

¹ Budburst timing within a functional trait framework

²

³ Running title: Budburst responses associated with traits

⁴ **Summary**

- ⁵ 1. Phenologies—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 we can infer 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.
- ¹⁵ 2. Using a modelling framework that accommodates this variability we performed a meta-analysis using phenological data from **a database of controlled environment experiments** and tree traits 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).
- ¹⁹ 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—were shorter with high nitrogen leaves. Seed mass showed no relationships to budburst cues, while the effect of specific leaf area exhibited a relationship with only photoperiod, but in the opposite direction to our predictions.
- ²⁴ 4. Synthesis: Our findings show how spring leafout phenology fits within a functional trait framework of acquisitive to conservative growth strategies, and better predicts how communities may shift in their growth strategies alongside changing phenology with climate change.

²⁷ ²⁸ Key Words: Leafout, spring phenology, traits, trees, climate change, forest communities

²⁹ **Introduction**

³⁰ The timing of life history events—phenology—can shape both ecosystem services and community
³¹ dynamics. Spring phenology, for example, defines the start and overall length of the growing season—
³² shaping forest carbon storage and species interactions (Beard *et al.*, 2019; Cleland *et al.*, 2007; Gu
³³ *et al.*, 2022). Shifts in phenology with climate change across systems (Menzel *et al.*, 2006; Vitasse
³⁴ *et al.*, 2021) have thus led to growing concerns over their possible impacts.

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³⁶ Predicting these changes requires understanding the drivers of phenology both at a proximate scale—
³⁷ the environmental triggers of phenology each year, such as temperature and daylength—and at an
³⁸ ultimate scale, where long-term environmental pressures may select for different phenologies across
³⁹ species, (e.g., certain species are early or late relative to other species each year Ovaskainen *et al.*,
⁴⁰ 2013; Wolkovich & Donahue, 2021). At the proximate level, environmental conditions throughout the
⁴¹ winter and spring cause species to start growth at different times. While similar environmental condi-
⁴² tions appear to trigger the start of growth in woody plants each year, differences in species responses to
⁴³ conditions may drive generalizable trends in variation across species of different successional strategies
⁴⁴ (Laube *et al.*, 2014a) or architecture (Flynn & Wolkovich, 2018). But current work provides limited
⁴⁵ insights into the drivers of these differences across species and how these can be used to predict future
⁴⁶ changes in community dynamics (Chuine *et al.*, 2016; Flynn & Wolkovich, 2018; Laube *et al.*, 2014a).

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⁴⁸ At the ultimate level, plant phenologies may vary due to changing pressures across the growing sea-
⁴⁹ son. Species that start growth early often risk high tissue loss—due to frost damage (Augspurger,
⁵⁰ 2009; Sakai & Larcher, 1987) or high herbivore apparenacy (Wainwright *et al.*, 2012)—but benefit from
⁵¹ higher resource availability (Hufkens *et al.*, 2012; Rathcke & Lacey, 1985). In contrast, later active
⁵² species face greater biotic pressures, especially from high competition for resources (Lopez *et al.*, 2008;
⁵³ Wolkovich & Ettinger, 2014). This variation in early to late season growth may mirror the stressors
⁵⁴ from early to late successional communities, and may similarly shape phenology (Laube *et al.*, 2014a).
⁵⁵ Different pressures could shape physical and phenological traits related to species growth strategies and
⁵⁶ fitness (Violle *et al.*, 2007). Species leaf and wood traits can reflect trade-offs between the construction
⁵⁷ costs and longevity of tissue (Reich *et al.*, 1997; Wright *et al.*, 2004), with cheaper to construct tissue
⁵⁸ being associated with faster growth rates (Westoby & Wright, 2006; Wright *et al.*, 2004). Previous
⁵⁹ studies have predicted associations between trade-offs in traits and phenology (Sporbert *et al.*, 2022;
⁶⁰ Wolkovich & Ettinger, 2014) (Fig 1), with the potential for species traits to similarly range from the
⁶¹ acquisitive (fast) to more conservative (slow) growth strategies associated with existing trait frame-
⁶² works (Chave *et al.*, 2009; Wright *et al.*, 2004).

63

64 Globally, gradients from acquisitive to conservative strategies appear common, and form the foun-
65 dation of the leaf economic and the wood economic spectra (Chave *et al.*, 2009; Díaz *et al.*, 2016;
66 Westoby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004), but they can make limited predictions
67 of trait variability (Violle *et al.*, 2012). As a result, highly variable traits like phenology are often
68 excluded from trait studies, leaving the relationships between broader trait syndromes and phenology
69 largely unknown. Understanding these relationships is critical to forecasting community dynamics and
70 responses to climate change. To the best of our knowledge, studies have generally only examined
71 the relationship between traits and phenology for a single or limited number of sites (as reviewed by
72 Wolkovich & Cleland (2014) and Wolkovich & Donahue (2021), but see Sporbert *et al.* (2022) and
73 Rauschkolb *et al.* (2024)) where the problem of proximate drivers causing phenological variation can
74 be more easily ignored. Adding phenology to broader trait frameworks becomes more complex when
75 high levels of variation occurs across large spatial and temporal ranges.

76

77 Recent climate change has caused plant phenology to shift earlier with warming (Fitter & Fitter, 2002;
78 Menzel *et al.*, 2006), but shifts across individual species have been shown to vary substantially in both
79 space (Vitasse, 2013) and time (Rudolf, 2019; Yu *et al.*, 2010). But experiments conducted under
80 controlled environments have shown that it is possible to consistently defining early to late phenol-
81 ogy from the known underlying cues (Chuine & Cour, 1999; Flynn & Wolkovich, 2018; Harrington
82 & Gould, 2015). This work has found early species to generally have smaller advances in phenology
83 when the three major cues of spring leafout are weaker: low spring temperatures (forcing), insufficient
84 winter temperatures (chilling) and shorter daylengths (photoperiod). In contrast, later species have
85 larger responses to high chilling and/or long photoperiods (Flynn & Wolkovich, 2018; Laube *et al.*,
86 2014a), and likely larger forcing responses. The consistency of these relationships allows us to better
87 understand the drivers of phenological variation both across plant communities and spatial scales.

88

89 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-
90 nology into functional trait research. In addition to how well we understand the environmental cues
91 that trigger early versus late leafout, spring in many forests includes strong gradients in frost risk or
92 nutrient availability (Fig 1). We might predict some variability in how traits relate to different growth
93 strategies based on differences across groups of species (Horbach *et al.*, 2023; Sporbert *et al.*, 2022;
94 Wang *et al.*, 2021) or strategies for responding to selective pressures, such as the differences in traits
95 that facilitate frost tolerance versus avoidance (Bucher & Rosbakh, 2021; Lenz *et al.*, 2013; Sakai &
96 Larcher, 1987) or to herbivory (Coley *et al.*, 1985). But broadly we predict acquisitive species to be
97 shorter, with leaf traits favorable to low light conditions found in the understory later in the growing

98 season, producing cheap leaves with high specific leaf area (SLA) that are nitrogen rich (Díaz *et al.*,
99 2016; Reich *et al.*, 1997; Wright *et al.*, 2004) (Fig 1). We would predict such species would exhibit early
100 phenology, budbursting under low chilling, cool spring conditions with shorter photoperiods. Canopy
101 species that budburst later via larger cue responses and when competition for soil resources is greater,
102 would then have traits associated with conservative growth—taller with denser wood (Chave *et al.*,
103 2009; Laughlin *et al.*, 2010)—with leaf traits suited for the high light conditions of the canopy (low
104 SLA and low LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative
105 continuum, as acquisitive species produce smaller seeds and the taller and more conservative species
106 produce larger—better provisioned—seeds (Díaz *et al.*, 2016) Fig 1).

107

108 To test our predicted relationships between budburst responses to environmental cues and common
109 functional traits (height, SLA, seed mass, and LNC), we merged available data from [global databases](#)
110 [of plant traits](#)—BIEN (Maitner *et al.*, 2018) and TRY (Kattge *et al.*, 2020)—with global budburst
111 [data](#) from the OSPREE database of controlled environment studies (Ettinger *et al.*, 2020). We devel-
112 oped a hierarchical Bayesian joint model that predicts phenological responses to forcing, chilling and
113 photoperiod treatments based on species-level trait values, while allowing additional variation due to
114 species. This approach takes a step towards predicting variation via species traits instead of species
115 identity (when traits explain a significant portion of the variation, species identity will explain only a
116 small amount), which could help forecast species phenological responses based on trait values alone.

117

118 Methods

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

125

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

128

129 We then scraped the data from all articles of woody species [reporting experiments that manipulated](#)
130 both photoperiod and/or temperature cues of budburst, leafout, or flowering phenology, and for which

131 there was a quantifiable response to each cue. We updated this database in July 2019 reviewing all new
132 articles found using the previous search terms. Additional details on the methods used to assemble,
133 clean, and update this database are discussed by Ettinger *et al.* (2020) and Morales-Castilla *et al.*
134 (2024). For the purpose of this study, we used a subset of the OSPREE database, using data only for
135 budburst phenology and for the subset of 234 species used in Morales-Castilla *et al.* (2024).

136

137 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020; Maitner *et al.*,
138 2018), both of which are large trait databases that include plant trait data across many individuals,
139 species, and studies (Table S1). We obtained data from both databases on 5 December, 2018, and
140 requested an updated version of the TRY data on 10 April, 2019. We again focused our search for trait
141 data on the subset of 234 OSPREE species used in Morales-Castilla *et al.* (2024). Using the BIEN
142 R package (v. 1.2.5) (Maitner *et al.*, 2018), we downloaded all available trait data for the 94 species
143 available, for which there were 13 unique traits. From the TRY database we received data for 10
144 unique traits for 96 of our focal species (Kattge *et al.*, 2020). Given our focus on the phenology of
145 adult trees, we subset the available data to only include traits measured from adult individuals with
146 heights greater than 1.38, as these individuals were more likely to have DBH measured at the standard
147 measurement height used in North America (Powell, 2016). We further removed all data from manipu-
148 lative experiments or from plants growing in non-natural habitats. We also grouped trait values where
149 appropriate, for example pooling trait values for specific leaf area (SLA) with those denoted as "SLA
150 with petioles", and "SLA without petioles" in our analysis (see Table S1). We also removed data that
151 was duplicated in both the TRY and BIEN datasets ($n = 434905$). For a full depiction of our data
152 cleaning process and decisions see S3.

153

154 For our analysis, we only include species for which we had a complete trait profile (i.e., all traits
155 measured for all species). We initially considered six commonly measured traits—SLA, leaf dry matter
156 content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species had
157 at least one trait measurement for each trait. We then used a principle component analysis (PCA)
158 to identify which of our six traits were strongly correlated. The first principal component explained
159 32% of variation while the second explained 24.2% of the variation (Fig. S2), with high correlations
160 between SLA and LDMC, and between height and SSD (Fig. S2). By excluding the trait from each
161 of these highly correlated trait pairs with the least amount of data (specifically LDMC and SSD) we
162 were able to increase the number of species in our dataset from the 26 species with complete data for
163 six traits, to 37 species with complete data for four traits. The data for these 37 species were from
164 24 unique studies (samples sizes: height $n = 47781$, seed mass $n = 281$, LNC $n = 3853$, SLA $n =$
165 7656). We subsampled the height measurements of the 13 most frequently measured tree to reduce

166 their influence on our height model. Since these species were measured 19 times more frequently than
167 most other species, we randomly sampled 3000 height measurements for each of these 13 species, while
168 including all height data for the remaining 24 species.

169 Joint model of trait and phenology

170

171 To understand connections between phenology and species traits, we developed a [Bayesian](#) joint model
172 for each trait: height, SLA, LNC, and seed mass. Our model is a joint model insofar as it involves
173 two sub-models—one that models trait observations and a second that uses shared latent processes
174 to model [how a given trait relates to the cues that shape the phenological observations](#). In particular,
175 we assume that trait values are the result of multiple sources of variation, including species (α_{species})
176 and study-level variation (α_{study}), that combine into one observed trait value (trait sub-model). This
177 trait value (α_{trait}) has a separate interaction with the three cues (β_{chilling} , β_{forcing} , $\beta_{\text{photoperiod}}$) that
178 determines phenology—specifically the day of year of budburst (phenology sub-model). Below we
179 describe the two sub-models, noting which parameters are shared across sub-models and which are
180 independent.

181 Trait sub-model

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

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

186 with

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

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

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

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

188 The latent parameter or overall mean trait value, $\alpha_{\text{grand trait}}$ represents a trait value that is independent
 189 of the species ($\alpha_{\text{species},i}$) and study-level ($\alpha_{\text{study},j}$) offsets from that trait value. The σ_m^2 parameter
 190 is the measurement error, and $\sigma_{\text{species}}^2$ and σ_{study}^2 represent species and study-level variances in trait
 191 values. Of these parameters, the α_{trait} are shared by the phenology sub-model.

192 Phenology sub-model

193 Our phenology sub-model describes the processes that determine the relationships between traits and
 194 environment cues and their effects on phenological observations for 1 to n species, specifically the
 195 timing (day of year) of budburst from the updated OSPREE dataset. We assume that an observation
 196 of budburst for species k under g treatments levels of chilling, forcing, and photoperiod (c_g, f_g, p_g),
 197 parameter $Y_{\text{pheno}_{k,g}}$ representing the observed day of budburst (which we z -scored to allow direct
 198 comparison of cues) has the following normal distribution:

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

199 with

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

200 and

$$\begin{aligned} \beta_{\text{chilling}_k} &= \alpha_{\text{chilling},k} + \beta_{\text{trait.chilling}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{forcing}_k} &= \alpha_{\text{forcing},k} + \beta_{\text{trait.forcing}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{photoperiod}_k} &= \alpha_{\text{photoperiod},k} + \beta_{\text{trait.photoperiod}} \cdot \alpha_{\text{trait},k} \end{aligned} \quad (7)$$

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

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

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

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

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

202 The model partitions day of budburst for species (k) as combination of their overall mean day of
 203 budburst without the influence of chilling, forcing, or photoperiod treatments ($\alpha_{\text{pheno},k}$, normally
 204 distributed with a mean of μ_{pheno} and variance σ_{pheno}^2) combined with the effects of treatments both
 205 dependent and independent of trait values.

206 The parameters $\alpha_{\text{chilling},k}$, $\alpha_{\text{forcing},k}$, and $\alpha_{\text{photoperiod},k}$ represent the trait-independent responses of
207 species k to chilling, forcing, and photoperiod treatments respectively, each with an associated mean
208 (μ_{chilling} , μ_{forcing} , $\mu_{\text{photoperiod}}$) and variance ($\sigma^2_{\text{chilling}}$, $\sigma^2_{\text{forcing}}$, $\sigma^2_{\text{photoperiod}}$) across species. The shared
209 parameter between the trait and phenology sub-model, $\alpha_{\text{trait},k}$, represents the effect of the species trait
210 value on its responses to chilling ($\beta_{\text{trait.chilling}}$), forcing ($\beta_{\text{trait.forcing}}$), and photoperiod ($\beta_{\text{trait.photoperiod}}$).
211 Finally, σ^2_d is the variance arising from measurement error.

212

213 The model was coded in the Stan programming language **StanCite**, which is a probabilistic program-
214 ming language enabling custom building of accurate and interpretable Bayesian models. We used the
215 rstan package (Stan Development Team, 2018) to interface with and run the Stan code in R version
216 3.3.6 **R**. For our model, we chose weakly informative priors, and validated them using a series of prior
217 predictive checks. The model was fit with 1,000 iterations per chain across 4 chains (4,000 total sam-
218 pling iterations), and all models met basic diagnostic checks, including no divergences, high effective
219 sample size (n_{eff}), and \hat{R} close to 1, fitting the data well (Fig S4). Here we present our model esti-
220 mates as the means and 90% posterior uncertainty intervals (UI), with additional UI included in the
221 supplementary tables and figures to allow for comparison and to assess the strength of relationships
222 (). We consider parameters with UI that overlap to be similar to each other and those that include
223 zero in the 90% UI to have weak effects.

224 Results

225 Across traits, height, SLA, and LNC strongly related to one or more environmental cue ($\beta_{\text{chilling}_k}$,
226 β_{forcing_k} , or $\beta_{\text{photoperiod}_k}$, Fig 2 a-f & j-l), with only LNC showing a relationship with all three cues
227 (Fig. 2 j-l). As we predicted, height was negatively related to chilling ($\beta_{\text{chilling}_k}$) and photoperiod
228 ($\beta_{\text{photoperiod}_k}$), with taller species having larger responses to high chilling and longer photoperiods
229 conditions (-1 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per
230 standardized photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). We found height to have a strong
231 relationship with the timing of budburst (as estimated by $\mu_{k,g}$), with later budburst estimated for
232 taller trees under increasing chilling and photoperiods (Fig. S5). We illustrate this relationship using
233 *Alnus incana*—a shorter and characteristically acquisitive species—and *Quercus rubra*—a taller and
234 characteristically conservative species—as examples (Fig 2,S5). In contrast, seed mass had a negligible
235 relationship with budburst and all three cues (Fig. 2 g-i), producing a relatively small differences
236 between estimates of budburst when the effects of seed mass are considered or not (for which estimate
237 are made using a trait effect of zero, Fig S5 d-f & Table S4).

238

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

251

252 In partitioning the measurement error in the trait values from variation from species and study-level
253 effects, we found that the species-level variation across traits (σ_{trait}^2) were comparable to, or greater
254 than variation across studies (σ_{study}^2 , Fig 3). In particular, variation across studies was greatest for
255 height, with an estimated study level variation (σ_{study}^2) of 7.5 m, than caused by species-level variation
256 (σ_{trait}^2), with an estimate of 5.9 m (Fig 3a). For seed mass and LNC, study-level variation was less
257 than that of the species-level variation, with variation in seed mass observations of 1 mg and 1.6 mg
258 for study-level and species-level variation respectively and for LNC observations estimates of 3.6 mg
259 g⁻¹ for study-level variation and 5.1 mg g⁻¹ for the species-level variation (Fig 3c and d). Study-level
260 variation was smallest for observations of SLA, with the estimate of 3.3 mm² mg⁻¹ for study-level
261 variations being approximately half that of the estimated species-level variation of 7.8 mm² mg⁻¹ (Fig
262 3b). Across all traits, study-level variation (σ_{study}^2) made a considerable contribution to the overall
263 variation observed in our trait values and suggests that models using large trait databases that fail to
264 separate out study from species-level variation (σ_{trait}^2) may poorly estimate species traits.

265

266 Discussion

267 We found some species traits influenced the timing of budburst in response to one or more of the three
268 primary cues of spring phenology: chilling, forcing and photoperiod. While the relationships between
269 some traits and phenological cues differed from our predictions, several of the trait effects we con-
270 sidered were associated with earlier or later phenology, following well-established gradients in growth
271 strategies predicted by functional trait frameworks (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby,

272 1998; Westoby & Wright, 2006; Wright *et al.*, 2004). Early species—known to budburst under weak
273 forcing, chilling, and photoperiod cues—exhibited several traits associated with fast and acquisitive
274 growth strategies, while later budbursting species—that require stronger forcing, chilling, and pho-
275 toperiod cues—did exhibit several traits associated with conservative, slower growth strategies. We
276 found the largest budburst responses occurred for traits related to resource acquisition and structure,
277 with SLA, LNC, and height all showing large responses to at least one of our three cues. In con-
278 trast, our one reproductive trait—seed mass—showed the smallest response. Our results provide a
279 major step forward in integrating phenology into broader trait syndromes that shape species growth
280 strategies, and support previous findings from more local scales that found strong relationships be-
281 tween height and species phenology (Osada & Hiura, 2019; Seiwa, 1999). Our more global analysis
282 is also in agreement with previous studies of plant phenological events, in which no relation is found
283 between phenology and seed mass in woody plants (Bolmgren & D. Cowan, 2008; Ettinger *et al.*, 2018).

284

285 In addition to identifying traits that also relate to phenological cues and the timing of spring bud-
286 burst, our results also provide important insight into the use of data from large databases to estimate
287 ecological processes. By partitioning the different sources of variation that contribute to the observed
288 trait values, we were able to demonstrate the considerable effects study-level variation can have on
289 trait values, which for some traits even exceeded the species-level variation. This variation is the result
290 of a myriad of factors, including observer error or differences in methodologies, and persist in any
291 database pooling data from diverse sources. To the best of our knowledge, our results provide some
292 of the strongest evidence for why it is important for analyses using data from aggregate databases to
293 account for the effects of this and other sources of variation in their analyses.

294 Effects of phenology-trait relationships on community assembly

295 Our findings suggest the changing pressures across the early growing season may affect the temporal
296 assembly of communities. Species with cue responses associated with earlier budburst had some traits
297 indicative of acquisitive growth strategies (shorter heights and high LNC) that allow faster return on
298 resource investments (Chave *et al.*, 2009; Grime, 1977; Westoby, 1998). These traits should allow early
299 species benefit from greater light availability in the open canopy of many temperate forests in the
300 early spring. In contrast, later-budbursting species had traits associated with slower, more conserva-
301 tive, growth (Chave *et al.*, 2009; Grime, 1977; Westoby, 1998) (Fig 2), which may help them compete
302 for the more limited soil and light resources later in the growing season. These traits have also been
303 linked to other ecological processes and species characteristics that define community structure and
304 diversity, such as species successional position (Laube *et al.*, 2014b), and is in agreement with the

305 differences we observed for height and LNC between *Alnus incana* (a pioneer species) and *Quercus*
306 *rubra* (a later successional species); Fig 2).

307

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

319

320 Phenology-trait relationships under future climates

321 Incorporating phenology within broader trait syndromes could aid forecasting of species and commu-
322 nity responses to climate change. While decades of research have documented phenological shifts with
323 anthropogenic climate change, increasing research suggests a potential connection between phenolog-
324 ical responses to warming and performance with warming, where species that shift their phenology
325 more also perform better (Cleland *et al.*, 2012; Macgregor *et al.*, 2019).

326

327 Our results suggest this phenology-performance relationship could be driven in part by a suite of traits
328 that covary with phenological cues to determine how responsive species are to warming. Species with
329 smaller responses to all cues, especially chilling and photoperiod, would tend to advance more with
330 warming, which our results suggest would allow these species to also grow more quickly. These results
331 could further aid in predicting the potential for invasion, as communities with similar phenologies
332 and suites of traits, appear more susceptible to fast growing, phenologically more responsive invasive
333 species (Alexander & Levine, 2019; Schuster *et al.*, 2021; Wolkovich & Cleland, 2011).

334

335 Our analytical approach and results may be especially useful to help forecast changes in forest dy-
336 namics. Identifying the varying trait syndromes of forest communities over a spring season can aid
337 predictions of how climate change will alter species growth and productivity. For example, our results

338 suggest that, by favoring more phenologically responsive species (i.e., with small chilling and pho-
339 toperiod responses), warming may also favor species with acquisitive growth strategies. In contrast,
340 conservative species, which appear less phenologically responsive to changes in temperature (due to
341 larger chilling and photoperiod responses) could face greater abiotic and biotic stress (Guy, 2014).

342

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

353

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357 Author Contributions Statement

358 DL, FAMJ, GL, MG, DS, and EMW planned and designed the study. All authors conducted the
359 literature review and cleaned the database. DL, FAMJ, GL, and EMW performed the data analysis
360 and contributed code. DL, FAMJ, and GL created the figures. DL and EMW wrote the initial draft
361 and all authors reviewed and revised the manuscript.

362 Competing Interests Statement

363 The authors declare no competing interests.

³⁶⁴ **Data availability statement**

³⁶⁵ The phenological data used for this manuscript is a subset of the existing OSPREE dataset (doi:10.5063/F1CZ35KB)
³⁶⁶ and the trait data a subset of the the TRY database (doi:10.1111/gcb.14904) and the BIEN database
³⁶⁷ (doi: 10.1111/2041-210X.1286).

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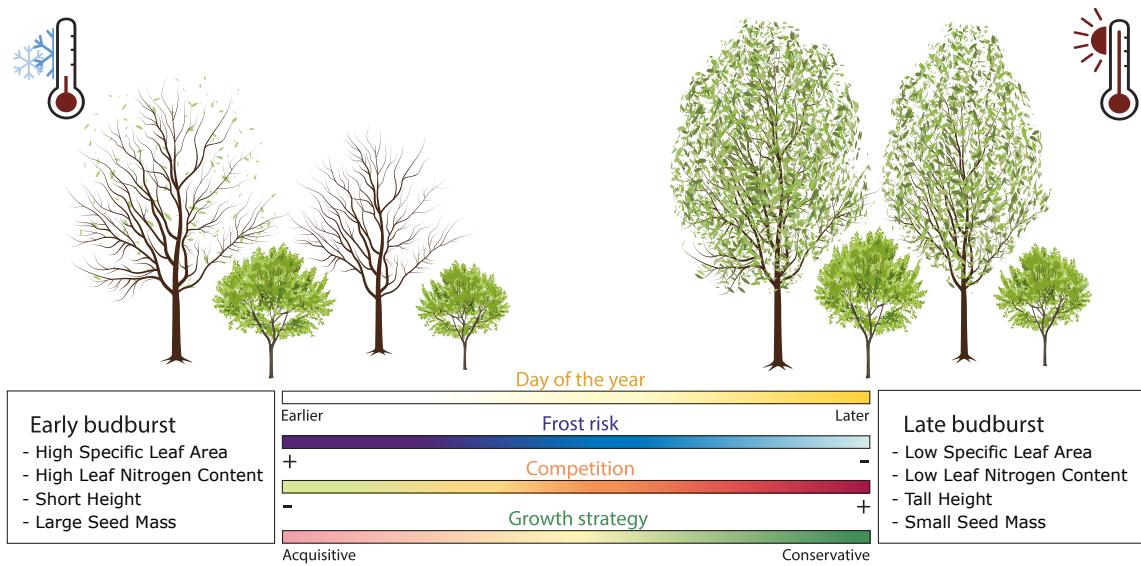


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater abiotic and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

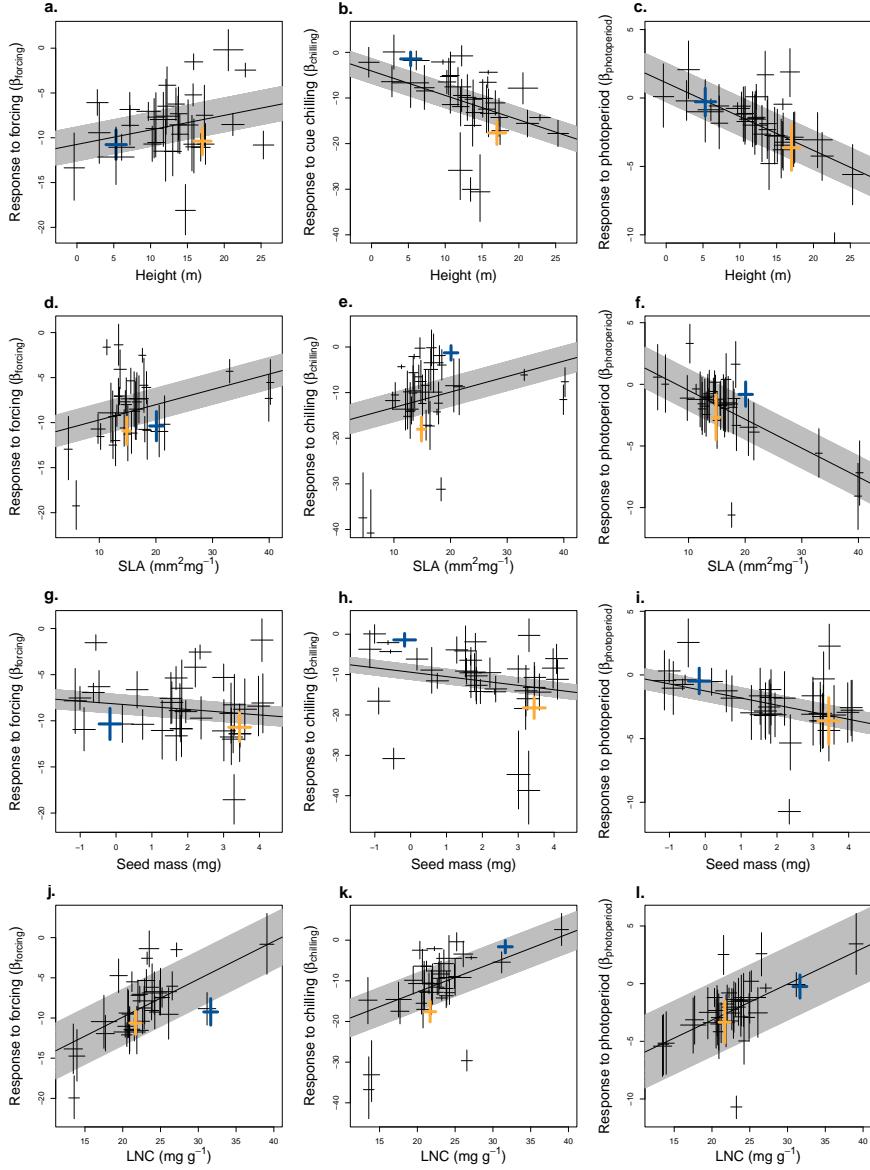


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third 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 cues) 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. The two example species depicted in Fig S5 are colored in each panel, with the acquisitive species (*Alnus incana*) shown in blue, and the conservative species (*Quercus rubra*) shown in yellow.

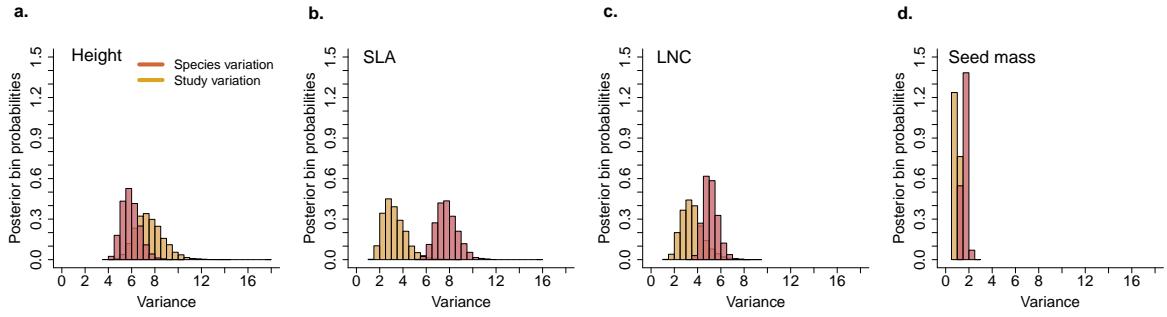


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf area, **c**, leaf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