

<sup>1</sup> Budburst timing within a functional trait framework

<sup>2</sup>

<sup>3</sup> Running title: Budburst responses associated with traits

<sup>4</sup> **Summary**

- <sup>5</sup> 1. Phenology, **the timing of recurring life history events**, can vary substantially in different environments and for different species. While climate change has shifted phenology by altering its environmental triggers, **such as temperature**, changes in the drivers that select for species-level variation remain poorly explained. Theory suggests that species-level variation in phenology can result from shifting environmental pressures that favour different strategies across the spring growing season: from the early season, where higher abiotic risks and greater availability of nutrients and light favour cheaper leaves and acquisitive growth strategies, to later when a more benign environment and lower levels of light and nutrients favour conservative growth strategies. This framework predicts a suite of traits that may co-vary with species phenologies, but the high variability in **phenology** across environments has made testing its role within a trait framework challenging.
- <sup>15</sup> 2. Using a modelling framework that accommodates this variability, with phenological data from a database of controlled environment experiments and tree trait data from two major databases we tested for relationships between traits and spring phenology in trees. Specifically, we examined the cues that drive early to late budburst: spring temperatures (forcing), winter temperatures (chilling), and daylength (photoperiod).
- <sup>20</sup> 3. We found mixed support for our predictions for how traits relate to budburst timing and phenology. Species with cues that lead to earlier budburst (**small responses to experimental chilling and photoperiod**) were shorter with **higher leaf nitrogen content**, both traits related to acquisitive strategies and thus in line with our predictions. However our one reproductive trait of seed mass showed no relationship with phenology, and other traits (e.g., specific leaf area) showed relationships in the opposite direction to our predictions.
- <sup>26</sup> 4. Synthesis: Our findings show how spring budburst phenology partially fits within a functional trait framework of acquisitive to conservative growth strategies. Leveraging these relationships could improve predictions of how communities shift in their growth strategies alongside changing phenology

29 with future warming.

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

32 

## Introduction

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

38

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

47

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

62 strategies associated with existing trait frameworks (Chave *et al.*, 2009; Wright *et al.*, 2004, Fig 1).

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, can improve forecasts of 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 across sites for herbaceous species (Rauschkolb  
73 *et al.*, 2024; Sporbert *et al.*, 2022). At more local spatial scales the problem of disentangling the local  
74 environmental triggers that shape traits (and vary across sites) and cause variation within or across  
75 species, can be more easily ignored in some systems (but see Albert *et al.*, 2011; Siefert *et al.*, 2015;  
76 Zuleta *et al.*, 2022, for discussion of systems with high variation within one species, site, or year).

77 Adding phenology to broader trait frameworks therefore becomes more complex as high levels of  
78 variation occur across larger spatial and temporal scales.

79 Recent climate change has highlighted how variable plant phenology is when observed over time and  
80 space across different species (Rudolf, 2019; Vitasse, 2013; Yu *et al.*, 2010), with many studies docu-  
81 menting how quickly phenology can shift with warming (Fitter & Fitter, 2002; Menzel *et al.*, 2006).  
82 But experiments conducted under controlled environments have shown that it is possible to consis-  
83 tently define early to late phenology from the known underlying cues (Chuine & Cour, 1999; Flynn &  
84 Wolkovich, 2018; Harrington & Gould, 2015). This work has found early species have small responses  
85 to the three major cues that determine woody plant budburst: forcing (accumulated warm tempera-  
86 tures usually in the spring), chilling (cool temperatures usually accumulated in the fall and winter),  
87 and photoperiod, while later species generally have larger responses to these cues (Flynn & Wolkovich,  
88 2018; Laube *et al.*, 2014). These responses suggest early species require lower amounts of forcing, chill-  
89 ing and shorter photoperiods to budburst, while species that budburst later require higher amounts of  
90 forcing, chilling and longer photoperiods (see Flynn & Wolkovich, 2018, for further details). The con-  
91 sistency of these relationships, alongside increasing evidence that intra-specific variation in tree spring  
92 phenology is low given the same climate (Aitken & Bemmels, 2016; Zeng & Wolkovich, 2024), allows  
93 us to estimate early to later active species across plant communities and diverse species assemblages.  
94 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phenol-  
95 ogy into functional trait research. In addition to how well we understand the environmental cues that  
96 lead to early versus late budburst, in many forests strong gradients in frost risk or nutrient availability

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

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

121

## 122 Methods

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

130

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

133

134 We then scraped the data from all articles reporting experiments that manipulated both photoperiod  
135 and/or temperature cues of woody species budburst, leafout, or flowering phenology, and for which  
136 there was a quantifiable response to each cue. We updated this database in July 2019 reviewing all  
137 new articles found using the previous search terms. Additional details on the methods used to as-  
138 semble, clean, and update this database are discussed by Ettinger *et al.* (2020) and Morales-Castilla  
139 *et al.* (2024). For the purpose of this study, we obtained a subset of the budburst data from OSPREE  
140 database and initially aimed to use data for 234 species used in Morales-Castilla *et al.* (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 is  
146 requested. **We obtained data from the BIEN databases on 5 December 2018 and the TRY data on 10**  
147 **April 2019.** We initially searched for trait data on the subset of 234 OSPREE species used in Morales-  
148 Castilla *et al.* (2024). From BIEN, this resulted in 94 of the 234 species available in the database, for  
149 which there were 13 unique traits. From the TRY database we received data for 10 unique traits for  
150 96 of the 234 requested species (Kattge *et al.*, 2020). As we were interested in the trait-phenology re-  
151 lationships of adult trees we subsetted the available data to **remove any observations denoted as being**  
152 **from juvenile individuals or with heights less than 2 m (following Natural Resources Canada, 2020, we**  
153 **assume this removes most individuals that were saplings when measured; analyses using an alternative**  
154 **cut-off of 1.37 m showed similar results).** We further removed all data from manipulative experiments  
155 or from plants growing in non-natural habitats. We then grouped trait values where appropriate, for  
156 example pooling trait values for specific leaf area (SLA) with those denoted as ‘SLA with petioles’,  
157 and ‘SLA without petioles’ in our analysis (see Table S1). We also removed data that was duplicated  
158 in both the TRY and BIEN datasets ( $n = 434,905$ ). For a full depiction of our data cleaning process  
159 and decisions see Fig. S2.

160

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

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

## **Joint model of trait and phenology**

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

### **Trait sub-model**

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

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

195 with

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

$$\alpha_{\text{trait}} = \alpha_{\text{grand trait}} + \alpha_{\text{species}_i} \quad (3)$$

196 where  $\alpha_{\text{species}_i}$  and  $\alpha_{\text{study}_j}$  are elements of the normal random vectors:

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

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

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 overall mean trait value. The  $\sigma_m^2$  parameter is the mea-  
 200 surement error for the observed trait values, and  $\sigma_{\text{species}}^2$  and  $\sigma_{\text{study}}^2$  represent species and study-level  
 201 variances in trait values. Of these parameters, we combine the mean trait value ( $\alpha_{\text{grand trait}}$ ) with  
 202 species-specific offsets from the mean trait value ( $\alpha_{\text{species},i}$ ) to form  $\boldsymbol{\alpha}_{\text{trait}}$ , which is shared by the  
 203 phenology sub-model 3.

## 204 Phenology sub-model

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

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

211 with

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

<sup>212</sup> and

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

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

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

<sup>213</sup> where  $\alpha_{\text{pheno}_k}$ ,  $\alpha_{\text{chilling}_k}$ ,  $\alpha_{\text{forcing}_k}$ , and  $\alpha_{\text{photoperiod}_k}$  are elements of the normal random vectors:

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

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

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

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

(13)

<sup>214</sup> The model partitions day of budburst for species ( $k$ ) as a combination of the overall mean day of  
<sup>215</sup> budburst without the influence of chilling, forcing, or photoperiod treatments ( $\alpha_{\text{pheno},k}$ , normally dis-  
<sup>216</sup> tributed with a mean of  $\mu_{\text{pheno}}$  and variance  $\sigma_{\text{pheno}}^2$ ) combined with the effects of treatments both  
<sup>217</sup> dependent and independent of trait values. The parameters  $\alpha_{\text{chilling}_k}$ ,  $\alpha_{\text{forcing}_k}$ , and  $\alpha_{\text{photoperiod}_k}$   
<sup>218</sup> represent the trait-independent responses of species  $k$  to chilling, forcing, and photoperiod treat-  
<sup>219</sup> ments respectively, each with an associated mean ( $\mu_{\text{chilling}}$ ,  $\mu_{\text{forcing}}$ ,  $\mu_{\text{photoperiod}}$ ) and variance ( $\sigma_{\text{chilling}}^2$ ,  
<sup>220</sup>  $\sigma_{\text{forcing}}^2$ ,  $\sigma_{\text{photoperiod}}^2$ ) across species. The shared parameter between the trait and phenology sub-model,  
<sup>221</sup>  $\alpha_{\text{trait}_k}$ , represents the effect of the species trait value on its responses to chilling ( $\beta_{\text{trait.chilling}}$ ), forcing  
<sup>222</sup> ( $\beta_{\text{trait.forcing}}$ ), and photoperiod ( $\beta_{\text{trait.photoperiod}}$ ). Finally, our model provides an estimate of  $\sigma_d^2$ , which

223 is the variance arising from measurement error for the observed day of budburst.

224

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

## 236 Results

237 Across traits, height, SLA, and LNC were related to one or more environmental cue ( $\beta_{chilling_k}$ ,  $\beta_{forcing_k}$ ,  
238 or  $\beta_{photoperiod_k}$ , Fig 2 a-f & j-l), with only LNC showing a relationship with all three cues (Fig. 2 j-l).  
239 As we predicted, height was negatively related to chilling ( $\beta_{chilling_k}$ ) and photoperiod ( $\beta_{photoperiod_k}$ ),  
240 with taller species having larger responses to high chilling and longer photoperiod conditions (-0.5  
241 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized  
242 photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). These large responses in the timing of budburst  
243 (as estimated by  $\mu_{k,g}$ ), in response to chilling and photoperiod treatments likely reflect that taller tree  
244 species require more chilling and forcing to budburst (conditions that are often met later in the growing  
245 season), while shorter species budburst earlier, under the lower chilling and photoperiod conditions  
246 that occur earlier in the spring . In contrast, seed mass had a negligible relationship with budburst  
247 and all three cues (Fig. 2 g-i & Table S4).

248

249 Of the studied leaf traits, we found that SLA related to photoperiod ( $\beta_{photoperiod_k}$ , -0.2 mm<sup>2</sup>/mg per  
250 standardized photoperiod; 90% UI: -0.5, 0.0, Table S3), but with larger responses to longer photoperi-  
251 ods for high SLA species (Fig. 2 f). We did not find strong responses to chilling ( $\beta_{chilling_k}$ ) or forcing  
252 treatments ( $\beta_{forcing_k}$ , Fig. 2 d & e) however. The relationship between LNC and budburst cues, was  
253 in line with our predictions, with high LNC species being less responsive to chilling (0.7 mg/g per  
254 standardized chilling; 90% UI: 0.2, 1.2, Table S5), forcing (0.5 mg/g per standardized forcing; 90%  
255 UI: 0.1, 0.8), and photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6, Fig 2 j-l).

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

259

260 We found that the species-level variance across traits were comparable to, or greater than, variance  
261 across studies (using our model that partitions the measurement error in the trait values from variance  
262 from species and study-level effects; Fig 3). For height, variance across studies ( $\sigma_{\text{study}}^2$ ) was greater (7.5  
263 m; 90% UI: 5.7, 9.8), than the variance caused by species ( $\sigma_{\text{species}}^2$ , 6 m; 90% UI: 4.9, 7.3, Fig 3a). For  
264 seed mass and LNC, study-level variance was less than that of the species-level variance, with variance  
265 in seed mass observations of 1 mg (90% UI: 0.8, 1.1) and 1.6 mg (90% UI: 0.8, 1.1) for study-level and  
266 species-level variance respectively and for LNC 3.6 mg g<sup>-1</sup> (90% UI: 2.2, 5.3) for study-level variance  
267 and 5.1 mg g<sup>-1</sup> for the species-level variance (90% UI: 2.2, 5.3, Fig 3c and d). The difference between  
268 species and study-level variance was greatest for SLA, with the estimate of 3.3 mm<sup>2</sup> mg<sup>-1</sup> (90% UI: 2,  
269 5.1) for study-level variance being approximately half that of the estimated species-level variance of  
270 7.8 mm<sup>2</sup> mg<sup>-1</sup> (90% UI: 6.4, 9.4, Fig 3b).

271

## 272 Discussion

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

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

290

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

301

### 302 Effects of phenology-trait relationships on community assembly

303 Our findings suggest that changing pressures across the early growing season may affect the temporal  
304 assembly of communities. Early-active species had traits indicative of acquisitive growth strategies  
305 that allow faster return on resource investments, like shorter heights and high LNC (Chave *et al.*,  
306 2009; Grime, 1977; Westoby, 1998). **In deciduous forests**, these traits would allow early-budbursting  
307 species to benefit from greater light availability in the open forest canopy in the early spring and  
308 to withstand the low light conditions later in the season. In contrast, later-budbursting species had  
309 traits associated with slower, more conservative, growth (Chave *et al.*, 2009; Grime, 1977; Westoby,  
310 1998), which may help them compete for the more limited soil and light resources later in the growing  
311 season. Similar trait-phenology relationships have also been linked to other ecological processes and  
312 species characteristics that define community structure and diversity, such as species successional  
313 position (Laube *et al.*, 2014), leading to the differences we observed for height and LNC in our example  
314 comparing *Alnus incana* (a pioneer species) and *Quercus rubra* (a later successional species; Fig 2).  
315 While our study focuses mainly on early versus later spring phenology, our approach and findings may  
316 provide insights into potential trade-offs between traits and the phenological cues that underlie early  
317 versus late budburst timing. In particular the relationships between traits and specific phenological  
318 cues that deviated from our expectations may offer novel insights. This is the case for tree height,  
319 which is related to mechanical strength and water transport (Chave *et al.*, 2009) Our finding that  
320 tree height was associated with chilling and photoperiod cues (but not forcing)suggests that species  
321 use of these two cues may be tied to preventing frost damage or xylem cavitation under a late spring

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

332 Our findings highlight the complexity and challenges in determining the drivers of species trait profiles  
333 to understand how phenology fits within a functional trait framework, but expanding to more diverse  
334 species and ecosystems could help. Major trait frameworks today, such as the leaf and wood economic  
335 spectra, generally emerged from studies across highly different ecosystems CITES, while relationships  
336 within certain habitats or regions often show much weaker relationships CITES. Our focus on bud-  
337 burst timing for temperate woody species leverages the largest databases of traits and phenological  
338 experiments, but still has a limited sample size of species and focuses on only one major ecosystem,  
339 which is primarily controlled by temperature CITES. Extending into other types of plant communities  
340 controlled by other factors, such as in savannas or tropical forests, which may be shaped by cues other  
341 than light or seasonal temperatures, could greatly expand how we understand the role of phenology  
342 within trait syndromes.

343

## 344 Future outlook and applications

345 Incorporating phenology within broader trait syndromes could aid in forecasting species and commu-  
346 nity responses to climate change. Decades of research have documented phenological advances with  
347 anthropogenic climate change (Fitter & Fitter, 2002; Menzel *et al.*, 2006), however, increasing research  
348 suggests a potential benefit to advancing, as plant species that shift their phenology with warming  
349 also perform better (Cleland *et al.*, 2012). Our results suggest phenology-performance relationships  
350 could be driven in part by a suite of traits that covary with phenology to determine how responsive  
351 species are to warming. Our results suggest that early-active species—which other studies have found  
352 to also be those that advance more with warming CITES)—are likely to have acquisitive traits (such  
353 as shorter heights and high LNC) that allow them to grow quickly, accumulate resources more quickly  
354 and possibly greater carbon sequestration over a longer growing season. How much these relation-

ships continue in the future also depends on how warming in the winter and spring continues and complexities of exactly how chilling and photoperiod cues operate, which is an area of active debate. Studies to date suggest chilling may increase or decrease in most places with warming (Guy, 2014; ?) while research on photoperiod has variously suggested photoperiod cues could stall responses for some later-active species (CITES) or have at most a relatively small effect (Ettinger *et al.*, 2020; ?). The insight that understanding trait-phenology relationships provides into how climate change may alter species coexistence and create novel species assemblages across communities (Rudolf, 2019; Wolkovich & Donahue, 2021) could have important implication for restoration ecology, including for pollinator communities and invasive plant management. For example, applying our approach to flower and fruit traits may help link plant phenology to pollinator communities, with the opportunity to better predict shifts in phenology and pollination services with climate change (CITES). Opportunities to better manage invasive plants may come from their tendency to have earlier phenologies (Alexander & Levine, 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019) and traits that facilitate fast growth (Fridley *et al.*, 2022). By identifying the trait-cue relationships that shape phenology, we could use existing trait data from invasive species to better predict whether they are likely to out-compete native species by growing earlier in the season and drawing down soil nutrients and/or light resources that later-active native species may rely on (CITES?). This could lead to better identifying which species may be of most concern and thus lead to effective management practices that protect native plant communities under future climate conditions.

374    **References**

- 375    Aitken, S.N. & Bemmels, J.B. (2016) Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications* **9**, 271–290.
- 377    Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violette, C. (2011) When and how should  
378    intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology,  
379    Evolution and Systematics* **13**, 217–225.
- 380    Alexander, J.M. & Levine, J.M. (2019) Earlier phenology of a nonnative plant increases impacts on  
381    native competitors. *PNAS* **116**, 6199–6204.
- 382    Augspurger, C.K. (2009) Spring 2007 warmth and frost : phenology , damage and refoliation in a  
383    temperate deciduous forest. *Functional Ecology* **23**, 1031–1039.
- 384    Beard, K.H., Kelsey, K.C., Leffler, A.J. & Welker, J.M. (2019) The Missing Angle : Ecosystem Con-  
385    sequences of Phenological Mismatch. *Trends in Ecology and Evolution* **34**, 885–888.
- 386    Bolmgren, K. & D. Cowan, P. (2008) Time – size tradeoffs: a phylogenetic comparative study of  
387    flowering time, plant height and seed mass in a north-temperate flora. *Oikos* **117**, 424–429.
- 388    Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a  
389    worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.
- 390    Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A. &  
391    Améglio, T. (2016) Can phenological models predict tree phenology accurately in the future? The  
392    unrevealed hurdle of endodormancy break. *Global change biology* **22**, 3444–3460.
- 393    Chuine, I. & Cour, P. (1999) Climatic determinants of budburst seasonality in four temperate-zone  
394    tree species. *New Phytologist* **143**, 339–349.
- 395    Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S.  
396    & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate  
397    change.pdf. *Ecology* **93**, 1765–1771.
- 398    Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology  
399    in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.
- 400    Clements, J.R., Fraser, J. W. & Yeatman, C.W. (1972) Frost Damage to White Spruce Buds. *Canadian  
401    Journal of Forest Research* **2**, 62–63.
- 402    Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource Availability and Plant Antiherbivore Defense.  
403    *Science* **230**, 895–899.

- 404 Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth,  
405 C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T.,  
406 Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel,  
407 H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S.,  
408 Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of  
409 plant form and function. *Nature* **529**, 167–171.
- 410 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F., Savas, T.,  
411 Samaha, J.A. & Wolkovich, E.M. (2020) Winter temperatures predominate in spring phenological  
412 responses to warming. *Nature Climate Change* **10**, 1137–1142.
- 413 Ettinger, A.K., Gee, S. & Wolkovich, E.M. (2018) Phenological sequences: how early-season events  
414 define those that follow. *American Journal of Botany* **105**, 1771–1780.
- 415 Fitter, A.H. & Fitter, R.S.R. (2002) Rapid Changes in Flowering Time in British Plants. *Science* **296**,  
416 1689–1691.
- 417 Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across  
418 all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.
- 419 Fridley, J.D., Bauerle, T.L., Craddock, A., Ebert, A.R., Frank, D.A., Heberling, J.M., Hinman, E.D.,  
420 Jo, I., Martinez, K.A., Smith, M.S., Woolhiser, L.J. & Yin, J. (2022) Fast but steady: An integrated  
421 leaf-stem-root trait syndrome for woody forest invaders. *Ecology Letters* **25**, 900–912.
- 422 Grime, J.P. (1977) Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance  
423 to Ecological and Evolutionary Theory Author ( s ): J . P . Grime Source : The American Naturalist  
424 , Vol . 111 , No . 982 ( Nov . - Dec ., 1977 ), pp . 1169-1194 Published. *The American Naturalist*  
425 **111**, 1169–1194.
- 426 Gu, H., Qiao, Y., Xi, Z., Rossi, S., Smith, N.G., Liu, J. & Chen, L. (2022) Warming-induced in-  
427 crease in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. *Nature  
428 Communications* **13**, 1–8.
- 429 Guy, R.D. (2014) The early bud gets to warm. *New Phytologist* **202**, 7–9.
- 430 Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying dormancy  
431 requirements for Pacific Northwest tree species. *Frontiers in Plant Science* **6**, 1–12.
- 432 Horbach, S., Rauschkolb, R. & Römermann, C. (2023) Flowering and leaf phenology are more variable  
433 and stronger associated to functional traits in herbaceous compared to tree species. *Flora* **300**, 1–9.

- 434 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'keefe, J. & Richardson, A.D.  
435 (2012) Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change*  
436 *Biology* **18**, 2365–2377.
- 437 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C. & et al. (2020) TRY plant trait database  
438 – enhanced coverage and open access. *Global Change Biology* **26**, 119–188.
- 439 Laube, J., Sparks, T.H., Estrella, N., Höfle, J., Ankerst, D.P. & Menzel, A. (2014) Chilling outweighs  
440 photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- 441 Laughlin, D.C., Leppert, J.J., Moore, M.M. & Sieg, C.H. (2010) A multi-trait test of the leaf-height-  
442 seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* **24**, 493–501.
- 443 Lenz, A., Hoch, G., Vitasse, Y. & Körner, C. (2013) European deciduous trees exhibit similar safety  
444 margins against damage by spring freeze events along elevational gradients. *New Phytologist* **200**,  
445 1166–1175.
- 446 Lopez, O.R., Farris-Lopez, K., Montgomery, R.A. & Givnish, T.J. (2008) Leaf phenology in relation  
447 to canopy closure in southern Appalachian trees. *American Journal of Botany* **95**, 1395–1407.
- 448 Lusk, C.H., Clearwater, M.J., Laughlin, D.C., Harrison, S.P., Prentice, I.C., Nordenstahl, M. & Smith,  
449 B. (2018) Frost and leaf-size gradients in forests: global patterns and experimental evidence. *New*  
450 *Phytologist* **219**, 565–573.
- 451 Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S.M., Guaderrama, D., Hinchliff,  
452 C.E., Jørgensen, P.M., Kraft, N.J., McGill, B., Merow, C., Morueta-Holme, N., Peet, R.K., Sandel,  
453 B., Schildhauer, M., Smith, S.A., Svenning, J.C., Thiers, B., Violette, C., Wiser, S. & Enquist, B.J.  
454 (2018) The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN)  
455 database. *Methods in Ecology and Evolution* **9**, 373–379.
- 456 Marquis, B., Bergeron, Y., Simard, M. & Tremblay, F. (2020) Growing-season frost is a better predictor  
457 of tree growth than mean annual temperature in boreal mixedwood forest plantations. *Global Change*  
458 *Biology* **26**, 6537–6554.
- 459 Maynard, D.S., Bialic-Murphy, L., Zohner, C.M., Averill, C., Van Den Hoogen, J., Ma, H., Mo, L.,  
460 Smith, G.R., Acosta, A.T.R., Aubin, I., Berenguer, E., Boonman, C.C.F., Catford, J.A., Cerabolini,  
461 B.E.L., Dias, A.S., González-Melo, A., Hietz, P., Lusk, C.H., Mori, A.S., Niinemets, Ü., Pillar, V.D.,  
462 Pinho, B.X., Rosell, J.A., Schurr, F.M., Sheremetev, S.N., Da Silva, A.C., Sosinski, É., Van Bode-  
463 gom, P.M., Weiher, E., Bönisch, G., Kattge, J. & Crowther, T.W. (2022) Global relationships in  
464 tree functional traits. *Nature Communications* **13**, 3185.

- 465 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P.,  
466 Bralslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C.,  
467 Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P.,  
468 Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J., Wielgolaski, F.E., Zach, S. &  
469 Zust, A. (2006) European phenological response to climate change matches the warming pattern.  
470 *Global Change Biology* **12**, 1969–1976.
- 471 Morales-Castilla, I., Davies, T.J., Legault, G., Buonaiuto, D.M., Chamberlain, C.J., Ettinger, A.K.,  
472 Garner, M., Jones, F.A.M., Loughnan, D., Pearse, W.D., Sodhi, D. & Wolkovich, E.M. (2024)  
473 Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate  
Change* **14**, 989–995.
- 475 Natural Resources Canada (2020) Forestry glossary: Sapling.
- 476 Osada, N. & Hiura, T. (2019) Intraspecific differences in spring leaf phenology in relation to tree size  
477 in temperate deciduous trees. *Tree Physiology* **39**, 782–791.
- 478 Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N.,  
479 Shcherbakov, A., Meyke, E. & del Mar Delgado, M. (2013) Community-level phenological response  
480 to climate change. *PNAS* **110**, 13434–13439.
- 481 Polgar, C., Gallinat, A. & Primack, R.B. (2014) Drivers of leaf-out phenology and their implications  
482 for species invasions: insights from thoreau's concord. *New Phytologist* **202**, 106–115.
- 483 R Development Core Team (2017) R: A language and environment for statistical computing. *R Foundation  
484 for Statistical Computing*, Vienna, Austria .
- 485 Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology  
and Systematics* **16**, 179–214.
- 487 Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka,  
488 D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädtter, A., Shafee, F.,  
489 Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M.,  
490 Stevens, A.D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg,  
491 M., Knickmann, B., Nordt, B., Wirth, C. & Römermann, C. (2024) Spatial variability in herbaceous  
492 plant phenology is mostly explained by variability in temperature but also by photoperiod and  
493 functional traits. *International Journal of Biometeorology* **68**, 761–775.
- 494 Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal  
495 of Ecology* **102**, 275–301.

- 496 Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in  
497 plant functioning. *Proceedings of the National Academy of Sciences* **94**, 13730–13734.
- 498 Rudolf, V.H.W. (2019) The role of seasonal timing and phenological shifts for species coexistence.  
499 *Ecology Letters* **22**, 1324–1338.
- 500 Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants: Responses and adaptation to freezing stress*.  
501 Springer-Verlag, Berlin, Heidelberg.
- 502 Seiwa, K. (1999) Changes in leaf phenology are dependent on tree height in Acer mono, a deciduous  
503 broad-leaved tree. *Annals of Botany* **83**, 355–361.
- 504 Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Bar-  
505 aloto, C., Carlucci, M.B., Cianciaruso, M.V., De L. Dantas, V., De Bello, F., Duarte, L.D.S., Fonseca,  
506 C.R., Freschet, G.T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama,  
507 Katabuchi, M., Kembel, S.W., Kichenin, E., Kraft, N.J.B., Lagerström, A., Bagousse-Pinguet,  
508 Y.L., Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J.M., Peltzer, D.A., Pérez-Ramos,  
509 I.M., Pillar, V.D., Prentice, H.C., Richardson, S., Sasaki, T., Schamp, B.S., Schöb, C., Shipley, B.,  
510 Sundqvist, M., Sykes, M.T., Vandewalle, M. & Wardle, D.A. (2015) A global meta-analysis of the  
511 relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**, 1406–1419.
- 512 Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., Konig, A., Nordt, B.,  
513 Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstadter, A., Maskova, T., Primack,  
514 R., Rosche, C., Shah, M.A., Stevens, A.D., Teilborger, K., Trager, S., Wirth, C. & Romermann,  
515 C. (2022) Functional traits influence patterns in vegetative and reproductive plant phenology – a  
516 multi-botanical garden study. *New Phytologist* **235**, 2199–2210.
- 517 Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3.
- 518 Stan Development Team (2024) Stan reference manual, v2.36.0.
- 519 Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J.  
520 (2012) The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology  
521 and Evolution* **27**, 244–252.
- 522 Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the  
523 concept of trait be functional! *Oikos* **116**, 882–892.
- 524 Vitasse, Y. (2013) Ontogenetic changes rather than difference in temperature cause understorey trees to  
525 leaf out earlier. *New Phytologist* **198**, 149–155.

- 526 Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat,  
527 C., Rebetez, M., Rixen, C., Strelbel, N., Schmidt, B.R., Wipf, S., Wohlgemuth, T., Yoccoz, N.G.  
528 & Lenoir, J. (2021) Phenological and elevational shifts of plants , animals and fungi under climate  
529 change in the European Alps. *Biological Reviews* **96**, 1816–1835.
- 530 Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2012) Seasonal priority effects : implications for  
531 invasion and restoration in a semi-arid system. *Journal of Applied Ecology* **49**, 234–241.
- 532 Wang, L., Han, X., Yin, Q., Wang, G., Xu, J., Chai, Y. & Yue, M. (2021) Differences in leaf phenological  
533 traits between trees and shrubs are closely related to functional traits in a temperate forest. *Acta  
534 Oecologica* **112**, 103760.
- 535 Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**,  
536 213–227.
- 537 Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in  
538 Ecology & Evolution* **21**, 261–268.
- 539 Wolkovich, E.M. & Cleland, E.E. (2014) Phenological niches and the future of invaded ecosystems  
540 with climate change. *AoB PLANTS* **6**, 1–16.
- 541 Wolkovich, E.M. & Donahue, M.J. (2021) How phenological tracking shapes species and communities  
542 in non-stationary environments. *Biological Reviews* **96**, 2810–2827.
- 543 Wolkovich, E.M. & Ettinger, A.K. (2014) Back to the future for plant phenology research. *New Phy-  
544 tologist* **203**, 1021–1024.
- 545 Wright, I.J., Westoby, M., Reich, P.B., Oleksyn, J., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-  
546 Bares, J., Chapin, T., Cornellissen, J.H.C., Diemer, M., Flexas, J., Gulias, J., Garnier, E., Navas,  
547 M.L., Roumet, C., Groom, P.K., Lamont, B.B., Hikosaka, K., Lee, T., Lee, W., Lusk, C., Midgley,  
548 J.J., Niinemets, Ü., Osada, H., Poorter, H., Pool, P., Veneklaas, E.J., Prior, L., Pyankov, V.I.,  
549 Thomas, S.C., Tjoelker, M.G. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*  
550 **428**, 821–827.
- 551 Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology  
552 on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* **107**, 22151–22156.
- 553 Zeng, Z.A. & Wolkovich, E.M. (2024) Weak evidence of provenance effects in spring phenology across  
554 Europe and North America. *New Phytologist* **242**, 1957–1964.
- 555 Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019) Phenology in a warming world: differences  
556 between native and non-native plant species. *Ecology Letters* **22**, 1253–1263.

557 Zuleta, D., Muller-Landau, H.C., Duque, A., Caro, N., Cardenas, D., Castaño, N., León-Peláez, J.D.  
558 & Feeley, K.J. (2022) Interspecific and intraspecific variation of tree branch, leaf and stomatal traits  
559 in relation to topography in an aseasonal Amazon forest. *Functional Ecology* **36**, 2955–2968.

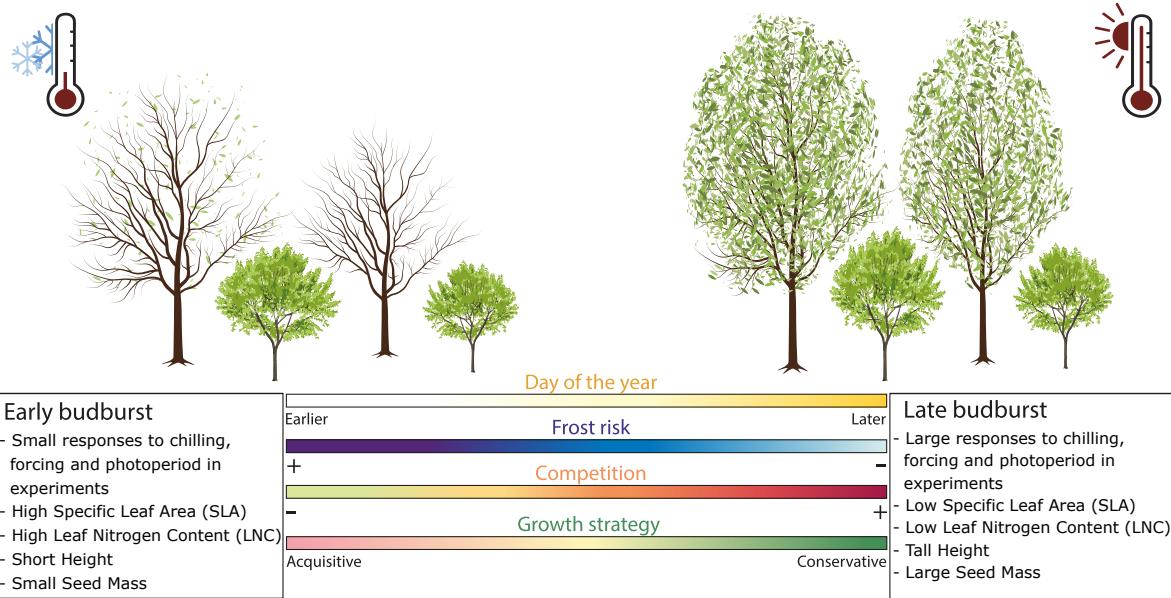


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies (Chave *et al.*, 2009; Westoby & Wright, 2006; Wright *et al.*, 2004), which may also include phenology. Drawing on previous research in plants, we predicted that early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater abiotic and biotic risk but reduced competition. In contrast, we expected later-budbursting species would have traits associated with conservative growth, as they are more likely to experience greater competition but a more climatically benign environment. Previous studies looking at different phenological events, such as flowering, or suites of non-woody species, have found varying relationships between traits and phenology, highlighting the complexity that may shape species timings.

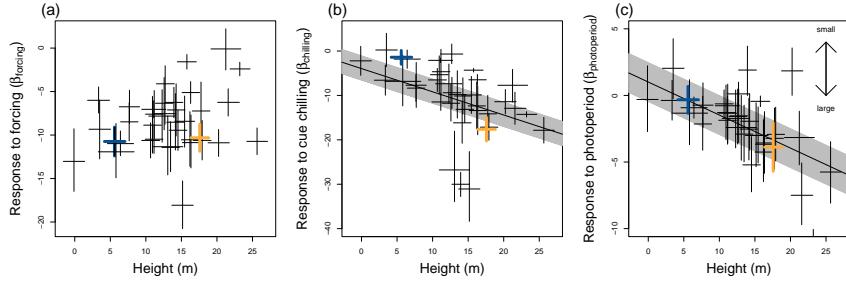


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the solid black lines showing the relationship between estimated trait effects and the responses to phenological cues (either  $\beta_{\text{chilling}}$ ,  $\beta_{\text{forcing}}$ ,  $\beta_{\text{photoperiod}}$  for each trait, shown only where this relationship does not include zero within the 90% UI) with the gray band the 50% uncertainty interval. As illustrated by the arrows in panel a, species with smaller responses to cues (chilling, forcing, photoperiod) have more positive values, while species with larger responses to cues have more negative values. Each set of crossed lines represents one species (with each line spanning the 50% uncertainty interval), depicting how well our model fits the data across all species. To illustrate the relationship between traits and the three phenological cues, we highlight two example species that differ greatly in their growth forms and life history. *Alnus incana*, shown in blue,<sup>22</sup> 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.

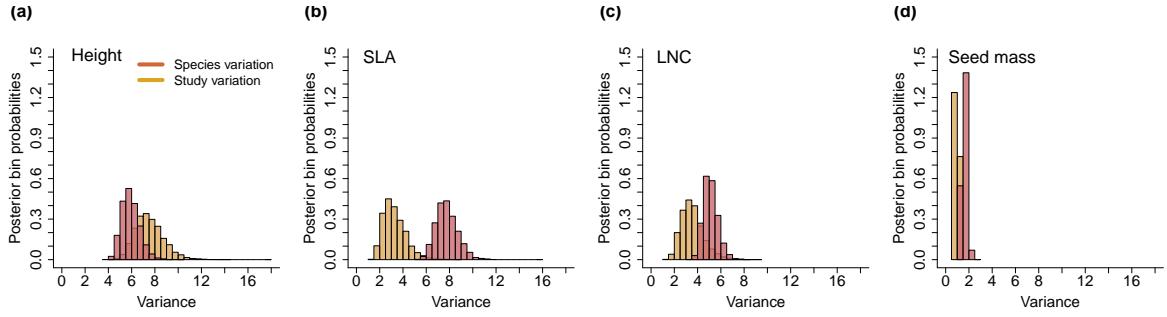


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ( $\sigma_{\text{species}}^2$  and  $\sigma_{\text{study}}^2$  respectively), with only (a) the height model estimating greater study-level variation than species-level, while our (b) specific leaf area,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