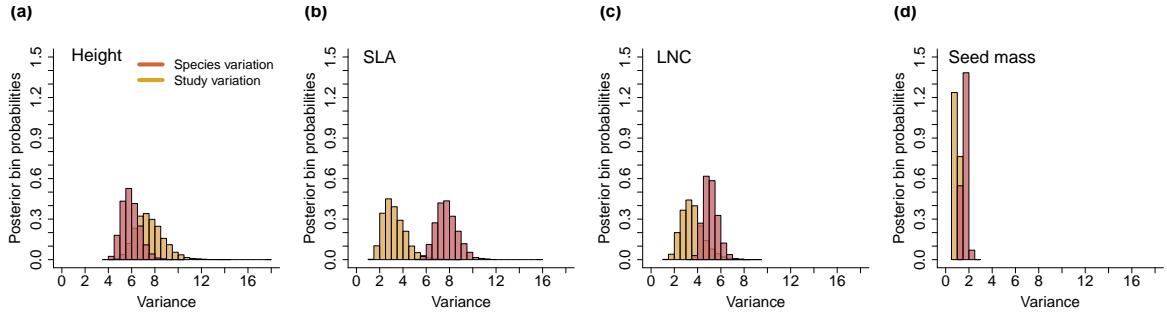


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only (a) the height model estimating greater study-level variation than species-level, while our (b) specific leaf area, (c) leaf nitrogen 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.