

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 low chilling and photoperiod cues—indicative of earlier budburst—had some traits related to acquisitive strategies (they were shorter with higher nitrogen leaves). Our one reproductive trait (seed mass), however showed no relationships to budburst 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
³² dynamics. Spring phenology, for example, defines the start and overall length of the growing season—
³³ shaping forest carbon storage and species interactions (Beard *et al.*, 2019; Cleland *et al.*, 2007; Gu
³⁴ *et al.*, 2022). Shifts in phenology with climate change across systems (Menzel *et al.*, 2006; Vitasse
³⁵ *et al.*, 2021) have thus led to growing concerns over their possible impacts.

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³⁷ Predicting these changes requires understanding the drivers of phenology both at a proximate scale—
³⁸ the environmental triggers that determine phenology each year, such as temperature and daylength—
³⁹ and, at an ultimate scale, where long-term environmental pressures may select for different phenologies
⁴⁰ across species, (e.g., certain species are early or late relative to other species each year, Ovaskainen
⁴¹ *et al.*, 2013; Wolkovich & Donahue, 2021). At the proximate level, environmental conditions through-
⁴² out the winter and spring cause species to start growth at different times. Groups of species may
⁴³ have more similar responses, however, because they are from similar functional groups, successional
⁴⁴ stages (Laube *et al.*, 2014) or architectures (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 sea-
⁵⁰ son that select for different growth strategies. Species that start growth early often risk high tissue
⁵¹ loss—due to frost damage (Augspurger, 2009; Sakai & Larcher, 1987) or high herbivore apparen-
⁵² cy (Wainwright *et al.*, 2012)—but benefit from higher resource availability (Hufkens *et al.*, 2012; Rathcke
⁵³ & Lacey, 1985). In contrast, later active species face greater biotic pressures, especially from high
⁵⁴ competition for resources (Lopez *et al.*, 2008; Wolkovich & Ettinger, 2014). Such differences could
⁵⁵ shape physical and phenological traits related to species growth strategies and fitness (Violle *et al.*,
⁵⁶ 2007). Species leaf and wood traits can reflect trade-offs between the construction costs and longevity
⁵⁷ of tissue (Reich *et al.*, 1997; Wright *et al.*, 2004), with cheaper-to-construct tissue being associated
⁵⁸ with faster growth rates (Westoby & Wright, 2006; Wright *et al.*, 2004). Previous studies have high-
⁵⁹ lighted associations between trade-offs in major wood and leaf traits and phenology (Sporbert *et al.*,
⁶⁰ 2022; Wang *et al.*, 2021; Wolkovich & Ettinger, 2014) (Fig 1), and hypothesized that phenology may
⁶¹ fit within the acquisitive (fast) to more conservative (slow) growth strategies associated with existing

62 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, is critical to forecasting 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 but see Rauschkolb *et al.* (2024); Sporbert *et al.* (2022)). At these spatial scales the problem of proximate
73 drivers causing phenological variation can be more easily ignored. Adding phenology to broader
74 trait frameworks becomes more complex because high levels of variation occur across large spatial and
75 temporal ranges.

76

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

89

90 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-
91 nology into functional trait research. In addition to how well we understand the environmental cues
92 that trigger early versus late leafout, spring in many forests includes strong gradients in frost risk
93 or nutrient availability (Fig 1). We might predict some variability in how traits relate to different
94 growth strategies (driven by different selective pressures), which then lead to differences across groups
95 of species (Horbach *et al.*, 2023; Sporbert *et al.*, 2022; Wang *et al.*, 2021)—such as the differences in
96 traits that facilitate frost tolerance versus avoidance (Bucher & Rosbakh, 2021; Lenz *et al.*, 2013; Sakai

& Larcher, 1987) or to 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) that are nitrogen rich (Díaz *et al.*, 2016; Reich *et al.*, 1997; Wright *et al.*, 2004) (Fig 1). We would predict such species to exhibit early phenology, budbursting under 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).

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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 species. 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), which could help forecast species phenological responses based on trait values alone.

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119 Methods

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

127

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

130

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

139

140 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020; Maitner
141 *et al.*, 2018), both of which are large trait databases that include plant trait observations across many
142 individuals, species, and studies (Table S1) and are available through slightly different mechanisms.
143 BIEN is accessible via the BIEN R package (here we used v. 1.2.5, Maitner *et al.*, 2018), and TRY
144 is requested. We obtained data from both databases on 5 December 2018, and requested an updated
145 version of the TRY data on 10 April 2019. We initially searched for trait data on the subset of 234
146 OSPREE species used in Morales-Castilla *et al.* (2024). From BIEN, this resulted in 94 of the 234
147 species available in the database, for which there were 13 unique traits. From the TRY database we
148 received data for 10 unique traits for 96 of the 234 requested species (Kattge *et al.*, 2020). As we
149 were interested in the trait-phenology relationships of adult trees we subset the available data to only
150 include traits measured from adult individuals. We assumed that by subsetting tree heights to be 1.38
151 m or greater the individuals in our analysis would be old enough to meet the standard measurement
152 height used in North America when measuring DBH (Powell, 2016). We further removed all data from
153 manipulative experiments or from plants growing in non-natural habitats. We also grouped trait values
154 where appropriate, for example pooling trait values for specific leaf area (SLA) with those denoted as
155 ‘SLA with petioles’, and ‘SLA without petioles’ in our analysis (see Table S1). We also removed data
156 that was duplicated in both the TRY and BIEN datasets ($n = 434,905$). For a full depiction of our
157 data cleaning process and decisions see Fig. S3.

158

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

165 (Fig. S2), with high correlations between SLA and LDMC, and between height and SSD (Fig. S2).
 166 By excluding the trait from each of these highly correlated trait pairs with the least amount of data
 167 (specifically LDMC and SSD) we were able to increase the number of species in our dataset from the
 168 26 species with complete data for six traits, to 37 species with complete data for four traits. The
 169 data for these 37 species were from 24 unique studies (sample sizes: height $n = 47781$, seed mass
 170 $n = 281$, LNC $n = 3853$, SLA $n = 7656$). We subsampled the height measurements of the 13
 171 most frequently measured trees to reduce their influence on our height model. Since each of these 13
 172 species were measured 19 times more frequently than most other species, we randomly sampled 3000
 173 height measurements for each individual species, while including all height data for the remaining, less
 174 frequently measured, 24 species.

175 **Joint model of trait and phenology**

176
 177 To understand connections between phenology and species traits, we developed a Bayesian joint model
 178 for each trait: height, SLA, LNC, and seed mass to relate to species budburst responses. We consider
 179 this a ‘joint’ model because it involves two sub-models—one that models trait observations and a
 180 second that uses shared latent processes to model how a given trait relates to the cues that shape
 181 the phenological observations. In particular, we assume that trait values are the result of multiple
 182 sources of variation, including species (α_{species}) and study-level variation (α_{study}), that combine into
 183 one observed trait value (trait sub-model). This trait value (α_{trait}) has a separate interaction with
 184 the three cues (β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$) that determines phenology—specifically the day of year
 185 of budburst (phenology sub-model). Below we describe the two sub-models, noting which parameters
 186 are shared across sub-models and which are independent.

187 **Trait sub-model**

188 Our trait sub-model describes the processes that shape a given trait observations for 1 to n species
 189 across each of the 1 to m studies in our trait dataset. We use hierarchical modeling to partition trait
 190 values by measurement error (σ_m^2), species identity ($\alpha_{\text{species}_i}$), and study (α_{study_j}). In particular, we
 191 assume that a trait observation for species i from study j , $Y_{\text{trait}_{i,j}}$, has the following normal distribution:

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

192 with

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

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

$$\boldsymbol{\alpha}_{\text{trait}} = \alpha_{\text{grand trait}} + \alpha_{\text{species}_i} \\ \boldsymbol{\alpha}_{\text{species}} = \{\alpha_{\text{species}_1}, \dots, \alpha_{\text{species}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{species}} \sim \mathcal{N}(0, \sigma_{\text{species}}^2) \quad (3)$$

$$\boldsymbol{\alpha}_{\text{study}} = \{\alpha_{\text{study}_1}, \dots, \alpha_{\text{study}_m}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \mathcal{N}(0, \sigma_{\text{study}}^2) \quad (4)$$

194 The latent parameter or overall mean trait value ($\alpha_{\text{grand trait}}$) represents a trait value that is indepen-
 195 dent of the species ($\alpha_{\text{species},i}$) and study-level ($\alpha_{\text{study},j}$) offsets from that trait value. The σ_m^2 parameter
 196 is the measurement error, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and study-level variances in trait
 197 values. Of these parameters, the $\boldsymbol{\alpha}_{\text{trait}}$ is shared by the phenology sub-model.

198 Phenology sub-model

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

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

205 with

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

206 and

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

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

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

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

$$\boldsymbol{\alpha}_{\text{pheno}} = \{\alpha_{\text{pheno}_1}, \dots, \alpha_{\text{pheno}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \mathcal{N}(\mu_{\text{pheno}}, \sigma_{\text{pheno}}^2) \quad (8)$$

$$\boldsymbol{\alpha}_{\text{chilling}} = \{\alpha_{\text{chilling}_1}, \dots, \alpha_{\text{chilling}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chilling}} \sim \mathcal{N}(\mu_{\text{chilling}}, \sigma_{\text{chilling}}^2)$$

$$\boldsymbol{\alpha}_{\text{forcing}} = \{\alpha_{\text{forcing}_1}, \dots, \alpha_{\text{forcing}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{forcing}} \sim \mathcal{N}(\mu_{\text{forcing}}, \sigma_{\text{forcing}}^2)$$

$$\boldsymbol{\alpha}_{\text{photoperiod}} = \{\alpha_{\text{photoperiod}_1}, \dots, \alpha_{\text{photoperiod}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photoperiod}} \sim \mathcal{N}(\mu_{\text{photoperiod}}, \sigma_{\text{photoperiod}}^2)$$

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

218
 219 The model was coded in the Stan (Stan Development Team, 2024), which is a probabilistic program-
 220 ming language for building Bayesian models. We used the rstan package (Stan Development Team,
 221 2018) to interface with and run the Stan code in R version 3.3.6 (R Development Core Team, 2017).
 222 For our model, we chose weakly informative priors, and validated them using a series of prior predictive
 223 checks. The model was fit with 1,000 iterations per chain across 4 chains (4,000 total sampling iter-
 224 ations), and all models met basic diagnostic checks, including no divergences, high effective sample size
 225 (n_{eff}), and \hat{R} close to 1, fitting the data well (Fig S4). Here we present our model estimates as the
 226 means and 90% posterior uncertainty intervals (UI), with the 50% UI included in the supplementary
 227 tables and figures to allow for comparison and to assess the strength of relationships. We consider
 228 parameters with UI that overlap to be similar to each other and those that include zero in the 90% UI
 229 to have small effects.

230 Results

231 Across traits, height, SLA, and LNC were related to one or more environmental cue ($\beta_{\text{chilling}_k}$, β_{forcing_k} ,
 232 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).
 233 As we predicted, height was negatively related to chilling ($\beta_{\text{chilling}_k}$) and photoperiod ($\beta_{\text{photoperiod}_k}$),
 234 with taller species having larger responses to high chilling and longer photoperiod conditions (-0.5 m

235 per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized pho-
236 toperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). We found height to have a larger relationship with
237 the timing of budburst (as estimated by $\mu_{k,g}$), with later budburst estimated for taller trees under
238 increasing chilling and photoperiods (Fig. S5). In contrast, seed mass had a negligible relationship
239 with budburst and all three cues (Fig. 2 g-i & Table S4).

240

241 Of our leaf traits, we found that SLA related to photoperiod ($\beta_{\text{photoperiod}_k}$, -0.2 mm²/mg per stan-
242 dardized photoperiod; 90% UI: -0.5, 0.0, Fig. 2 f, Table S3), but did not strongly predict responses
243 to chilling ($\beta_{\text{chilling}_k}$) or forcing treatments (β_{forcing_k} , Fig. 2 d & e). Contrary to our predictions,
244 species with high SLA—indicative of larger, thin leaves and a lower investment in leaf mass and asso-
245 ciated with more acquisitive growth strategies—exhibited larger responses to photoperiod commonly
246 observed in late budbursting species (Fig. 2 f). The relationship between LNC and budburst cues,
247 were in line with our predictions, with high LNC species being less responsive to chilling (0.7 mg/g
248 per standardized chilling; 90% UI: 0.2, 1.2, Table S5), forcing (0.5 mg/g per standardized forcing; 90%
249 UI: 0.1, 0.8, and photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6), Fig 2 j-l &
250 Fig S5 d-f). This suggests that species that produce leaves with high nitrogen content, which relates
251 generally to high photosynthetic rates and acquisitive growth, are likely to budburst early based on
252 the relationships between this trait and environmental cues.

253

254 We found that the species-level variation across traits (σ_{trait}^2) were comparable to, or greater than
255 variation across studies (using our model that partitions the measurement error in the trait values
256 from variation from species and study-level effects, σ_{study}^2 , Fig 3). For height, variation across studies
257 (σ_{study}^2) was greater (7.5 m; 90% UI: 5.8, 9.7), than the variation caused by species (σ_{trait}^2 , 5.9 m;
258 90% UI: 4.8, 7.3, Fig 3a). For seed mass and LNC, study-level variation was less than that of the
259 species-level variation, with variation in seed mass observations of 1 mg (90% UI: 0.8, 1.1) and 1.6 mg
260 (90% UI: 0.8, 1.1) for study-level and species-level variation respectively and for LNC 3.6 mg g⁻¹ (90%
261 UI: 2.2, 5.3) for study-level variation and 5.1 mg g⁻¹ for the species-level variation (90% UI: 2.2, 5.3,
262 Fig 3c and d). Study-level variation was smallest for SLA, with the estimate of 3.3 mm² mg⁻¹ (90% UI:
263 2, 5.1) for study-level variation being approximately half that of the estimated species-level variation
264 of 7.8 mm² mg⁻¹ (90% UI: 6.4, 9.4, Fig 3b). Across all traits, the effect of study-level variation (σ_{study}^2)
265 made a considerable contribution to the overall variation observed in our trait values and suggests that
266 models using large trait databases that fail to separate out study from species-level variation (σ_{trait}^2)
267 may poorly estimate species traits.

268

²⁶⁹ **Discussion**

²⁷⁰ We found several species traits influenced the timing of budburst in response to one or more of the
²⁷¹ three primary cues of spring phenology: chilling, forcing and photoperiod. While the relationships
²⁷² between SLA and seed mass with phenological cues differed from our predictions, the trait effects of
²⁷³ height and LNC were associated with earlier or later phenology, following well-established gradients in
²⁷⁴ growth strategies predicted by functional trait frameworks (Chave *et al.*, 2009; Díaz *et al.*, 2016; West-
²⁷⁵ oby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004). Early species—which generally budburst
²⁷⁶ given small levels of forcing, chilling, and shorter photoperiod—exhibited relationships with several
²⁷⁷ traits associated with fast and acquisitive growth strategies, while later budbursting species—which
²⁷⁸ require larger levels of forcing, chilling, and longer photoperiods to initiate growth—exhibited traits
²⁷⁹ indicative of conservative, slower growth strategies. We found the largest budburst responses occurred
²⁸⁰ for traits related to resource acquisition and structure, with SLA, LNC, and height all showing large
²⁸¹ responses to at least one of our three cues. In contrast, our one reproductive trait—seed mass—showed
²⁸² the smallest response. Our results provide a major step forward in integrating phenology into broader
²⁸³ trait syndromes that shape species growth strategies, and support previous findings from more local
²⁸⁴ scales that found large relationships between height and species phenology (Osada & Hiura, 2019;
²⁸⁵ Seiwa, 1999). Our more global analysis supports previous studies of plant phenological events, which
²⁸⁶ found no relationship between phenology and seed mass in woody plants (Bolmgren & D. Cowan, 2008;
²⁸⁷ Ettinger *et al.*, 2018).

²⁸⁸

²⁸⁹ In addition to identifying trait-phenology relationships shaping the timing of spring budburst, our
²⁹⁰ results also provide important insights into the use of data from large databases to estimate ecological
²⁹¹ processes. By partitioning the different sources of variation that contribute to observed trait values,
²⁹² we found considerable effects of study-level variation. For one of our traits, the differences due to
²⁹³ study exceeded those due to species. Such study-level variation is likely the result of myriad factors,
²⁹⁴ including observer error and differences in methodologies, that are present in any dataset that pools
²⁹⁵ data from diverse sources. Our findings thus highlight that analyses using data from aggregate trait
²⁹⁶ databases may need to account for this variation to make the most accurate predictions.

²⁹⁷ **Effects of phenology-trait relationships on community assembly**

²⁹⁸ Our findings suggest the changing pressures across the early growing season may affect the temporal
²⁹⁹ assembly of communities. Species with small cue responses, an indication of earlier budburst, had
³⁰⁰ some traits indicative of acquisitive growth strategies (shorter heights and high LNC) that allow faster
³⁰¹ return on resource investments (Chave *et al.*, 2009; Grime, 1977; Westoby, 1998). These traits should

allow early species to benefit from greater light availability in the open forest canopy in the early spring and withstand the low light conditions later in the season. In contrast, later-budbursting species had traits associated with slower, more conservative, growth (Chave *et al.*, 2009; Grime, 1977; Westoby, 1998), which may help them compete for the more limited soil and light resources later in the growing season. Similar trait-phenology relationships have also been linked to other ecological processes and species characteristics that define community structure and diversity, such as species successional position (Laube *et al.*, 2014), providing support to the differences we observed for height and LNC in our example comparing *Alnus incana* (a pioneer species) and *Quercus rubra* (a later successional species; Fig 2).

311

The trait by cue relationships that deviated from our expectations also offer novel insights into the tradeoffs between traits and environmental cues. All of our traits are associated with multiple aspects of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our predictions, we found large responses to forcing for short trees, which could prevent frost damage or xylem cavitation under a late spring frost (Clements *et al.*, 1972; Marquis *et al.*, 2020) and influence annual cambial meristem growth (Lenz *et al.*, 2016). Similarly, the lack of a relationship between SLA and chilling and forcing could be driven by other physiological constraints or tradeoffs with selection by other cues—as variation in SLA also reflects differences in species relative growth rates or leaf longevity—and not just photosynthetic potential (Reich, 2014; Westoby, 1998). These findings highlight the complexity of determining the drivers of species trait profiles.

322 Phenology-trait relationships under future climates

323 Incorporating phenology within broader trait syndromes could aid forecasting of species and community responses to climate change. While decades of research have documented phenological shifts with 324 anthropogenic climate change (Fitter & Fitter, 2002; Menzel *et al.*, 2006), increasing research suggests 325 a potential connection between phenological responses to warming and performance with warming, 326 where species that shift their phenology more also perform better (Cleland *et al.*, 2012; Macgregor 327 *et al.*, 2019).

329

330 Our results suggest this phenology-performance relationship could be driven in part by a suite of 331 traits that covary with phenological cues to determine how responsive species are to warming. Species 332 with smaller responses to all cues, especially chilling and photoperiod, would tend to advance more 333 with warming (Guy, 2014). Our results suggest that these same species are likely to have acquisitive 334 traits, such as short heights and high LNC that allow them to grow quickly and benefit from the

335 greater availability of nutrients in the early spring. Understanding these trait-phenology relationships
336 may provide insight into how climate change may alter species coexistence (Rudolf, 2019; Wolkovich
337 & Donahue, 2021). A greater understanding of trait-phenology relationships may also improve our
338 ability to manage species invasions. Invasive species tend to have earlier phenologies (Alexander &
339 Levine, 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019), but possibly also a unique suite of traits
340 that facilitate fast growth (Fridley *et al.*, 2022), thus understanding how much early phenology versus
341 fast growth drive their success could aid management decisions.

342

343 Our analytical approach and results may be especially useful to help forecast changes in forest dy-
344 namics. Identifying the varying trait syndromes of forest communities over a spring season can aid
345 predictions of how climate change will alter species growth and productivity. For example, our results
346 suggest that, by favoring more phenologically responsive species (i.e., with small chilling and pho-
347 toperiod responses), warming may also favor species with acquisitive growth strategies. In contrast,
348 conservative species, which appear less phenologically responsive to changes in temperature (due to
349 larger chilling and photoperiod responses) could face greater abiotic and biotic stress (Guy, 2014).

350

351 Our results could further help identify which species are most likely to be negatively impacted under
352 future climates, and develop better strategies for climate change mitigation and conservation. Species
353 that fail to advance phenologically with warming might experience more competition (Alexander &
354 Levine, 2019; Carter *et al.*, 2018), as species that begin growth increasingly earlier with warming have
355 more time to deplete resources. In addition to altering the timing and interactions between species
356 within a season, species trait syndromes have the potential to further redefine the environmental
357 conditions under which growth occurs and, as a result, shape community assembly and productivity
358 within ecological communities (Rudolf, 2019; Wolkovich & Donahue, 2021). By identifying the species
359 most vulnerable to climate change impacts, we can develop more effective management practices that
360 prevent the loss of critical ecosystem services and preserve community diversity under future conditions.

361

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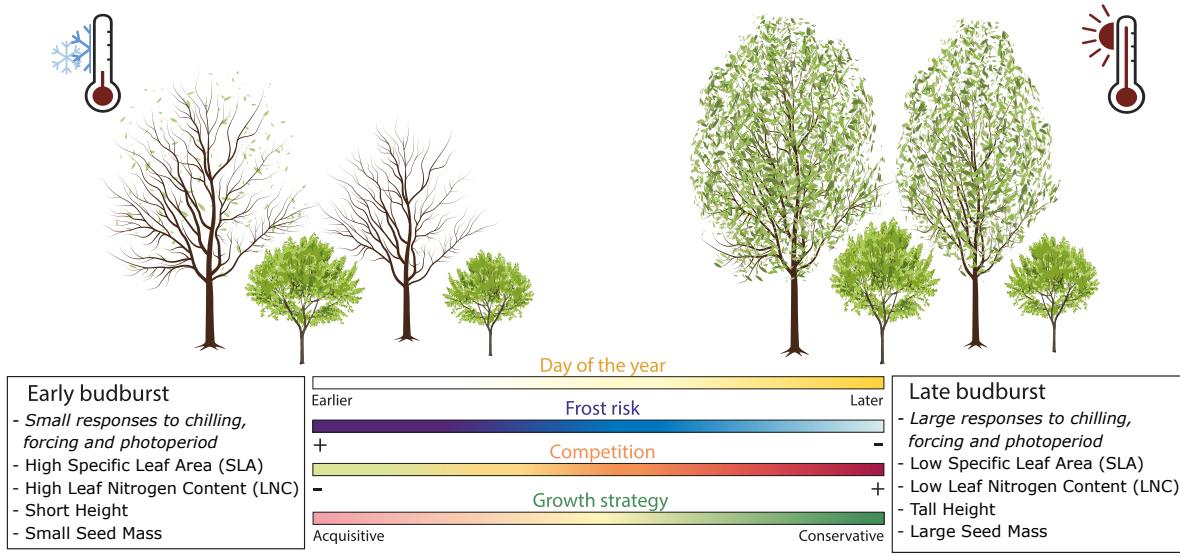


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater abiotic and 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. However 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 temporal niche.

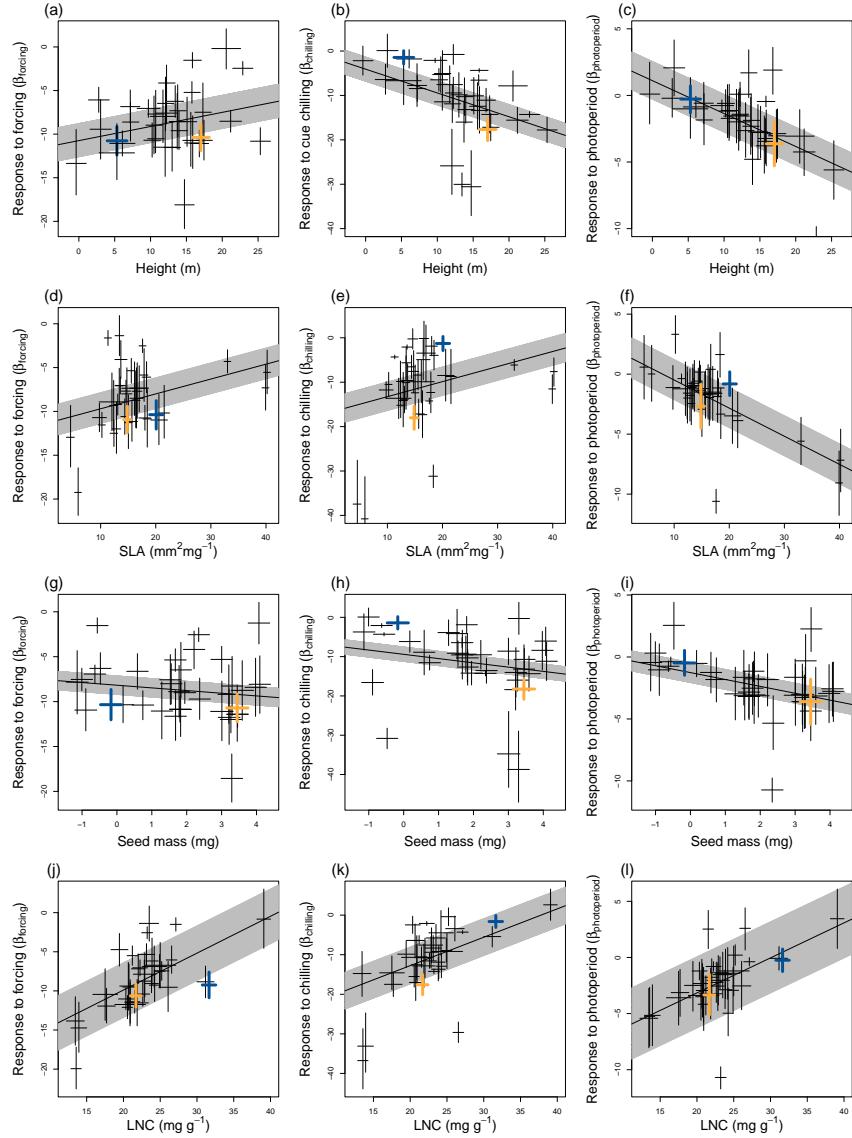


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the black line depicting the mean linear relationship between estimated trait effects and the slope of the cue response (either β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$ for each respective trait) and the gray band the 50% uncertainty interval. 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—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 (see also Fig S5).

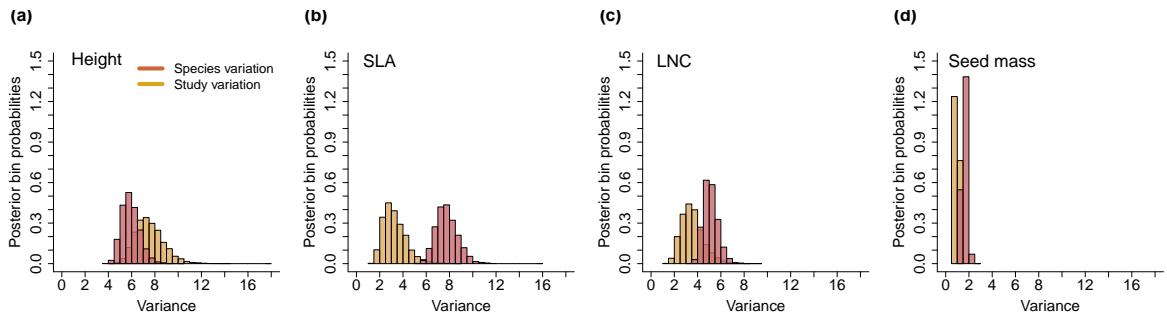


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only (a) the height model estimating greater study-level variation than species-level, while our (b) specific leaf area, (c) leaf nitrogen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