

¹ Budburst timing within a functional trait framework

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²⁸ Running title: Budburst responses associated with traits

²⁹ Summary

³⁰ 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.

⁴⁰ 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).

⁴⁵ 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.

⁵¹ 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 with future warming.

⁵⁵

⁵⁶ Key words: Leafout, spring phenology, traits, trees, climate change, forest communities

57 **Introduction**

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

63

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

71

72 Understanding these species-level differences requires considering how long-term environmental and
73 biotic pressures may select for certain species to be early or late relative to other species each year
74 (Ovaskainen *et al.*, 2013; Wolkovich & Donahue, 2021). Species that start growth early often risk high
75 tissue loss due to frost damage (Augspurger, 2009; Sakai & Larcher, 1987) or high herbivore apparen-
76 cy (Wainwright *et al.*, 2012), but benefit from higher resource availability (Hufkens *et al.*, 2012; Rathcke
77 & Lacey, 1985). In contrast, later active species face greater biotic pressures, especially from high
78 competition for resources (Lopez *et al.*, 2008; Wolkovich & Ettinger, 2014). Such differences could
79 shape physical and phenological traits related to species growth strategies and fitness (Violle *et al.*,
80 2007). Species leaf and wood traits can reflect trade-offs between the construction costs and longevity
81 of tissue (Reich *et al.*, 1997; Wright *et al.*, 2004), with cheaper-to-construct tissue being associated
82 with faster growth rates (Westoby & Wright, 2006; Wright *et al.*, 2004). Previous studies have high-
83 lighted associations between trade-offs in phenology with structural and leaf traits in both woody
84 (Wang *et al.*, 2021; Wolkovich & Ettinger, 2014) and herbaceous species (Sporbert *et al.*, 2022), and
85 hypothesized that phenology may fit within the acquisitive (fast) to more conservative (slow) growth
86 strategies associated with existing trait frameworks (Chave *et al.*, 2009; Wright *et al.*, 2004, Fig 1).

87

88 Globally, gradients from acquisitive to conservative strategies appear common and form the foundation
89 of the leaf and wood economic spectra (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby &
90 Wright, 2006; Wright *et al.*, 2004), but they make limited predictions of trait variability (Violle *et al.*,

91 As a result, highly variable traits like phenology are often excluded from trait studies, leaving
92 the relationships between broader trait syndromes and phenology largely unknown. Understanding
93 these relationships, however, can improve forecasts of community dynamics and responses to climate
94 change. Most studies have examined the relationship between traits and phenology for a single or
95 limited number of sites (as reviewed by Wolkovich & Cleland, 2014; Wolkovich & Donahue, 2021),
96 though recent studies have explored these relationships across sites for herbaceous species (Rauschkolb
97 *et al.*, 2024; Sporbert *et al.*, 2022). At more local spatial scales the problem of disentangling the local
98 environmental triggers that shape traits (and vary across sites) and cause variation within or across
99 species, can be more easily ignored in some systems (but see Albert *et al.*, 2011; Siefert *et al.*, 2015;
100 Zuleta *et al.*, 2022, for discussion of systems with high trait variation within one species, site, or year).
101 Adding phenology to broader trait frameworks therefore becomes more complex as high levels of vari-
102 ation occur across larger spatial and temporal scales.

103

104 Recent climate change has highlighted how variable plant phenology is when observed over time and
105 space across different species (Rudolf, 2019; Vitasse, 2013; Yu *et al.*, 2010), with many studies docu-
106 menting how quickly phenology can shift with warming (Fitter & Fitter, 2002; Menzel *et al.*, 2006).
107 But experiments conducted under controlled environments have shown that it is possible to consist-
108 ently define early to late phenology from the known underlying cues (Chuine & Cour, 1999; Flynn
109 & Wolkovich, 2018; Harrington & Gould, 2015). This work has found that early species have small
110 responses in experiments to the three major cues that determine woody plant budburst: forcing (accu-
111 mulated warm temperatures usually in the spring), chilling (cool temperatures usually accumulated in
112 the fall and winter), and photoperiod, while later species generally have larger responses to these cues
113 (Flynn & Wolkovich, 2018; Laube *et al.*, 2014). These responses suggest early species require lower
114 amounts of forcing, chilling and shorter photoperiods to budburst, while species that budburst later
115 require higher amounts of forcing, chilling and longer photoperiods (see Flynn & Wolkovich, 2018,
116 for further details). The consistency of these relationships, alongside increasing evidence that intra-
117 specific variation in tree spring phenology is low given the same climate (Aitken & Bemmels, 2016;
118 Zeng & Wolkovich, 2024), allows us to estimate early to later active species across plant communities
119 and diverse species assemblages.

120

121 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-
122 nology into functional trait research. In addition to how well we understand the environmental cues
123 that lead to early versus late budburst, in many forests strong gradients in frost risk or nutrient avail-
124 ability from the start to the end of the spring growing season likely shape other traits (Fig 1). These
125 gradients should drive differences in growth strategies of early versus late species, and thus be related

126 to differences in traits (Horbach *et al.*, 2023; Wang *et al.*, 2021), such as the differences in traits that
127 facilitate frost tolerance versus avoidance (Lenz *et al.*, 2013; Sakai & Larcher, 1987) or in herbivory
128 (Coley *et al.*, 1985). Broadly we predict acquisitive species to be shorter, with leaf traits favorable to
129 the low light conditions of the understory later in the growing season—that is, they should produce
130 leaves with high specific leaf area (SLA) and leaf nitrogen content (LNC) (Díaz *et al.*, 2016; Reich
131 *et al.*, 1997; Wright *et al.*, 2004). We would predict such species to exhibit early budburst phenology.
132 Canopy species that budburst later when competition for soil resources is greater, would then have
133 traits associated with conservative growth, being taller with denser wood (Chave *et al.*, 2009; Laughlin
134 *et al.*, 2010) and leaf traits suited for the higher light conditions of the canopy (low SLA and low
135 LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative continuum,
136 as acquisitive species produce smaller seeds and taller and more conservative species produce larger,
137 better provisioned seeds (Díaz *et al.*, 2016).

138

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

148

149 Methods

150 We merged three major databases for our analysis. We gathered phenological data from the OSPREE
151 database (Ettinger *et al.*, 2020), which contains data from experiments of dormant plant tissue from
152 woody plants growing either in the field or in controlled environments. From OSPREE, we used the
153 available budburst data for temperate tree species from studies that each manipulated forcing, chilling
154 and photoperiod. We originally constructed the OSPREE database by performing a systematic review
155 of the literature, and searched both ISI Web of Science and Google Scholar using the following two
156 search terms:

157

- 158 1. TOPIC = (budburst OR leafout) AND (photoperiod or daylength) AND temperature*

¹⁵⁹ 2. TOPIC = (budburst OR leafout) AND dorman*

¹⁶⁰

¹⁶¹ We then scraped the data from all articles reporting experiments that manipulated both photoperiod
¹⁶² and/or temperature cues of woody species budburst, leafout, or flowering phenology, and for which
¹⁶³ there was a quantifiable response to each cue. We updated this database in July 2019 reviewing all
¹⁶⁴ new articles found using the previous search terms. Additional details on the methods used to as-
¹⁶⁵ semble, clean, and update this database are discussed by Ettinger *et al.* (2020) and Morales-Castilla
¹⁶⁶ *et al.* (2024). For the purpose of this study, we obtained a subset of the budburst data from the OS-
¹⁶⁷ PREE database and initially aimed to use data for the 234 species used in Morales-Castilla *et al.* (2024).

¹⁶⁸

¹⁶⁹ We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020; Maitner
¹⁷⁰ *et al.*, 2018), both of which are large trait databases that include plant trait observations across many
¹⁷¹ individuals, species and studies (Table S1) and are available through slightly different mechanisms.
¹⁷² BIEN is accessible via the BIEN R package (here we used v. 1.2.5, Maitner *et al.*, 2018), and TRY is
¹⁷³ requested. We obtained data from the BIEN databases on 5 December 2018 and the TRY data on 10
¹⁷⁴ April 2019. We initially searched for trait data on the subset of 234 OSPREE species used in Morales-
¹⁷⁵ Castilla *et al.* (2024). From BIEN, this resulted in 94 of the 234 species available in the database, for
¹⁷⁶ which there were 13 unique traits. From the TRY database we received data for 10 unique traits for
¹⁷⁷ 96 of the 234 requested species (Kattge *et al.*, 2020). As we were interested in the trait-phenology re-
¹⁷⁸ lationships of adult trees we subsetted the available data to remove any observations denoted as being
¹⁷⁹ from juvenile individuals or with heights less than 2 m (following Natural Resources Canada, 2020, we
¹⁸⁰ assume this removes most individuals that were saplings when measured; analyses using an alternative
¹⁸¹ cut-off of 1.37 m showed similar results). We further removed all data from manipulative experiments
¹⁸² or from plants growing in non-natural habitats. We then grouped trait values where appropriate, for
¹⁸³ example pooling trait values for specific leaf area (SLA) with those denoted as ‘SLA with petioles’,
¹⁸⁴ and ‘SLA without petioles’ in our analysis (see Table S1). We also removed data that was duplicated
¹⁸⁵ in both the TRY and BIEN datasets ($n = 434,905$). For a full depiction of our data cleaning process
¹⁸⁶ and decisions see Fig. S1.

¹⁸⁷

¹⁸⁸ For our analysis, we only included species for which we had a complete trait profile (i.e., all traits
¹⁸⁹ measured for all species). For this profile, we initially considered six commonly measured traits: SLA,
¹⁹⁰ leaf dry matter content (LDMC), height, seed mass, stem specific density (SSD), and LNC. There were
¹⁹¹ 26 species that had at least one trait measurement for each of these traits. We then used a principle
¹⁹² component analysis (PCA) to identify which (if any) of our six traits were strongly correlated. The
¹⁹³ first principal component explained 32% of variation while the second explained 24.2% of the variation,

194 with high correlations between SLA and LDMC, and between height and SSD (Fig. S2). By excluding
 195 the trait from each of these highly correlated trait pairs with the least amount of data (specifically
 196 LDMC and SSD) we were able to increase the number of species in our dataset from the 26 species
 197 with complete data for six traits, to 37 species with complete data for four traits. The data for these 37
 198 species were from 24 unique studies (Fig S3, sample sizes: height $n = 47781$, seed mass $n = 281$, LNC
 199 $n = 3853$, SLA $n = 7656$). Our dataset of tree height included 13 species that were measured over
 200 19 times more frequently than most other species. We therefore subsampled the height measurements
 201 of these 13 most frequently measured trees to reduce their influence on our height model, randomly
 202 sampling 3000 height measurements for each individual species while including all height data for the
 203 remaining, less frequently measured, 24 species. This subsampling was not required for any of the
 204 other traits included in our study.

205 **Joint model of trait and phenology**

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

216 **Trait sub-model**

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

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

²²² with

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

(3)

²²³ where $\alpha_{\text{species}_i}$ and α_{study_j} are elements of the normal random vectors:

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

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

²²⁴ Mathematically, the latent parameter or overall mean trait value ($\alpha_{\text{grand trait}}$) represents a trait value
²²⁵ that is independent of the other parameters in the model, namely the parameters for species and
²²⁶ study-level (α_{species} and α_{study} , respectively), from that overall mean trait value. The σ_m^2 parameter
²²⁷ is the measurement error for the observed trait values, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and
²²⁸ study-level variances in trait values. Of these parameters, we combine the mean trait value ($\alpha_{\text{grand trait}}$)
²²⁹ with species-specific effects from the mean trait value (α_{species}) to form $\boldsymbol{\alpha}_{\text{trait}}$, which is shared by the
²³⁰ phenology sub-model.

²³¹ Phenology sub-model

²³² Our phenology sub-model describes the processes that determine the relationships between traits and
²³³ environmental cues and their effects on phenological observations for 1 to n species, specifically the
²³⁴ timing (day of year) of budburst from the updated OSPREE dataset. The observations of budburst
²³⁵ for species k under g treatment levels of each cue (c_g, f_g, p_g , for chilling, forcing and photoperiod
²³⁶ treatments respectively, which we z -scored to allow direct comparison between cues) is represented by
²³⁷ parameter $Y_{\text{pheno}_{k,g}}$, and assumed to follow a normal distribution:

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

²³⁸ with

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

²³⁹ and

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

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

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

²⁴⁰ where α_{pheno_k} , $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$ are elements of the normal random vectors:

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

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

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

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

(13)

²⁴¹ The model partitions day of budburst for species (k) as a combination of the overall mean day of
²⁴² budburst without the influence of chilling, forcing, or photoperiod treatments ($\alpha_{\text{pheno},k}$, normally dis-
²⁴³ tributed with a mean of μ_{pheno} and variance σ_{pheno}^2) combined with the effects of treatments both de-
²⁴⁴ pending and independent of trait values. The parameters $\alpha_{\text{chilling}_k}$, $\alpha_{\text{forcing}_k}$, and $\alpha_{\text{photoperiod}_k}$ represent
²⁴⁵ the trait-independent responses of species k to chilling, forcing and photoperiod treatments respectively,
²⁴⁶ each with an associated mean (μ_{chilling} , μ_{forcing} , $\mu_{\text{photoperiod}}$) and variance ($\sigma_{\text{chilling}}^2$, $\sigma_{\text{forcing}}^2$, $\sigma_{\text{photoperiod}}^2$)
²⁴⁷ across species. The shared parameter between the trait and phenology sub-model, α_{trait_k} , represents
²⁴⁸ the effect of the species trait value on its responses to chilling ($\beta_{\text{trait.chilling}}$), forcing ($\beta_{\text{trait.forcing}}$), and
²⁴⁹ photoperiod ($\beta_{\text{trait.photoperiod}}$). Finally, our model provides an estimate of σ_d^2 , which is the variance

250 arising from measurement error for the observed day of budburst.

251

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

263 Results

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

275

276 Of the studied leaf traits, we found that SLA related to photoperiod ($\beta_{photoperiod_k}$, -0.2 mm²/mg per
277 standardized photoperiod; 90% UI: -0.5, 0.0, Table S4), but with larger responses to longer photope-
278 riodes for high SLA species (Fig. 2 f). But we did not find strong responses to chilling ($\beta_{chilling_k}$) or
279 forcing treatments ($\beta_{forcing_k}$, Fig. 2 d & e). The relationship between LNC and budburst cues, was
280 in line with our predictions, with high LNC species being less responsive to chilling (0.7 mg/g per
281 standardized chilling; 90% UI: 0.2, 1.2, Table S5), forcing (0.5 mg/g per standardized forcing; 90%
282 UI: 0.1, 0.8), and photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6, Fig 2 j-l).

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

286

287 We found that the species-level variance across traits were comparable to, or greater than, variance
288 across studies (using our model that partitions the measurement error in the trait values from variance
289 from species and study-level effects; Fig 3). For height, variance across studies (σ_{study}^2) was greater
290 (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
291 3a). But for seed mass and LNC, study-level variance was less than that of the species-level variance,
292 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)
293 for study-level and species-level variance respectively and for LNC 3.6 mg g⁻¹ (90% UI: 2.2, 5.3) for
294 study-level variance and 5.1 mg g⁻¹ for the species-level variance (90% UI: 2.2, 5.3, Fig 3c and d).
295 The difference between species and study-level variance was greatest for SLA, with the estimate of 3.3
296 mm² mg⁻¹ (90% UI: 2, 5.1) for study-level variance being approximately half that of the estimated
297 species-level variance of 7.8 mm² mg⁻¹ (90% UI: 6.4, 9.4, Fig 3b).

298

299 Discussion

300 We found several species traits influenced the timing of budburst in response to one or more of the
301 three primary cues of spring phenology. In general, early species (those with smaller responses to
302 chilling, forcing and photoperiod in experiments Flynn & Wolkovich, 2018; Laube *et al.*, 2014), had
303 relationships with several traits associated with fast and acquisitive growth strategies. Later bud-
304 bursting species (those with larger responses to chilling, forcing and photoperiod in experiments Flynn
305 & Wolkovich, 2018; Laube *et al.*, 2014), however, had traits indicative of conservative, slower growth
306 strategies. Specifically, the trait effects of height and LNC on the timing of budburst followed well-
307 established gradients in growth strategies predicted by functional trait frameworks (Chave *et al.*, 2009;
308 Díaz *et al.*, 2016; Westoby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004). But in the case of
309 SLA, its relationship to spring phenological cues was opposite of our predictions. Species with high
310 SLA—as a result of having the larger, thin leaves, with low investment in leaf mass, and generally
311 indicative of acquisitive growth strategies—had larger responses to photoperiod. Seed mass, which was
312 our one reproductive trait, showed the weakest response to all three cues, suggesting no connection
313 between seed mass and spring phenology. Our results are in line with previous studies conducted
314 at more local scales that found large relationships between height and species phenology (Osada &
315 Hiura, 2019; Seiwa, 1999), as well as findings from large-scale research which found no relationship

³¹⁶ between phenology and seed mass in woody plants (Bolmgren & D. Cowan, 2008; Ettinger *et al.*, 2018).

³¹⁷

³¹⁸ In addition to identifying trait-phenology relationships shaping the timing of spring budburst, our
³¹⁹ results provide further insights into the use of data from large databases to estimate ecological pro-
³²⁰ cesses. By partitioning the different sources of variation that contribute to observed trait values, we
³²¹ found study-level variance made a considerable contribution to the overall variance. Such study-level
³²² variance is likely the result of several factors, including differences across sites, observer error, and
³²³ differences in methodologies, that are present in any dataset that pools data from diverse sources. We
³²⁴ found a particularly strong effect in our height data, as the variance due to study differences exceeded
³²⁵ the estimated species-level variance. This suggests that models using large trait databases that fail to
³²⁶ separate out study from species-level variance may poorly estimate species traits, especially for species
³²⁷ observed in a single study.

³²⁸

³²⁹ Effects of phenology-trait relationships on community assembly

³³⁰ Our findings suggest that changing pressures across the early growing season may affect the temporal
³³¹ assembly of communities. Early-active species had traits indicative of acquisitive growth strategies
³³² that allow faster return on resource investments, like shorter heights and high LNC (Chave *et al.*,
³³³ 2009; Grime, 1977; Westoby, 1998). In deciduous forests, these traits would allow early-budbursting
³³⁴ species to benefit from greater light availability in the open forest canopy in the early spring and
³³⁵ to withstand the low light conditions later in the season. In contrast, later-budbursting species had
³³⁶ traits associated with slower, more conservative growth (Chave *et al.*, 2009; Grime, 1977; Westoby,
³³⁷ 1998), which may help them compete for the more limited soil and light resources later in the grow-
³³⁸ ing season. Similar trait-phenology relationships have also been linked to other ecological processes
³³⁹ and species characteristics that define community structure and diversity, such as species successional
³⁴⁰ position (Laube *et al.*, 2014), leading to the differences we observed for height and LNC in our exam-
³⁴¹ ple comparing *Alnus incana* (a pioneer species) and *Quercus rubra* (a later successional species; Fig 2).

³⁴²

³⁴³ While our study focuses mainly on early versus later spring phenology, our approach and findings may
³⁴⁴ provide insights into potential trade-offs between traits and the phenological cues that underlie early
³⁴⁵ versus late budburst timing. This is particularly true for the relationships that deviated from our ex-
³⁴⁶ pectations. Our finding that tree height (which is related to mechanical strength and water transport
³⁴⁷ (Chave *et al.*, 2009)) was associated with chilling and photoperiod cues (but not forcing) suggests that
³⁴⁸ species use of these two cues may be tied to preventing frost damage or xylem cavitation under a late

349 spring frost (Clements *et al.*, 1972; Marquis *et al.*, 2020). Similarly, the lack of a relationship between
350 SLA and temperature cues (chilling and forcing) was surprising, given that differences in leaf area can
351 also affect heat transfer, such that thicker leaves with higher SLA may have an increased risk of frost
352 damage (Lusk *et al.*, 2018). Many different traits may contribute to decreasing the risk of frost damage
353 (e.g., trichome density, cuticle type, Sakai & Larcher (1987)) and thus a composite of many traits may
354 give better insights into links between traits and frost damage. Further, well-studied traits, such as
355 SLA, often reflect multiple aspects of growth and function (Maynard *et al.*, 2022), and may be adaptive
356 for reasons other than those we predicted. Variation in SLA can also capture differences in species rel-
357 ative growth rates or leaf longevity, and not just photosynthetic potential (Reich, 2014; Westoby, 1998).

358

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

371

372 Future outlook and applications

373 Incorporating phenology within broader trait syndromes could aid in forecasting species and commu-
374 nity responses to climate change. Decades of research have documented phenological advances with
375 anthropogenic climate change (Fitter & Fitter, 2002; Menzel *et al.*, 2006), however, increasing research
376 suggests a potential benefit to earlier phenologies, as plant species that shift their phenology with
377 warming also perform better (Cleland *et al.*, 2012). Our results suggest phenology-performance rela-
378 tionships could be driven in part by a suite of traits that covary with phenology to determine how
379 responsive species are to warming. Our results suggest that early-active species—which other studies
380 have found to also be those that advance more with warming (Fuccillo Battle *et al.*, 2022; Menzel *et al.*,
381 2020)—are likely to have acquisitive traits (such as shorter heights and high LNC) that allow them to

382 grow quickly, accumulate resources faster and possibly have greater carbon sequestration over a longer
383 growing season. How much these relationships continue in the future also depends on how warming
384 in the winter and spring continues, and the complexities of exactly how chilling and photoperiod cues
385 operate, which is an area of active debate. Studies to date suggest chilling may decrease in most places
386 with warming (Guy, 2014; Wang *et al.*, 2022) while research on photoperiod has variously suggested
387 photoperiod cues could stall responses for some later-active species (Ettinger *et al.*, 2021) or have at
388 most a relatively small effect (Ettinger *et al.*, 2021, 2020).

389

390 The insight that understanding trait-phenology relationships provides regarding how climate change
391 may alter species coexistence and create novel species assemblages across communities (Rudolf, 2019;
392 Wolkovich & Donahue, 2021) could have important implication for restoration ecology, including for
393 pollinator communities and invasive plant management. For example, applying our approach to flower
394 and fruit traits may help link plant phenology to pollinator communities, with the opportunity to better
395 predict shifts in phenology and pollination services with climate change (Leclerc *et al.*, 2024; Pareja-
396 Bonilla *et al.*, 2025). Opportunities to better manage invasive plants may come from their tendency
397 to have earlier phenologies (Alexander & Levine, 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019)
398 and traits that facilitate fast growth (Fridley *et al.*, 2022). By identifying the trait-cue relationships
399 that shape phenology, we could use existing trait data from invasive species to better predict whether
400 they are likely to out-compete native species by growing earlier in the season and drawing down soil
401 nutrients and/or light resources that later-active native species may rely on (Buonaiuto & Wolkovich,
402 2023; Dawson-Glass *et al.*, 2025; Hess *et al.*, 2019; Weidlich *et al.*, 2021). This could lead to better
403 identifying which species may be of most concern and thus lead to effective management practices that
404 protect native plant communities under future climate conditions.

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⁴¹² **Author Contributions Statement**

⁴¹³ Deirdre Loughnan, Faith Jones, Geoffrey Legault, Mira Garner, Darwin Sodhi, and E M Wolkovich
⁴¹⁴ planned and designed the study. All authors conducted the literature review and cleaned the database.
⁴¹⁵ Deirdre Loughnan, Faith Jones, Geoffrey Legault, and E M Wolkovich performed the data analysis and
⁴¹⁶ contributed code. Deirdre Loughnan, Faith Jones, and Geoffrey Legault created the figures. Deirdre
⁴¹⁷ Loughnan and E M Wolkovich wrote the initial draft and all authors reviewed and approved the
⁴¹⁸ manuscript for publication.

⁴¹⁹ **Competing Interests Statement**

⁴²⁰ The authors declare no competing interests.

⁴²¹ **Data availability statement**

⁴²² The phenological data used for this manuscript is a subset of the existing public OSPREE dataset
⁴²³ (doi:10.5063/F1CZ35KB, Ettinger *et al.*, 2020) and the trait data a subset of the TRY database
⁴²⁴ (doi:10.1111/gcb.14904, Kattge *et al.*, 2020) and the BIEN database (doi: 10.1111/2041-210X.1286,
⁴²⁵ Maitner *et al.*, 2018). A full list of referenced studies obtained from each trait database is provided in
⁴²⁶ Table S1.

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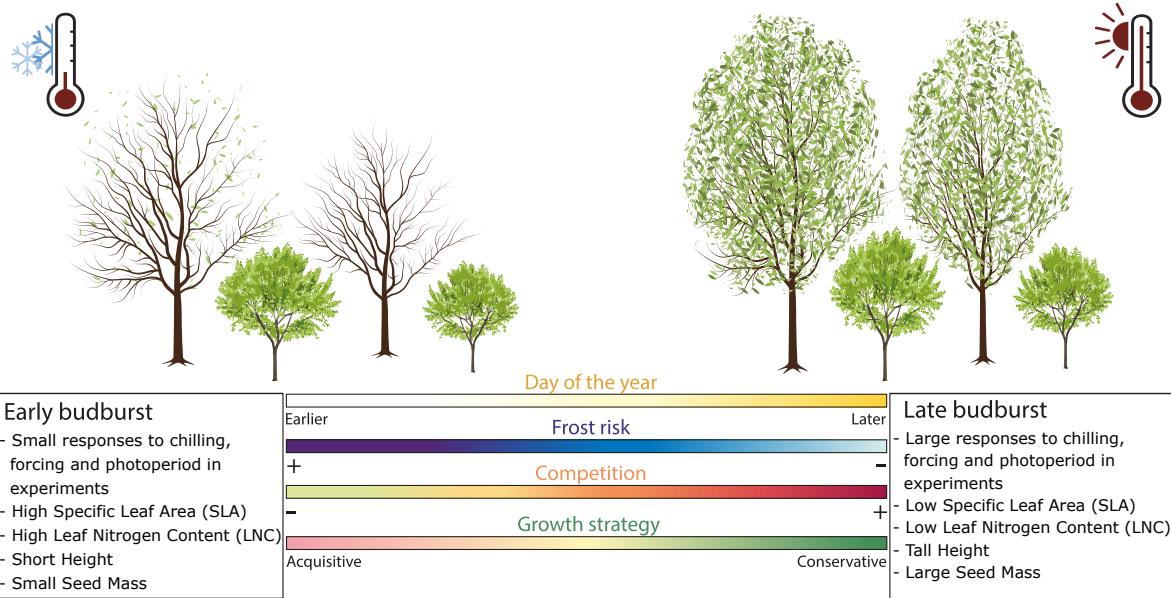


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies (Chave *et al.*, 2009; Westoby & Wright, 2006; Wright *et al.*, 2004), which may also include phenology. Drawing on previous research in plants, we predicted that early-budbursting species 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.

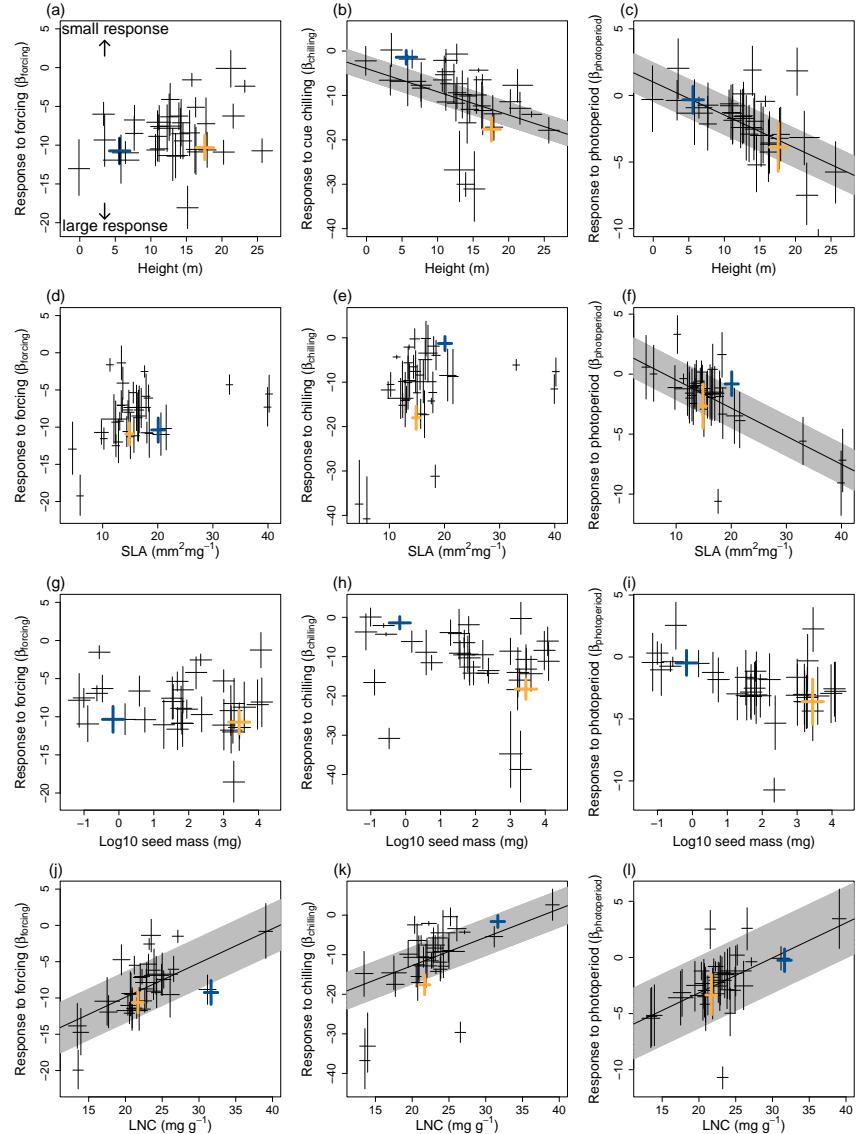


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA ($\text{mm}^2 \text{mg}^{-1}$) (second row: 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, 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.

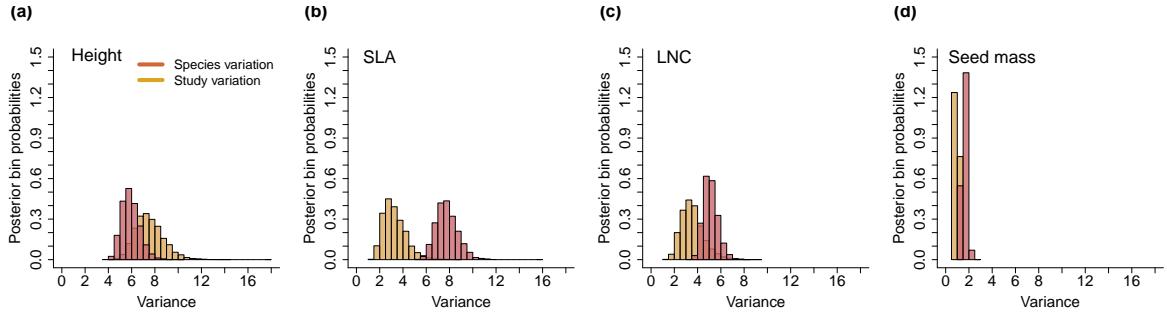


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only (a) the height model estimating greater study-level variation than species-level, while our (b) specific leaf area, (c) leaf nitrogen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