

¹ Budburst timing within a functional trait framework

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³ Running title: Budburst responses associated with traits

⁴ **Summary**

- ⁵ 1. Phenology, **the timing of recurring life history events**, can vary substantially in different environments and for different species. While climate change has shifted phenology by altering its proximate drivers, **such as temperature**, changes in the ultimate drivers that select for species-level variation remain poorly explained. Theory suggests that species-level variation in phenology can result from shifting environmental pressures that favour different strategies across the spring growing season: from the early season, where higher abiotic risks and greater availability of nutrients and light favour cheaper leaves and acquisitive growth strategies, to later when a more benign environment and lower levels of light and nutrients favour conservative growth strategies. From this framework we can predict suites of traits that may co-vary with species phenologies, but the high variability in traits, **and especially phenology**, across environments, have made testing the role of phenology within a trait framework challenging.
- ¹⁶ 2. Using a modelling framework that accommodates this variability, we used phenological data from a database of controlled environment experiments and tree trait data from two trait databases to test the relationships between traits and three cues for tree budburst: spring temperatures (forcing), winter temperatures (chilling), and daylength (photoperiod).
- ²⁰ 3. We found mixed support for our predictions for how traits relate to budburst timing and cues. Species with cues indicative of earlier budburst, like low chilling and photoperiod, had some traits related to acquisitive strategies (they were shorter with higher leaf nitrogen content). 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 dynam-
³² ics. Spring phenology, for example, defines the start and overall length of the growing season—shaping
³³ forest carbon storage and species interactions (Beard *et al.*, 2019; Cleland *et al.*, 2007; Gu *et al.*, 2022).
³⁴ Shifts in phenology with climate change across systems (Menzel *et al.*, 2006; Vitasse *et al.*, 2021) have
³⁵ thus led to growing concerns over their possible impacts.

³⁶

³⁷ Predicting these changes requires understanding the drivers of phenology both at a proximate scale (**the**
³⁸ **environmental triggers that determine phenology each year, such as temperature and daylength**) and at
³⁹ an ultimate scale, where long-term environmental pressures may select for different phenologies across
⁴⁰ species, **for example, 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 **growth forms** (Flynn & Wolkovich, 2018) that cause them to have similar
⁴⁵ growth strategies. But current work provides limited insights into the drivers of these differences across
⁴⁶ species and how they can be used to predict future changes in community dynamics (Chuine *et al.*,
⁴⁷ 2016; Flynn & Wolkovich, 2018; Laube *et al.*, 2014).

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⁴⁹ At the ultimate level, plant phenologies may vary due to changing pressures across the growing 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 of woody**
⁵⁹ **species have highlighted associations between trade-offs in major wood and leaf traits and phenology**
⁶⁰ (Wang *et al.*, 2021; Wolkovich & Ettinger, 2014) and herbaceous plants (Sporbert *et al.*, 2022) (Fig
⁶¹ 1), and hypothesized that phenology may fit within the acquisitive (fast) to more conservative (slow)

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

63

64 Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation
65 of the leaf and wood economic spectra (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby &
66 Wright, 2006; Wright *et al.*, 2004), but they make limited predictions of trait variability (Viole *et al.*,
67 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving
68 the relationships between broader trait syndromes and phenology largely unknown. Understanding
69 these relationships, however, 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 though recent studies have explored these relationships for herbaceous species (Rauschkolb *et al.*, 2024;
73 Sporbert *et al.*, 2022)). At these spatial scales the problem of proximate drivers causing phenological
74 variation can be more easily ignored, depending on the system. Adding phenology to broader trait
75 frameworks becomes more complex because high levels of variation occur across large spatial and tem-
76 poral ranges.

77

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

91

92 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-
93 nology into functional trait research. In addition to how well we understand the environmental cues
94 that trigger early versus late leafout, in many forests we see strong gradients in frost risk or nutrient
95 availability from the start to the end of the spring growing season (Fig 1). We might predict some
96 variability in how traits relate to different growth strategies (driven by different selective pressures),

97 which then lead to differences across groups of species (Horbach *et al.*, 2023; Wang *et al.*, 2021), such
98 as the differences in traits that facilitate frost tolerance versus avoidance (Lenz *et al.*, 2013; Sakai
99 & Larcher, 1987) or to herbivory (Coley *et al.*, 1985). Broadly we predict acquisitive species to be
100 shorter, with leaf traits favorable to the low light conditions of the understory later in the growing
101 season—that is, they should produce leaves with high specific leaf area (SLA) and leaf nitrogen content
102 (LNC)(Díaz *et al.*, 2016; Reich *et al.*, 1997; Wright *et al.*, 2004) (Fig 1). We would predict such species
103 to exhibit early phenology, budbursting under low chilling and cool spring conditions (low forcing)
104 when photoperiods are short. Canopy species that budburst later via larger cue responses and when
105 competition for soil resources is greater, would then have traits associated with conservative growth—
106 taller with denser wood (Chave *et al.*, 2009; Laughlin *et al.*, 2010) and leaf traits suited for the higher
107 light conditions of the canopy (low SLA and low LNC, Fig 1). Seed size may similarly be predicted
108 from this acquisitive to conservative continuum, as acquisitive species produce smaller seeds and the
109 taller and more conservative species produce larger, better provisioned, seeds (Díaz *et al.*, 2016) Fig 1).

110

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

120

121 Methods

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

129

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

132

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

141

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

159

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

165 first principal component explained 32% of variation while the second explained 24.2% of the variation
 166 (Fig. S3), with high correlations between SLA and LDMC, and between height and SSD (Fig. S3).
 167 By excluding the trait from each of these highly correlated trait pairs with the least amount of data
 168 (specifically LDMC and SSD) we were able to increase the number of species in our dataset from the
 169 26 species with complete data for six traits, to 37 species with complete data for four traits. The
 170 data for these 37 species were from 24 unique studies (sample sizes: height $n = 47781$, seed mass n
 171 = 281, LNC $n = 3853$, SLA $n = 7656$). We subsampled the height measurements of the 13 most
 172 frequently measured trees to reduce their influence on our height model. Since each of these 13 species
 173 were measured over 19 times more frequently than most other species, we randomly sampled 3000
 174 height measurements for each individual species, while including all height data for the remaining,
 175 less frequently measured, 24 species. **This subsampling was not required for any of the other traits**
 176 **included in our study.**

177 Joint model of trait and phenology

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

188 Trait sub-model

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

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

194 with

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

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

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

196

$$\boldsymbol{\alpha}_{\text{trait}} = \alpha_{\text{grand trait}} + \alpha_{\text{species}_i} \quad (4)$$

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

$$\boldsymbol{\alpha}_{\text{study}} = \begin{bmatrix} \alpha_{\text{study}_1} \\ \alpha_{\text{study}_2} \\ \vdots \\ \alpha_{\text{study}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{study}} \sim \text{Normal}(0, \sigma_{\text{study}}^2) \quad (6)$$

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

202 Phenology sub-model

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

$$Y_{\text{pheno}_{k,g}} \sim \text{Normal}(\mu_{k,g}, \sigma_d^2) \quad (7)$$

209 with

$$\mu_{k,g} = \alpha_{\text{pheno}_k} + \beta_{\text{chilling}_k} \cdot c_g + \beta_{\text{forcing}_k} \cdot f_g + \beta_{\text{photoperiod}_k} \cdot p_g \quad (8)$$

210 and

$$\beta_{\text{chilling}_k} = \alpha_{\text{chilling}_k} + \beta_{\text{trait.chilling}} \cdot \alpha_{\text{trait}_k} \quad (9)$$

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

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

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

$$\boldsymbol{\alpha}_{\text{pheno}} = \{\alpha_{\text{pheno}_1}, \dots, \alpha_{\text{pheno}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \text{Normal}(\mu_{\text{pheno}}, \sigma_{\text{pheno}}^2) \quad (10)$$

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

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

222

223 The model was coded in the Stan (Stan Development Team, 2024), which is a probabilistic program-
 224 ming language for building Bayesian models. We used the rstan package (Stan Development Team,
 225 2018) to interface with and run the Stan code in R version 3.3.6 (R Development Core Team, 2017).
 226 For our model, we chose weakly informative priors, and validated them using a series of prior predic-
 227 tive checks. The model was fit with 1,000 iterations per chain across 4 chains (4,000 total sampling
 228 iterations), and all models met basic diagnostic checks, including no divergences, high effective sample
 229 size (n_{eff}), and \hat{R} close to 1, fitting the data well (Fig S4). Here in our discussion of the results we

230 present our model estimates as the means and 90% posterior uncertainty intervals (UI), with the 50%
231 UI depicted in the figures and both included in the supplementary tables to allow for comparison and
232 to assess the strength of relationships. We consider parameters with UI that overlap to be similar to
233 each other and those that include zero in the 90% UI to have small effects.

234 Results

235 Across traits, height, SLA, and LNC were related to one or more environmental cue ($\beta_{\text{chilling}_k}$, β_{forcing_k} ,
236 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).
237 As we predicted, height was negatively related to chilling ($\beta_{\text{chilling}_k}$) and photoperiod ($\beta_{\text{photoperiod}_k}$),
238 with taller species having larger responses to high chilling and longer photoperiod conditions (-0.5 m
239 per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized pho-
240 toperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). We found height to have a larger relationship with
241 the timing of budburst (as estimated by $\mu_{k,g}$), line ??meaning that taller tree species will budburst
242 later as chilling and photoperiods increase, while shorter species will budburst under lower chilling and
243 photoperiod cues and therefore be earlier line ??(Fig. ??). In contrast, seed mass had a negligible
244 relationship with budburst and all three cues (Fig. 2 g-i & Table S4).

245
246 Of the studied leaf traits, we found that SLA related to photoperiod ($\beta_{\text{photoperiod}_k}$, -0.2 mm²/mg per
247 standardized photoperiod; 90% UI: -0.5, 0.0, Fig. 2 f, Table S3), but did not strongly predict responses
248 to chilling ($\beta_{\text{chilling}_k}$) or forcing treatments (β_{forcing_k} , Fig. 2 d & e). The relationship between LNC and
249 budburst cues, were in line with our predictions, with high LNC species being less responsive to chilling
250 (0.7 mg/g per standardized chilling; 90% UI: 0.2, 1.2, Table S5), forcing (0.5 mg/g per standardized
251 forcing; 90% UI: 0.1, 0.8, and photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6),
252 Fig 2 j-l & Fig ?? d-f). This suggests that species that produce leaves with high nitrogen content,
253 which relates generally to high photosynthetic rates and acquisitive growth, are likely to budburst
254 early based on the relationships between this trait and environmental cues.

255
256 We found that the species-level variance across traits (σ_{trait}^2) were comparable to, or greater than vari-
257 ance across studies (using our model that partitions the measurement error in the trait values from
258 variance from species and study-level effects, σ_{study}^2 , Fig 3). For height, variance across studies (σ_{study}^2)
259 was greater (7.5 m; 90% UI: 5.7, 9.8), than the variance caused by species (σ_{trait}^2 , 5.9 m; 90% UI: 4.9,
260 7.3, Fig 3a). For seed mass and LNC, study-level variance was less than that of the species-level
261 variance, with variance in seed mass observations of 1 mg (90% UI: 0.8, 1.1) and 1.6 mg (90% UI: 0.8,
262 1.1) for study-level and species-level variance respectively and for LNC 3.6 mg g⁻¹ (90% UI: 2.2, 5.3)

for study-level variance and 5.1 mg g^{-1} for the species-level variance (90% UI: 2.2, 5.3, Fig 3c and d). Study-level variance was smallest for SLA, with the estimate of $3.3 \text{ mm}^2 \text{ mg}^{-1}$ (90% UI: 2, 5.1) for study-level variance being approximately half that of the estimated species-level variance of $7.8 \text{ mm}^2 \text{ mg}^{-1}$ (90% UI: 6.4, 9.4, Fig 3b).

267

268 Discussion

We found several species traits influenced the timing of budburst in response to one or more of the three primary cues of spring phenology: chilling, forcing and photoperiod. **The relationships between SLA and phenological cues differed from our predictions, as species with high SLA that produce larger, thin leaves that invest less in leaf mass and are associated with more acquisitive growth strategies, exhibited larger responses to photoperiod indicative of late budbursting species.** But the trait effects of height and LNC on the timing of budburst did follow well-established gradients in growth strategies predicted by functional trait frameworks (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby & Wright, 2006; Wright *et al.*, 2004). Early species which generally budburst given small levels of forcing, chilling, and shorter photoperiod, exhibited relationships with several traits associated with fast and acquisitive growth strategies. Later budbursting species, which require larger levels of forcing, chilling, and longer photoperiods to initiate growth, however, exhibited traits indicative of conservative, slower growth strategies. We found the largest budburst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and height all showing large responses to at least one of our three cues. **Seed mass, which was our one reproductive trait, showed the smallest response to all cues.** Our results provide a major step forward in integrating phenology into broader trait syndromes that shape species growth strategies, and support previous findings from more local scales that found large relationships between height and species phenology (Osada & Hiura, 2019; Seiwa, 1999). Our **large-scale** analysis supports previous studies of plant phenological events, which found no relationship between phenology and seed mass in woody plants (Bolmgren & D. Cowan, 2008; Ettinger *et al.*, 2018).

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In addition to identifying trait-phenology relationships shaping the timing of spring budburst, our results also provide important insights into the use of data from large databases to estimate ecological processes. By partitioning the different sources of variation that contribute to observed trait values, we found study-level variance made a considerable contribution to the overall variance observed in our trait values. For height in particular, the differences due to study exceeded those due to species. Such study-level variance is likely the result of myriad factors, including observer error and differences in methodologies, that are present in any dataset that pools data from diverse sources. Our findings

²⁹⁶ thus suggests that models using large trait databases that fail to separate out study from species-level
²⁹⁷ variance may poorly estimate species traits and may need to account for this variance to make the
²⁹⁸ most accurate predictions. .

²⁹⁹ Effects of phenology-trait relationships on community assembly

³⁰⁰ Our findings suggest the changing pressures across the early growing season may affect the temporal
³⁰¹ assembly of communities. Species with small cue requirements, **as exemplified by their small responses**
³⁰² **to experimental cues and indication of earlier budburst**, had some traits indicative of acquisitive growth
³⁰³ strategies (shorter heights and high LNC) that allow faster return on resource investments (Chave *et al.*,
³⁰⁴ 2009; Grime, 1977; Westoby, 1998). These traits should allow early species to benefit from greater light
³⁰⁵ availability in the open forest canopy in the early spring and withstand the low light conditions later
³⁰⁶ in the season. In contrast, later-budbursting species had traits associated with slower, more conserva-
³⁰⁷ tive, growth (Chave *et al.*, 2009; Grime, 1977; Westoby, 1998), which may help them compete for the
³⁰⁸ more limited soil and light resources later in the growing season. Similar trait-phenology relationships
³⁰⁹ have also been linked to other ecological processes and species characteristics that define community
³¹⁰ structure and diversity, such as species successional position (Laube *et al.*, 2014), providing support
³¹¹ to the differences we observed for height and LNC in our example comparing *Alnus incana* (a pioneer
³¹² species) and *Quercus rubra* (a later successional species; Fig 2).

³¹³

³¹⁴ The trait by cue relationships that deviated from our expectations also offer novel insights into the
³¹⁵ potential tradeoffs between traits and environmental cues. All of our traits are associated with multiple
³¹⁶ aspects of species growth, and may be adaptive for reasons other than those we predicted. Contrary
³¹⁷ to our predictions, **we found a negligible response to forcing with tree height**, which could prevent
³¹⁸ frost damage or xylem cavitation under a late spring frost (Clements *et al.*, 1972; Marquis *et al.*, 2020)
³¹⁹ and influence annual cambial meristem growth (Lenz *et al.*, 2016). **Similarly, the lack of a relationship**
³²⁰ **between SLA and temperature was surprising, given that temperature does influence the rates of leaf**
³²¹ **growth and therefore SLA in the spring (CITES)**. Our findings may be indicative of other physiological
³²² constraints or tradeoffs between SLA and leaf development, with selection by other cues. Variation
³²³ in traits like SLA also reflects differences in species relative growth rates or leaf longevity, and not
³²⁴ just photosynthetic potential (Reich, 2014; Westoby, 1998). These findings highlight the complexity of
³²⁵ determining the drivers of species trait profiles.

³²⁶ **Phenology-trait relationships under future climates**

³²⁷ Incorporating phenology within broader trait syndromes could aid forecasting of species and commu-
³²⁸ nity responses to climate change. While decades of research have documented phenological shifts with
³²⁹ anthropogenic climate change (Fitter & Fitter, 2002; Menzel *et al.*, 2006), increasing research suggests
³³⁰ a potential connection between phenological responses to warming and performance with warming,
³³¹ where plant species that shift their phenology more also perform better (Cleland *et al.*, 2012).

³³²

³³³ **Future outlook and applications**

³³⁴ Our results suggest this phenology-performance relationship could be driven in part by a suite of traits
³³⁵ that covary with phenological cues to determine how responsive species are to warming. Species with
³³⁶ smaller responses to all cues, especially chilling and photoperiod, have smaller cue requirements and
³³⁷ as such would tend to advance more with warming (Guy, 2014). Our results suggest that these same
³³⁸ species are likely to have acquisitive traits, such as short heights and high LNC that allow them to
³³⁹ grow quickly and benefit from the greater availability of nutrients in the early spring. Understanding
³⁴⁰ these trait-phenology relationships may provide insight into how climate change may alter species
³⁴¹ coexistence (Rudolf, 2019; Wolkovich & Donahue, 2021). A greater understanding of trait-phenology
³⁴² relationships may also improve our ability to manage species invasions. Invasive species tend to have
³⁴³ earlier phenologies (Alexander & Levine, 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019), but pos-
³⁴⁴ sibly also a unique suite of traits that facilitate fast growth (Fridley *et al.*, 2022), thus understanding
³⁴⁵ how much early phenology versus fast growth drive their success could aid management decisions.

³⁴⁶

³⁴⁷ Our analytical approach and results may be especially useful to help forecast changes in forest dy-
³⁴⁸ namics. Identifying the varying trait syndromes of forest communities over a spring season can aid
³⁴⁹ predictions of how climate change will alter species growth and productivity. For example, our results
³⁵⁰ suggest that, by favoring more phenologically responsive species (i.e., with small chilling and pho-
³⁵¹ toperiod responses), warming may also favor species with acquisitive growth strategies. In contrast,
³⁵² conservative species, which appear less phenologically responsive to changes in temperature (due to
³⁵³ larger chilling and photoperiod responses) could face greater abiotic and biotic stress (Guy, 2014).

³⁵⁴

³⁵⁵ Our results could further help identify which species are most likely to be negatively impacted under
³⁵⁶ future climates, and develop better strategies for climate change mitigation and conservation. Species
³⁵⁷ that fail to advance phenologically with warming might experience more competition (Alexander &
³⁵⁸ Levine, 2019; Carter *et al.*, 2018), as species that begin growth increasingly earlier with warming have

359 more time to deplete resources. In addition to altering the timing and interactions between species
360 within a season, species trait syndromes have the potential to further redefine the environmental
361 conditions under which growth occurs and, as a result, shape community assembly and productivity
362 within ecological communities (Rudolf, 2019; Wolkovich & Donahue, 2021). By identifying the species
363 most vulnerable to climate change impacts, we can develop more effective management practices that
364 prevent the loss of critical ecosystem services and preserve community diversity under future conditions.

365

³⁶⁶ **References**

- ³⁶⁷ Alexander, J.M. & Levine, J.M. (2019) Earlier phenology of a nonnative plant increases impacts on
³⁶⁸ native competitors. *PNAS* **116**, 6199–6204.
- ³⁶⁹ Augspurger, C.K. (2009) Spring 2007 warmth and frost : phenology , damage and refoliation in a
³⁷⁰ temperate deciduous forest. *Functional Ecology* **23**, 1031–1039.
- ³⁷¹ Beard, K.H., Kelsey, K.C., Leffler, A.J. & Welker, J.M. (2019) The Missing Angle : Ecosystem Con-
³⁷² sequences of Phenological Mismatch. *Trends in Ecology and Evolution* **34**, 885–888.
- ³⁷³ Bolmgren, K. & D. Cowan, P. (2008) Time – size tradeoffs: a phylogenetic comparative study of
³⁷⁴ flowering time, plant height and seed mass in a north-temperate flora. *Oikos* **117**, 424–429.
- ³⁷⁵ Carter, S.K., Saenz, D. & Rudolf, V.H. (2018) Shifts in phenological distributions reshape interaction
³⁷⁶ potential in natural communities. *Ecology Letters* **21**, 1143–1151.
- ³⁷⁷ Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a
³⁷⁸ worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.
- ³⁷⁹ Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A. &
³⁸⁰ Améglio, T. (2016) Can phenological models predict tree phenology accurately in the future? The
³⁸¹ unrevealed hurdle of endodormancy break. *Global change biology* **22**, 3444–3460.
- ³⁸² Chuine, I. & Cour, P. (1999) Climatic determinants of budburst seasonality in four temperate-zone
³⁸³ tree species. *New Phytologist* **143**, 339–349.
- ³⁸⁴ Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S.
³⁸⁵ & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate
³⁸⁶ change.pdf. *Ecology* **93**, 1765–1771.
- ³⁸⁷ Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology
³⁸⁸ in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.
- ³⁸⁹ Clements, J.R., Fraser, J, W. & Yeatman, C.W. (1972) Frost Damage to White Spruce Buds. *Canadian*
³⁹⁰ *Journal of Forest Research* **2**, 62–63.
- ³⁹¹ Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource Availability and Plant Antiherbivore Defense.
³⁹² *Science* **230**, 895–899.
- ³⁹³ Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth,
³⁹⁴ C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T.,

- 395 Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel,
396 H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S.,
397 Günther, A., Falcuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of
398 plant form and function. *Nature* **529**, 167–171.
- 399 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F., Savas, T.,
400 Samaha, J.A. & Wolkovich, E.M. (2020) Winter temperatures predominate in spring phenological
401 responses to warming. *Nature Climate Change* **10**, 1137–1142.
- 402 Ettinger, A.K., Gee, S. & Wolkovich, E.M. (2018) Phenological sequences: how early-season events
403 define those that follow. *American Journal of Botany* **105**, 1771–1780.
- 404 Fitter, A.H. & Fitter, R.S.R. (2002) Rapid Changes in Flowering Time in British Plants. *Science* **296**,
405 1689–1691.
- 406 Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across
407 all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.
- 408 Fridley, J.D., Bauerle, T.L., Craddock, A., Ebert, A.R., Frank, D.A., Heberling, J.M., Hinman, E.D.,
409 Jo, I., Martinez, K.A., Smith, M.S., Woolhiser, L.J. & Yin, J. (2022) Fast but steady: An integrated
410 leaf-stem-root trait syndrome for woody forest invaders. *Ecology Letters* **25**, 900–912.
- 411 Grime, J.P. (1977) Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance
412 to Ecological and Evolutionary Theory Author (s): J . P . Grime Source : The American Naturalist
413 , Vol . 111 , No . 982 (Nov . - Dec ., 1977), pp . 1169-1194 Published. *The American Naturalist*
414 **111**, 1169–1194.
- 415 Gu, H., Qiao, Y., Xi, Z., Rossi, S., Smith, N.G., Liu, J. & Chen, L. (2022) Warming-induced in-
416 crease in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. *Nature
417 Communications* **13**, 1–8.
- 418 Guy, R.D. (2014) The early bud gets to warm. *New Phytologist* **202**, 7–9.
- 419 Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying dormancy
420 requirements for Pacific Northwest tree species. *Frontiers in Plant Science* **6**, 1–12.
- 421 Horbach, S., Rauschkolb, R. & Römermann, C. (2023) Flowering and leaf phenology are more variable
422 and stronger associated to functional traits in herbaceous compared to tree species. *Flora* **300**, 1–9.
- 423 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'keefe, J. & Richardson, A.D.
424 (2012) Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change
425 Biology* **18**, 2365–2377.

- 426 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C. & et al. (2020) TRY plant trait database
427 – enhanced coverage and open access. *Global Change Biology* **26**, 119–188.
- 428 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014) Chilling outweighs
429 photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- 430 Laughlin, D.C., Leppert, J.J., Moore, M.M. & Sieg, C.H. (2010) A multi-trait test of the leaf-height-
431 seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* **24**, 493–501.
- 432 Lenz, A., Hoch, G., Körner, C. & Vitasse, Y. (2016) Convergence of leaf-out towards minimum risk of
433 freezing damage in temperate trees. *Functional Ecology* **30**, 1480–1490.
- 434 Lenz, A., Hoch, G., Vitasse, Y. & Körner, C. (2013) European deciduous trees exhibit similar safety
435 margins against damage by spring freeze events along elevational gradients. *New Phytologist* **200**,
436 1166–1175.
- 437 Lopez, O.R., Farris-Lopez, K., Montgomery, R.A. & Givnish, T.J. (2008) Leaf phenology in relation
438 to canopy closure in southern Appalachian trees. *American Journal of Botany* **95**, 1395–1407.
- 439 Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S.M., Guaderrama, D., Hinchliff,
440 C.E., Jørgensen, P.M., Kraft, N.J., McGill, B., Merow, C., Morueta-Holme, N., Peet, R.K., Sandel,
441 B., Schildhauer, M., Smith, S.A., Svenning, J.C., Thiers, B., Violle, C., Wiser, S. & Enquist, B.J.
442 (2018) The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN)
443 database. *Methods in Ecology and Evolution* **9**, 373–379.
- 444 Marquis, B., Bergeron, Y., Simard, M. & Tremblay, F. (2020) Growing-season frost is a better predictor
445 of tree growth than mean annual temperature in boreal mixedwood forest plantations. *Global Change
446 Biology* **26**, 6537–6554.
- 447 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P.,
448 Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C.,
449 Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P.,
450 Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J., Wielgolaski, F.E., Zach, S. &
451 Zust, A. (2006) European phenological response to climate change matches the warming pattern.
452 *Global Change Biology* **12**, 1969–1976.
- 453 Morales-Castilla, I., Davies, T.J., Legault, G., Buonaiuto, D.M., Chamberlain, C.J., Ettinger, A.K.,
454 Garner, M., Jones, F.A.M., Loughnan, D., Pearse, W.D., Sodhi, D. & Wolkovich, E.M. (2024)
455 Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate
456 Change* **14**, 989–995.

- 457 Osada, N. & Hiura, T. (2019) Intraspecific differences in spring leaf phenology in relation to tree size
458 in temperate deciduous trees. *Tree Physiology* **39**, 782–791.
- 459 Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N.,
460 Shcherbakov, A., Meyke, E. & del Mar Delgado, M. (2013) Community-level phenological response
461 to climate change. *PNAS* **110**, 13434–13439.
- 462 Polgar, C., Gallinat, A. & Primack, R.B. (2014) Drivers of leaf-out phenology and their implications
463 for species invasions: insights from thoreau's concord. *New Phytologist* **202**, 106–115.
- 464 R Development Core Team (2017) R: A language and environment for statistical computing. *R Foundation
465 for Statistical Computing, Vienna, Austria*.
- 466 Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology
467 and Systematics* **16**, 179–214.
- 468 Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka,
469 D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F.,
470 Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M.,
471 Stevens, A.D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg,
472 M., Knickmann, B., Nordt, B., Wirth, C. & Römermann, C. (2024) Spatial variability in herbaceous
473 plant phenology is mostly explained by variability in temperature but also by photoperiod and
474 functional traits. *International Journal of Biometeorology* **68**, 761–775.
- 475 Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal
476 of Ecology* **102**, 275–301.
- 477 Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in
478 plant functioning. *Proceedings of the National Academy of Sciences* **94**, 13730–13734.
- 479 Rudolf, V.H.W. (2019) The role of seasonal timing and phenological shifts for species coexistence.
480 *Ecology Letters* **22**, 1324–1338.
- 481 Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants: Responses and adaptation to freezing stress*.
482 Springer-Verlag, Berlin, Heidelberg.
- 483 Seiwa, K. (1999) Changes in leaf phenology are dependent on tree height in Acer mono, a deciduous
484 broad-leaved tree. *Annals of Botany* **83**, 355–361.
- 485 Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., Konig, A., Nordt, B.,
486 Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstadter, A., Maskova, T., Primack,

- 487 R., Rosche, C., Shah, M.A., Stevens, A.D., Teilborger, K., Trager, S., Wirth, C. & Romermann,
488 C. (2022) Functional traits influence patterns in vegetative and reproductive plant phenology – a
489 multi-botanical garden study. *New Phytologist* **235**, 2199–2210.
- 490 Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3.
- 491 Stan Development Team (2024) Stan reference manual, v2.36.0.
- 492 Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J.
493 (2012) The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology
and Evolution* **27**, 244–252.
- 495 Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the
496 concept of trait be functional! *Oikos* **116**, 882–892.
- 497 Vitasse, Y. (2013) Ontogenetic changes rather than difference in temperature cause understory trees to
498 leaf out earlier. *New Phytologist* **198**, 149–155.
- 499 Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat,
500 C., Rebetez, M., Rixen, C., Strelbel, N., Schmidt, B.R., Wipf, S., Wohlgemuth, T., Yoccoz, N.G.
501 & Lenoir, J. (2021) Phenological and elevational shifts of plants , animals and fungi under climate
502 change in the European Alps. *Biological Reviews* **96**, 1816–1835.
- 503 Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2012) Seasonal priority effects : implications for
504 invasion and restoration in a semi-arid system. *Journal of Applied Ecology* **49**, 234–241.
- 505 Wang, L., Han, X., Yin, Q., Wang, G., Xu, J., Chai, Y. & Yue, M. (2021) Differences in leaf phenological
506 traits between trees and shrubs are closely related to functional traits in a temperate forest. *Acta
Oecologica* **112**, 103760.
- 508 Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**,
509 213–227.
- 510 Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in
511 Ecology & Evolution* **21**, 261–268.
- 512 Wolkovich, E.M. & Cleland, E.E. (2014) Phenological niches and the future of invaded ecosystems
513 with climate change. *AoB PLANTS* **6**, 1–16.
- 514 Wolkovich, E.M. & Donahue, M.J. (2021) How phenological tracking shapes species and communities
515 in non-stationary environments. *Biological Reviews* **96**, 2810–2827.

- 516 Wolkovich, E.M. & Ettinger, A.K. (2014) Back to the future for plant phenology research. *New Phy-*
517 *tologist* **203**, 1021–1024.
- 518 Wright, I.J., Westoby, M., Reich, P.B., Oleksyn, J., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-
519 Bares, J., Chapin, T., Cornellissen, J.H.C., Diemer, M., Flexas, J., Gulias, J., Garnier, E., Navas,
520 M.L., Roumet, C., Groom, P.K., Lamont, B.B., Hikosaka, K., Lee, T., Lee, W., Lusk, C., Midgley,
521 J.J., Niinemets, Ü., Osada, H., Poorter, H., Pool, P., Veneklaas, E.J., Prior, L., Pyankov, V.I.,
522 Thomas, S.C., Tjoelker, M.G. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*
523 **428**, 821–827.
- 524 Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology
525 on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* **107**, 22151–22156.
- 526 Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019) Phenology in a warming world: differences
527 between native and non-native plant species. *Ecology Letters* **22**, 1253–1263.

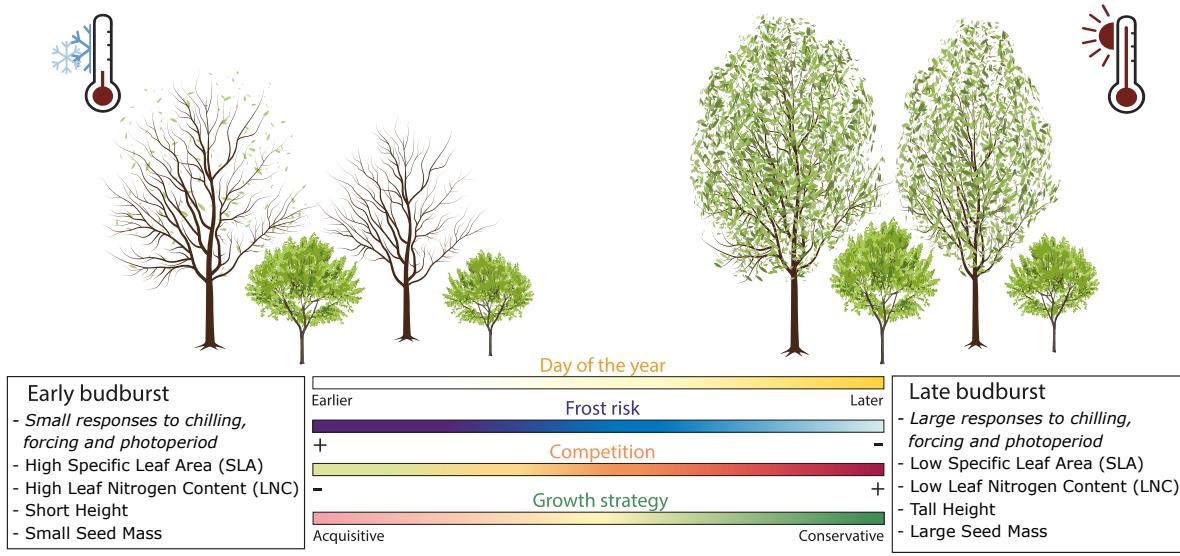


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies (Chave *et al.*, 2009; Westoby & Wright, 2006; Wright *et al.*, 2004), which may also include phenology (Wolkovich & Ettinger, 2014; ?). We predicted early-budbursting species would have 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.

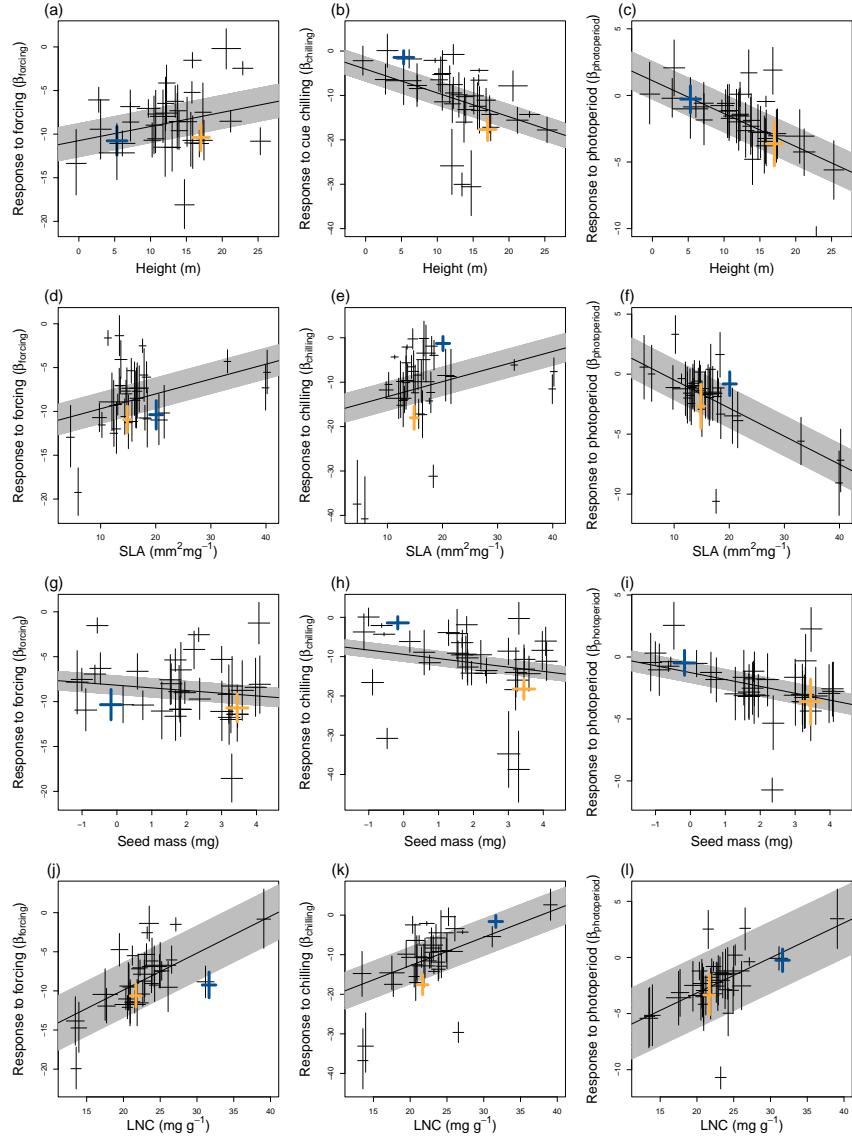


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, **with the black lines depicting strong linear relationships between estimated trait effects and the slopes of the cue responses** (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, 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.

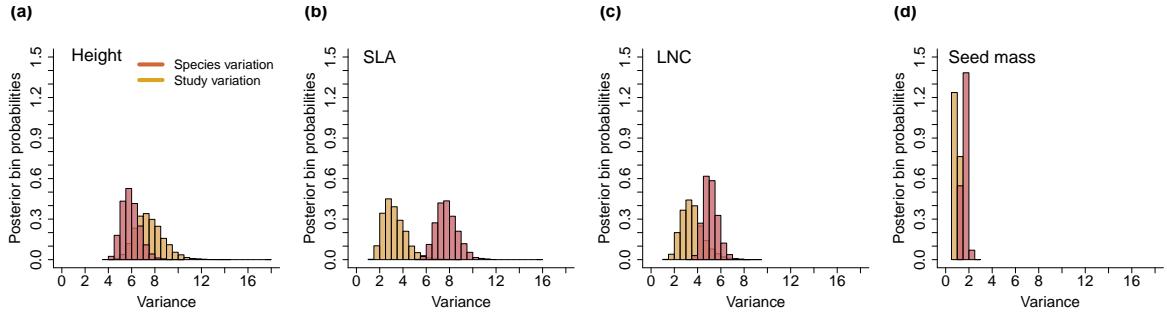


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ($\sigma_{\text{species}}^2$ and σ_{study}^2 respectively), with only (a) the height model estimating greater study-level variation than species-level, while our (b) specific leaf area, (c) leaf nitrogen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