

<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 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 infer suites of traits that may co-vary with species phenologies, but the high variability in traits—and especially phenology—across environments, have made testing the role of phenology within a trait framework challenging.

<sup>16</sup> 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).

<sup>20</sup> 3. We found mixed support for our predictions for how traits relate to budburst timing and cues. Species with low chilling and photoperiod cues—indicative of earlier budburst—had some traits related to acquisitive strategies (they were shorter with higher nitrogen leaves). Our one reproductive trait (seed mass), however showed no relationships to budburst cues, and other traits (e.g., specific leaf area) showed relationships in the opposite direction to our predictions.

<sup>25</sup> 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.

<sup>28</sup>

<sup>29</sup> Key Words: Leafout, spring phenology, traits, trees, climate change, forest communities

## <sup>30</sup> Introduction

<sup>31</sup> The timing of life history events—phenology—can shape both ecosystem services and community  
<sup>32</sup> dynamics. Spring phenology, for example, defines the start and overall length of the growing season—  
<sup>33</sup> shaping forest carbon storage and species interactions (Beard *et al.*, 2019; Cleland *et al.*, 2007; Gu  
<sup>34</sup> *et al.*, 2022). Shifts in phenology with climate change across systems (Menzel *et al.*, 2006; Vitasse  
<sup>35</sup> *et al.*, 2021) have thus led to growing concerns over their possible impacts.

<sup>36</sup>

<sup>37</sup> Predicting these changes requires understanding the drivers of phenology both at a proximate scale—  
<sup>38</sup> the environmental triggers that determine phenology each year, such as temperature and daylength—  
<sup>39</sup> and, at an ultimate scale, where long-term environmental pressures may select for different phenologies  
<sup>40</sup> across species, (e.g., certain species are early or late relative to other species each year Ovaskainen  
<sup>41</sup> *et al.*, 2013; Wolkovich & Donahue, 2021). At the proximate level, environmental conditions through-  
<sup>42</sup> out the winter and spring cause species to start growth at different times (as each species generally has  
<sup>43</sup> a unique response to the environment). Groups of species may have more similar responses, however,  
<sup>44</sup> because they are from similar functional groups, successional stages (Laube *et al.*, 2014a) or archi-  
<sup>45</sup> tectures (Flynn & Wolkovich, 2018) that cause them to have similar growth strategies. But current  
<sup>46</sup> work provides limited insights into the drivers of these differences across species and how they can be  
<sup>47</sup> used to predict future changes in community dynamics (Chuine *et al.*, 2016; Flynn & Wolkovich, 2018;  
<sup>48</sup> Laube *et al.*, 2014a).

<sup>49</sup>

<sup>50</sup> At the ultimate level, plant phenologies may vary due to changing pressures across the growing sea-  
<sup>51</sup> son that select for different growth strategies. Species that start growth early often risk high tissue  
<sup>52</sup> loss—due to frost damage (Augspurger, 2009; Sakai & Larcher, 1987) or high herbivore apparentency  
<sup>53</sup> (Wainwright *et al.*, 2012)—but benefit from higher resource availability (Hufkens *et al.*, 2012; Rathcke  
<sup>54</sup> & Lacey, 1985). In contrast, later active species face greater biotic pressures, especially from high  
<sup>55</sup> competition for resources (Lopez *et al.*, 2008; Wolkovich & Ettinger, 2014). Such differences could  
<sup>56</sup> shape physical and phenological traits related to species growth strategies and fitness (Viole *et al.*,  
<sup>57</sup> 2007). Species leaf and wood traits can reflect trade-offs between the construction costs and longevity  
<sup>58</sup> of tissue (Reich *et al.*, 1997; Wright *et al.*, 2004), with cheaper-to-construct tissue being associated with  
<sup>59</sup> faster growth rates (Westoby & Wright, 2006; Wright *et al.*, 2004). Previous studies have highlighted  
<sup>60</sup> the associations between trade-offs in traits and phenology (Sporbert *et al.*, 2022; Wang *et al.*, 2021;  
<sup>61</sup> Wolkovich & Ettinger, 2014) (Fig 1), and indicate the potential for species traits to similarly range

62 from the acquisitive (fast) to more conservative (slow) growth strategies associated with existing trait  
63 frameworks (Chave *et al.*, 2009; Wright *et al.*, 2004).

64

65 Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation  
66 of the leaf and wood economic spectra (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998; Westoby &  
67 Wright, 2006; Wright *et al.*, 2004), but they make limited predictions of trait variability (Viole *et al.*,  
68 2012). As a result, highly variable traits like phenology are often excluded from trait studies, leaving  
69 the relationships between broader trait syndromes and phenology largely unknown. Understanding  
70 these relationships, however, is critical to forecasting community dynamics and responses to climate  
71 change. Most studies have examined the relationship between traits and phenology for a single or lim-  
72 ited number of sites, Wolkovich & Cleland (as reviewed by 2014); Wolkovich & Donahue (as reviewed  
73 by 2021) but see Rauschkolb *et al.* (2024); Sporbert *et al.* (2022). At these spatial scales the problem  
74 of proximate drivers causing phenological variation can be more easily ignored. Adding phenology  
75 to broader trait frameworks becomes more complex when high levels of variation occurs across large  
76 spatial and temporal 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—usually spring—temperatures), chilling (accumu-  
85 lated cool—usually fall and winter—temperatures), and shorter photoperiod to leaf out, and thus have  
86 relatively small responses to each of these cues in experiments. In contrast, later species have larger  
87 responses to chilling and/or longer photoperiods, and larger forcing responses (Flynn & Wolkovich,  
88 2018; Laube *et al.*, 2014a). The consistency of these relationships allows us to better understand the  
89 drivers of phenological variation across plant communities and diverse species assemblages.

90

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

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

109

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

119

## 120 Methods

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

128

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

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

131

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

140

141 We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge *et al.*, 2020; Maitner  
142 *et al.*, 2018), both of which are large trait databases that include plant trait observations across many  
143 individuals, species, and studies (Table S1) and are available through slightly different mechanisms.  
144 BIEN is accessible via the BIEN R package (here we used v. 1.2.5 Maitner *et al.*, 2018), and TRY is  
145 requested. We obtained data from both databases on 5 December, 2018, and requested an updated  
146 version of the TRY data on 10 April 2019. We initially searched for trait data on the subset of 234  
147 OSPREE species used in Morales-Castilla *et al.* (2024). From BIEN, this resulted in 94 of the 234  
148 species available in the database, for which there were 13 unique traits. From the TRY database  
149 we received data for 10 unique traits for 96 of the 234 requested species (Kattge *et al.*, 2020). For our  
150 purposes, we were interested in the trait-phenology relationships of adult trees, and therefore subset  
151 the available data to only include traits measured from adult individuals. We assumed that by subset-  
152 ting tree heights to be 1.38 m or greater the individuals in our analysis would be old enough to meet  
153 the standard measurement height used in North America when measuring DBH (Powell, 2016). We  
154 further removed all data from manipulative experiments or from plants growing in non-natural habi-  
155 tats. We also grouped trait values where appropriate, for example pooling trait values for specific leaf  
156 area (SLA) with those denoted as "SLA with petioles", and "SLA without petioles" in our analysis  
157 (see Table S1). We also removed data that was duplicated in both the TRY and BIEN datasets ( $n =$   
158 434905). For a full depiction of our data cleaning process and decisions see Fig. S3.

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). We initially considered six commonly measured traits—SLA, leaf dry matter  
162 content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species  
163 had at least one trait measurement for each of the traits. We then used a principle component  
164 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 (Fig. S2), with high correlations between SLA and LDMC, and between height and SSD (Fig. S2). By excluding the one 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 (samples sizes: height  $n = 47781$ , seed mass  $n = 281$ , LNC  $n = 3853$ , SLA  $n = 7656$ ). We subsampled the height measurements of the 13 most frequently measured tree to reduce their influence on our height model. Since each of these species were measured 19 times more frequently than most other species, we randomly sampled 3000 height measurements for each individual species, while including all height data for the remaining, less frequently measured, 24 species.

## Joint model of trait and phenology

To understand connections between phenology and species traits, we developed a Bayesian joint model for each trait: height, SLA, LNC, and seed mass to relate to species budburst responses. 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). This trait value ( $\alpha_{\text{trait}}$ ) has a separate interaction with the three cues ( $\beta_{\text{chilling}}$ ,  $\beta_{\text{forcing}}$ ,  $\beta_{\text{photoperiod}}$ ) that determines phenology—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 measurement error ( $\sigma_m^2$ ), 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:

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

193 with

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

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

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

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

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

## 199 Phenology sub-model

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

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

206 with

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

207 and

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

208 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:

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

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

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

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

209 The model partitions day of budburst for species ( $k$ ) as a combination of the overall mean day of  
 210 budburst without the influence of chilling, forcing, or photoperiod treatments ( $\alpha_{\text{pheno},k}$ , normally  
 211 distributed with a mean of  $\mu_{\text{pheno}}$  and variance  $\sigma_{\text{pheno}}^2$ ) combined with the effects of treatments both  
 212 dependent and independent of trait values.

213 The parameters  $\alpha_{\text{chilling},k}$ ,  $\alpha_{\text{forcing},k}$ , and  $\alpha_{\text{photoperiod},k}$  represent the trait-independent responses of  
 214 species  $k$  to chilling, forcing, and photoperiod treatments respectively, each with an associated mean  
 215 ( $\mu_{\text{chilling}}$ ,  $\mu_{\text{forcing}}$ ,  $\mu_{\text{photoperiod}}$ ) and variance ( $\sigma_{\text{chilling}}^2$ ,  $\sigma_{\text{forcing}}^2$ ,  $\sigma_{\text{photoperiod}}^2$ ) across species. The shared  
 216 parameter between the trait and phenology sub-model,  $\alpha_{\text{trait},k}$ , represents the effect of the species trait  
 217 value on its responses to chilling ( $\beta_{\text{trait.chilling}}$ ), forcing ( $\beta_{\text{trait.forcing}}$ ), and photoperiod ( $\beta_{\text{trait.photoperiod}}$ ).  
 218 Finally,  $\sigma_d^2$  is the variance arising from measurement error for the observed day of budburst.

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

## 231 Results

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

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

241

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

254

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

269

**270 Discussion**

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

289

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

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

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

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

312

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

324

### 325 Phenology-trait relationships under future climates

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

332

Our results suggest this phenology-performance relationship could be driven in part by a suite of traits that covary with phenological cues to determine how responsive species are to warming. Species with smaller responses to all cues, especially chilling and photoperiod, would tend to advance more with

336 warming (Guy, 2014). Our results suggest that these same species are likely to have acquisitive traits,  
337 such as short heights and high LNC that allow them to grow quickly and benefit from the greater  
338 availability of nutrients in the early spring. Understanding these trait-phenology relationships may  
339 provide insight into how climate change may alter species coexistence (Rudolf, 2019; Wolkovich &  
340 Donahue, 2021). A greater understanding of trait-phenology relationships may also improve our abil-  
341 ity to manage species invasions, as invasive species tend to have earlier phenologies (Alexander & Levine,  
342 2019; Polgar *et al.*, 2014; Zettlemoyer *et al.*, 2019), but possibly a unique suite of traits that facilitate  
343 fast growth (Fridley *et al.*, 2022)..

344

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

352

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

363

## 364 Acknowledgements

365 We thank two anonymous reviewers and all the researchers who measured the traits and conducted  
366 the experiments producing the data used in this manuscript.

<sup>367</sup> **Author Contributions Statement**

<sup>368</sup> DL, FAMJ, GL, MG, DS, and EMW planned and designed the study. All authors conducted the  
<sup>369</sup> literature review and cleaned the database. DL, FAMJ, GL, and EMW performed the data analysis  
<sup>370</sup> and contributed code. DL, FAMJ, and GL created the figures. DL and EMW wrote the initial draft  
<sup>371</sup> and all authors reviewed and revised the manuscript.

<sup>372</sup> **Competing Interests Statement**

<sup>373</sup> The authors declare no competing interests.

<sup>374</sup> **Data availability statement**

<sup>375</sup> The phenological data used for this manuscript is a subset of the existing OSPREE dataset (doi:10.5063/F1CZ35KB)  
<sup>376</sup> and the trait data a subset of the the TRY database (doi:10.1111/gcb.14904) and the BIEN database  
<sup>377</sup> (doi: 10.1111/2041-210X.1286).

378    **References**

- 379    Alexander, J.M. & Levine, J.M. (2019) Earlier phenology of a nonnative plant increases impacts on  
380    native competitors. *PNAS* **116**, 6199–6204.
- 381    Augspurger, C.K. (2009) Spring 2007 warmth and frost : phenology , damage and refoliation in a  
382    temperate deciduous forest. *Functional Ecology* **23**, 1031–1039.
- 383    Beard, K.H., Kelsey, K.C., Leffler, A.J. & Welker, J.M. (2019) The Missing Angle : Ecosystem Con-  
384    sequences of Phenological Mismatch. *Trends in Ecology and Evolution* **34**, 885–888.
- 385    Bolmgren, K. & D. Cowan, P. (2008) Time – size tradeoffs: a phylogenetic comparative study of  
386    flowering time, plant height and seed mass in a north-temperate flora. *Oikos* **117**, 424–429.
- 387    Bucher, S.F. & Rosbakh, S. (2021) Foliar summer frost resistance measured via electrolyte leakage ap-  
388    proach as related to plant distribution, community composition and plant traits. *Functional Ecology*  
389    **35**, 590–600.
- 390    Carter, S.K., Saenz, D. & Rudolf, V.H. (2018) Shifts in phenological distributions reshape interaction  
391    potential in natural communities. *Ecology Letters* **21**, 1143–1151.
- 392    Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a  
393    worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.
- 394    Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A. &  
395    Améglio, T. (2016) Can phenological models predict tree phenology accurately in the future? The  
396    unrevealed hurdle of endodormancy break. *Global change biology* **22**, 3444–3460.
- 397    Chuine, I. & Cour, P. (1999) Climatic determinants of budburst seasonality in four temperate-zone  
398    tree species. *New Phytologist* **143**, 339–349.
- 399    Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S.  
400    & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate  
401    change.pdf. *Ecology* **93**, 1765–1771.
- 402    Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology  
403    in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.
- 404    Clements, J.R., Fraser, J. W. & Yeatman, C.W. (1972) Frost Damage to White Spruce Buds. *Canadian*  
405    *Journal of Forest Research* **2**, 62–63.
- 406    Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource Availability and Plant Antiherbivore Defense.  
407    *Science* **230**, 895–899.

- 408 Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth,  
409 C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T.,  
410 Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel,  
411 H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S.,  
412 Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D. (2016) The global spectrum of  
413 plant form and function. *Nature* **529**, 167–171.
- 414 Ettinger, A.K., Chamberlain, C.J., Morales-Castilla, I., Buonaiuto, D.M., Flynn, D.F., Savas, T.,  
415 Samaha, J.A. & Wolkovich, E.M. (2020) Winter temperatures predominate in spring phenological  
416 responses to warming. *Nature Climate Change* **10**, 1137–1142.
- 417 Ettinger, A.K., Gee, S. & Wolkovich, E.M. (2018) Phenological sequences: how early-season events  
418 define those that follow. *American Journal of Botany* **105**, 1771–1780.
- 419 Fitter, A.H. & Fitter, R.S.R. (2002) Rapid Changes in Flowering Time in British Plants. *Science* **296**,  
420 1689–1691.
- 421 Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across  
422 all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.
- 423 Fridley, J.D., Bauerle, T.L., Craddock, A., Ebert, A.R., Frank, D.A., Heberling, J.M., Hinman, E.D.,  
424 Jo, I., Martinez, K.A., Smith, M.S., Woolhiser, L.J. & Yin, J. (2022) Fast but steady: An integrated  
425 leaf-stem-root trait syndrome for woody forest invaders. *Ecology Letters* **25**, 900–912.
- 426 Grime, J.P. (1977) Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance  
427 to Ecological and Evolutionary Theory Author ( s ): J . P . Grime Source : The American Naturalist  
428 , Vol . 111 , No . 982 ( Nov . - Dec . , 1977 ), pp . 1169-1194 Published. *The American Naturalist*  
429 **111**, 1169–1194.
- 430 Gu, H., Qiao, Y., Xi, Z., Rossi, S., Smith, N.G., Liu, J. & Chen, L. (2022) Warming-induced in-  
431 crease in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. *Nature  
432 Communications* **13**, 1–8.
- 433 Guy, R.D. (2014) The early bud gets to warm. *New Phytologist* **202**, 7–9.
- 434 Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying dormancy  
435 requirements for Pacific Northwest tree species. *Frontiers in Plant Science* **6**, 1–12.
- 436 Horbach, S., Rauschkolb, R. & Römermann, C. (2023) Flowering and leaf phenology are more variable  
437 and stronger associated to functional traits in herbaceous compared to tree species. *Flora* **300**,  
438 152218.

- 439 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'keefe, J. & Richardson, A.D.  
440 (2012) Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change*  
441 *Biology* **18**, 2365–2377.
- 442 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C. & et al. (2020) TRY plant trait database  
443 – enhanced coverage and open access. *Global Change Biology* **26**, 119–188.
- 444 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014a) Chilling outweighs  
445 photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- 446 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014b) Chilling outweighs  
447 photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- 448 Laughlin, D.C., Leppert, J.J., Moore, M.M. & Sieg, C.H. (2010) A multi-trait test of the leaf-height-  
449 seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* **24**, 493–501.
- 450 Lenz, A., Hoch, G., Körner, C. & Vitasse, Y. (2016) Convergence of leaf-out towards minimum risk of  
451 freezing damage in temperate trees. *Functional Ecology* **30**, 1480–1490.
- 452 Lenz, A., Hoch, G., Vitasse, Y. & Körner, C. (2013) European deciduous trees exhibit similar safety  
453 margins against damage by spring freeze events along elevational gradients. *New Phytologist* **200**,  
454 1166–1175.
- 455 Lopez, O.R., Farris-Lopez, K., Montgomery, R.A. & Givnish, T.J. (2008) Leaf phenology in relation  
456 to canopy closure in southern Appalachian trees. *American Journal of Botany* **95**, 1395–1407.
- 457 Macgregor, C.J., Thomas, C.D., Roy, D.B., Beaumont, M.A., Bell, J.R., Brereton, T., Bridle, J.R.,  
458 Dytham, C., Fox, R., Gotthard, K., Hoffmann, A.A., Martin, G., Middlebrook, I., Nylin, S., Platts,  
459 P.J., Rasteiro, R., Saccheri, I.J., Villoutreix, R., Wheat, C.W. & Hill, J.K. (2019) Climate-induced  
460 phenology shifts linked to range expansions in species with multiple reproductive cycles per year.  
461 *Nature Communications* **10**, 1–10.
- 462 Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S.M., Guaderrama, D., Hinchliff,  
463 C.E., Jørgensen, P.M., Kraft, N.J., McGill, B., Merow, C., Morueta-Holme, N., Peet, R.K., Sandel,  
464 B., Schildhauer, M., Smith, S.A., Svenning, J.C., Thiers, B., Violle, C., Wiser, S. & Enquist, B.J.  
465 (2018) The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN)  
466 database. *Methods in Ecology and Evolution* **9**, 373–379.
- 467 Marquis, B., Bergeron, Y., Simard, M. & Tremblay, F. (2020) Growing-season frost is a better predictor  
468 of tree growth than mean annual temperature in boreal mixedwood forest plantations. *Global Change*  
469 *Biology* **26**, 6537–6554.

- 470 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P.,  
471 Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C.,  
472 Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P.,  
473 Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J., Wielgolaski, F.E., Zach, S. &  
474 Zust, A. (2006) European phenological response to climate change matches the warming pattern.  
475 *Global Change Biology* **12**, 1969–1976.
- 476 Morales-Castilla, I., Davies, T.J., Legault, G., Buonaiuto, D.M., Chamberlain, C.J., Ettinger, A.K.,  
477 Garner, M., Jones, F.A.M., Loughnan, D., Pearse, W.D., Sodhi, D. & Wolkovich, E.M. (2024)  
478 Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate  
479 Change* .
- 480 Osada, N. & Hiura, T. (2019) Intraspecific differences in spring leaf phenology in relation to tree size  
481 in temperate deciduous trees. *Tree Physiology* **39**, 782–791.
- 482 Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N.,  
483 Shcherbakov, A., Meyke, E. & del Mar Delgado, M. (2013) Community-level phenological response  
484 to climate change. *PNAS* **110**, 13434–13439.
- 485 Polgar, C., Gallinat, A. & Primack, R.B. (2014) Drivers of leaf-out phenology and their implications for  
486 species invasions: insights from <span style="font-variant:small-caps;">T</span> horeau's <span  
487 style="font-variant:small-caps;">C</span> oncord. *New Phytologist* **202**, 106–115.
- 488 Powell, D.C. (2016) How to measure a big tree. *USDA Forest Service* pp. 1–14.
- 489 R Development Core Team (2017) R: A language and environment for statistical computing. *R Foundation  
490 for Statistical Computing, Vienna, Austria* .
- 491 Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology  
492 and Systematics* **16**, 179–214.
- 493 Rauschkolb, R., Bucher, S.F., Hensen, I., Ahrends, A., Fernández-Pascual, E., Heubach, K., Jakubka,  
494 D., Jiménez-Alfaro, B., König, A., Koubek, T., Kehl, A., Khuroo, A.A., Lindstädter, A., Shafee, F.,  
495 Mašková, T., Platonova, E., Panico, P., Plos, C., Primack, R., Rosche, C., Shah, M.A., Sporbert, M.,  
496 Stevens, A.D., Tarquini, F., Tielbörger, K., Träger, S., Vange, V., Weigelt, P., Bonn, A., Freiberg,  
497 M., Knickmann, B., Nordt, B., Wirth, C. & Römermann, C. (2024) Spatial variability in herbaceous  
498 plant phenology is mostly explained by variability in temperature but also by photoperiod and  
499 functional traits. *International Journal of Biometeorology* **68**, 761–775.
- 500 Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal  
501 of Ecology* **102**, 275–301.

- 502 Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in  
503 plant functioning. *Proceedings of the National Academy of Sciences* **94**, 13730–13734.
- 504 Rudolf, V.H.W. (2019) The role of seasonal timing and phenological shifts for species coexistence.  
505 *Ecology Letters* **22**, 1324–1338.
- 506 Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants: Responses and adaptation to freezing stress*.  
507 Springer-Verlag, Berlin, Heidelberg.
- 508 Seiwa, K. (1999) Changes in leaf phenology are dependent on tree height in Acer mono, a deciduous  
509 broad-leaved tree. *Annals of Botany* **83**, 355–361.
- 510 Sporbert, M., Jakubka, D., Bucher, S.F., Hensen, I., Freiberg, M., Heubach, K., Konig, A., Nordt, B.,  
511 Plos, C., Blinova, I., Bonn, A., Knickmann, B., Koubek, T., Linstadter, A., Maskova, T., Primack,  
512 R., Rosche, C., Shah, M.A., Stevens, A.D., Teilborger, K., Trager, S., Wirth, C. & Romermann,  
513 C. (2022) Functional traits influence patterns in vegetative and reproductive plant phenology – a  
514 multi-botanical garden study. *New Phytologist* **235**, 2199–2210.
- 515 Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3.
- 516 Stan Development Team (2024) Stan reference manual, v2.36.0.
- 517 Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J.  
518 (2012) The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology  
and Evolution* **27**, 244–252.
- 520 Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the  
521 concept of trait be functional! *Oikos* **116**, 882–892.
- 522 Vitasse, Y. (2013) Ontogenetic changes rather than difference in temperature cause understory trees to  
523 leaf out earlier. *New Phytologist* **198**, 149–155.
- 524 Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat,  
525 C., Rebetez, M., Rixen, C., Strelbel, N., Schmidt, B.R., Wipf, S., Wohlgemuth, T., Yoccoz, N.G.  
526 & Lenoir, J. (2021) Phenological and elevational shifts of plants , animals and fungi under climate  
527 change in the European Alps. *Biological Reviews* **96**, 1816–1835.
- 528 Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2012) Seasonal priority effects : implications for  
529 invasion and restoration in a semi-arid system. *Journal of Applied Ecology* **49**, 234–241.
- 530 Wang, L., Han, X., Yin, Q., Wang, G., Xu, J., Chai, Y. & Yue, M. (2021) Differences in leaf phenological  
531 traits between trees and shrubs are closely related to functional traits in a temperate forest. *Acta  
Oecologica* **112**, 103760.

- 533 Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**,  
534 213–227.
- 535 Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in  
536 Ecology & Evolution* **21**, 261–268.
- 537 Wolkovich, E.M. & Cleland, E.E. (2014) Phenological niches and the future of invaded ecosystems  
538 with climate change. *AoB PLANTS* **6**, 1–16.
- 539 Wolkovich, E.M. & Donahue, M.J. (2021) How phenological tracking shapes species and communities  
540 in non-stationary environments. *Biological Reviews* **96**, 2810–2827.
- 541 Wolkovich, E.M. & Ettinger, A.K. (2014) Back to the future for plant phenology research. *New Phy-  
542 tologist* **203**, 1021–1024.
- 543 Wright, I.J., Westoby, M., Reich, P.B., Oleksyn, J., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-  
544 Bares, J., Chapin, T., Cornellissen, J.H.C., Diemer, M., Flexas, J., Gulias, J., Garnier, E., Navas,  
545 M.L., Roumet, C., Groom, P.K., Lamont, B.B., Hikosaka, K., Lee, T., Lee, W., Lusk, C., Midgley,  
546 J.J., Niinemets, Ü., Osada, H., Poorter, H., Pool, P., Veneklaas, E.J., Prior, L., Pyankov, V.I.,  
547 Thomas, S.C., Tjoelker, M.G. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*  
548 **428**, 821–827.
- 549 Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology  
550 on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* **107**, 22151–22156.
- 551 Zettlemoyer, M.A., Schultheis, E.H. & Lau, J.A. (2019) Phenology in a warming world: differences  
552 between native and non-native plant species. *Ecology Letters* **22**, 1253–1263.

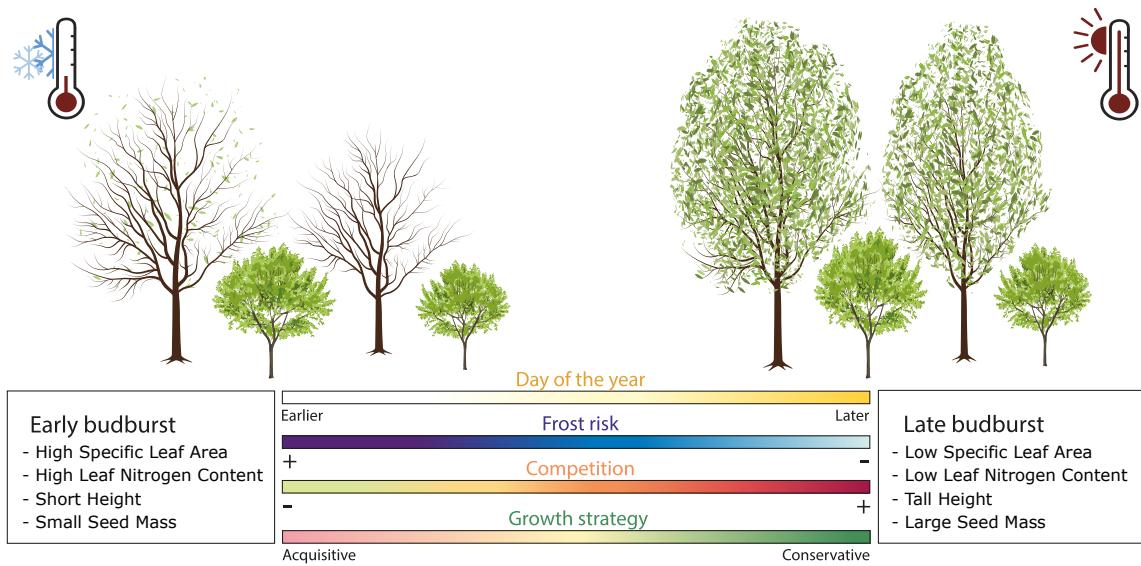


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater abiotic and biotic risk but reduced competition. In contrast, we expected later-budbursting species would have traits associated with conservative growth, as they experience greater competition but a more climatically benign environment. However previous studies looking at different phenological events, such as flowering, or suites of non-woody species, have found varying relationships between traits and phenology, highlighting the complexity that may shape species temporal niche.

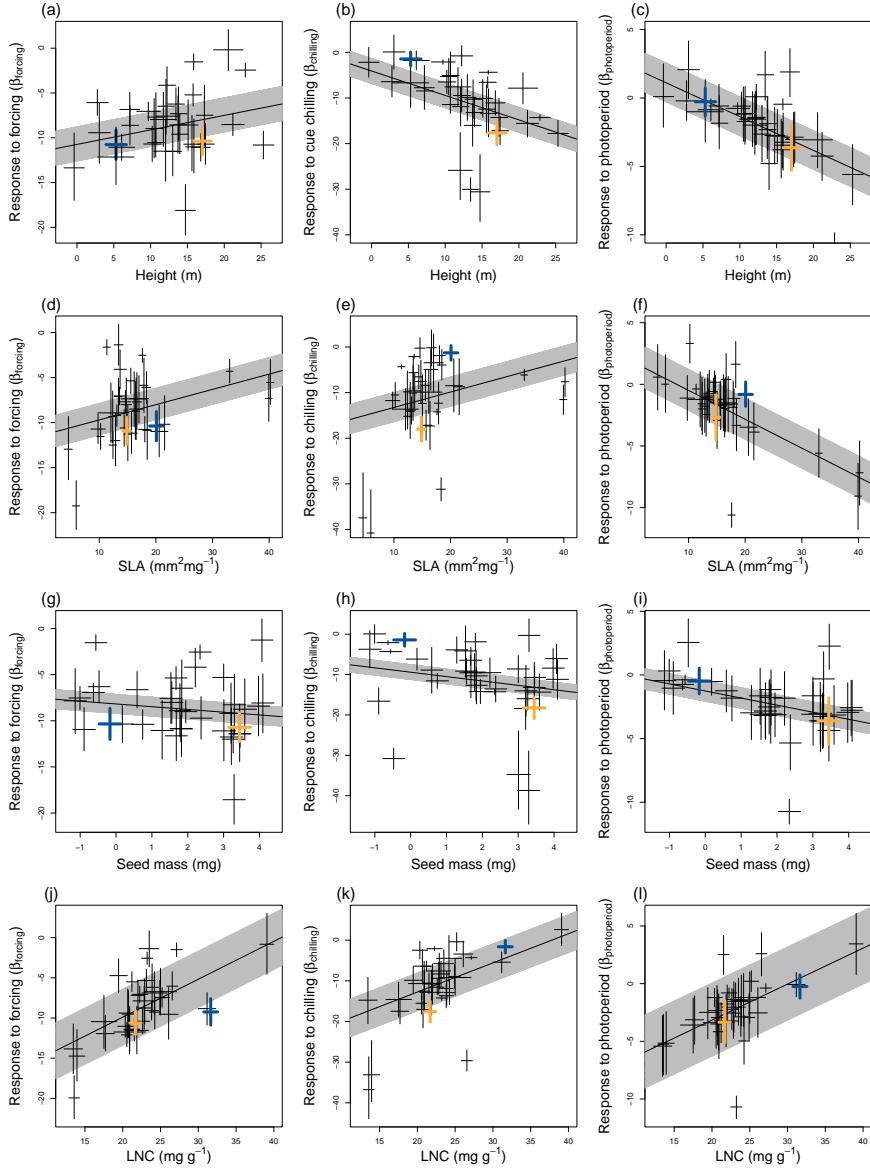


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the black line depicting the mean linear relationship between estimated trait effects and the slope of the cue response (either  $\beta_{\text{chilling}}$ ,  $\beta_{\text{forcing}}$ ,  $\beta_{\text{photoperiod}}$  for each respective trait) and the gray band the 50% uncertainty interval. Each set of crossed lines represents one species (with each line spanning the 50% uncertainty interval), depicting how well our model fits the data across all species. To illustrate the relationship between traits and the three phenological cues we highlight two example species that differ greatly in their architecture and life history—*Alnus incana*, shown in blue—a shorter, shrubby tree species with a growth strategy characteristic of an acquisitive species—and *Quercus rubra*, shown in yellow—a taller and characteristically conservative species (see also Fig 2 and S5).

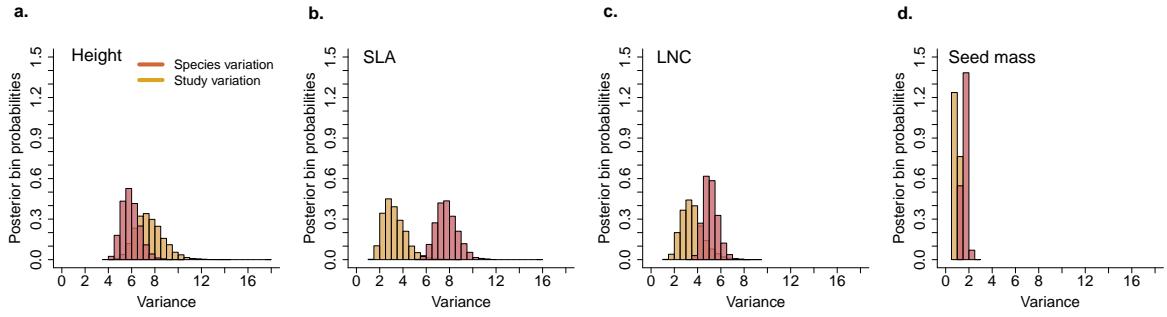


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ( $\sigma_{\text{species}}^2$  and  $\sigma_{\text{study}}^2$  respectively), with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf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