

<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. Phenologies—the timing of recurring life history events—can vary substantially in different environments and for different species. While climate change has shifted phenology by altering its proximate drivers—such as temperature—changes in the ultimate drivers that select for species-level variation remain poorly explained. Theory suggests that species-level variation in phenology can result from shifting environmental pressures that favour different strategies across the [spring growing season](#): from the early season, where higher abiotic risks and greater availability of nutrients and light favour cheaper leaves and acquisitive growth strategies, to later when a more benign environment and lower levels of light and nutrients favour conservative growth strategies. From this we can infer suites of traits that may co-vary with species phenologies, but the high variability in traits—and especially phenology—across environments, have made testing the role of phenology within a trait framework challenging.
- <sup>15</sup> 2. Using a modelling framework that accommodates this variability we performed a meta-analysis using phenological data from [a database of controlled environment experiments](#) and [tree 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>19</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—were shorter with high nitrogen leaves. Seed mass showed no relationships to budburst cues, while specific leaf area was only related to photoperiod, and in the opposite direction to our predictions.
- <sup>23</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.

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<sup>27</sup> Key Words: Leafout, spring phenology, traits, trees, climate change, forest communities

<sup>28</sup> **Introduction**

<sup>29</sup> The timing of life history events—phenology—can shape both ecosystem services and community  
<sup>30</sup> dynamics. Spring phenology, for example, defines the start and overall length of the growing season—  
<sup>31</sup> shaping forest carbon storage and species interactions (Beard *et al.*, 2019; Cleland *et al.*, 2007; Gu  
<sup>32</sup> *et al.*, 2022). Shifts in phenology with climate change across systems (Menzel *et al.*, 2006; Vitasse  
<sup>33</sup> *et al.*, 2021) have thus led to growing concerns over their possible impacts.

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<sup>35</sup> Predicting these changes requires understanding the drivers of phenology both at a proximate scale—  
<sup>36</sup> the environmental triggers of phenology each year, such as temperature and daylength—and at an  
<sup>37</sup> ultimate scale, where long-term environmental pressures may select for different phenologies across  
<sup>38</sup> species, (e.g., certain species are early or late relative to other species each year Ovaskainen *et al.*,  
<sup>39</sup> 2013; Wolkovich & Donahue, 2021). At the proximate level, environmental conditions throughout  
<sup>40</sup> the winter and spring cause species to start growth at different times. While similar environmental  
<sup>41</sup> conditions appear to trigger the start of growth in woody plants each year, it is increasingly clear that  
<sup>42</sup> some functional groups differ in their responses to conditions with generalizable found for species that  
<sup>43</sup> differ in their successional stages (Laube *et al.*, 2014a) or architecture (Flynn & Wolkovich, 2018).  
<sup>44</sup> But current work provides limited insights into the drivers of these differences across species and how  
<sup>45</sup> they can be used to predict future changes in community dynamics (Chuine *et al.*, 2016; Flynn &  
<sup>46</sup> Wolkovich, 2018; Laube *et al.*, 2014a).

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<sup>48</sup> At the ultimate level, plant phenologies may vary due to changing pressures across the growing sea-  
<sup>49</sup> son. Species that start growth early often risk high tissue loss—due to frost damage (Augspurger,  
<sup>50</sup> 2009; Sakai & Larcher, 1987) or high herbivore apprenency (Wainwright *et al.*, 2012)—but benefit from  
<sup>51</sup> higher resource availability (Hufkens *et al.*, 2012; Rathcke & Lacey, 1985). In contrast, later active  
<sup>52</sup> species face greater biotic pressures, especially from high competition for resources (Lopez *et al.*, 2008;  
<sup>53</sup> Wolkovich & Ettinger, 2014). Such differences could shape physical and phenological traits related  
<sup>54</sup> to species growth strategies and fitness (Violle *et al.*, 2007). Species leaf and wood traits can reflect  
<sup>55</sup> trade-offs between the construction costs and longevity of tissue (Reich *et al.*, 1997; Wright *et al.*,  
<sup>56</sup> 2004), with cheaper to construct tissue being associated with faster growth rates (Westoby & Wright,  
<sup>57</sup> 2006; Wright *et al.*, 2004). Previous studies have highlighted the associations between trade-offs in  
<sup>58</sup> traits and phenology (Sporbert *et al.*, 2022; Wang *et al.*, 2021; Wolkovich & Ettinger, 2014) (Fig 1),  
<sup>59</sup> and indicate the potential for species traits to similarly range from the acquisitive (fast) to more con-  
<sup>60</sup> servative (slow) growth strategies associated with existing trait frameworks (Chave *et al.*, 2009; Wright  
<sup>61</sup> *et al.*, 2004).

62

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

75

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

88

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

shorter, with leaf traits favorable to the low light conditions of the understory later in the growing season, producing cheap 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 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).

To test our predicted relationships 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.

117

## 118 Methods

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

126

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

129

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

137

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

156

157 For our analysis, we only include species for which we had a complete trait profile (i.e., all traits  
158 measured for all species). We initially considered six commonly measured traits—SLA, leaf dry matter  
159 content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species had  
160 at least one trait measurement for each of the traits. We then used a principle component analysis  
161 (PCA) to identify which of our six traits were strongly correlated. The first principal component  
162 explained 32% of variation while the second explained 24.2% of the variation (Fig. S2), with high  
163 correlations between SLA and LDMC, and between height and SSD (Fig. S2). By excluding the one  
164 trait from each of these highly correlated trait pairs with the least amount of data (specifically LDMC

165 and SSD) we were able to increase the number of species in our dataset from the 26 species with  
 166 complete data for six traits, to 37 species with complete data for four traits. The data for these 37  
 167 species were from 24 unique studies (samples sizes: height  $n = 47781$ , seed mass  $n = 281$ , LNC  $n =$   
 168 3853, SLA  $n = 7656$ ). We subsampled the height measurements of the 13 most frequently measured  
 169 tree to reduce their influence on our height model. Since each of these species were measured 19  
 170 times more frequently than most other species, we randomly sampled 3000 height measurements for  
 171 each individual species, while including all height data for the remaining, less frequently measured, 24  
 172 species.

## 173 Joint model of trait and phenology

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

### 185 Trait sub-model

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

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

190 with

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

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

$$\boldsymbol{\alpha}_{\text{trait}} = \alpha_{\text{grand trait}} + \alpha_{\text{species}_i}$$

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

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

(4)

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

## 196 Phenology sub-model

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

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

202 with

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

203 and

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

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

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

204 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:

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

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

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

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

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

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

215

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

## 227 Results

228 Across traits, height, SLA, and LNC strongly related to one or more environmental cue ( $\beta_{\text{chilling}_k}$ ,  
229  $\beta_{\text{forcing}_k}$ , or  $\beta_{\text{photoperiod}_k}$ , Fig 2 a-f & j-l), with only LNC showing a relationship with all three cues  
230 (Fig. 2 j-l). As we predicted, height was negatively related to chilling ( $\beta_{\text{chilling}_k}$ ) and photoperiod  
231 ( $\beta_{\text{photoperiod}_k}$ ), with taller species having larger responses to high chilling and longer photoperiods  
232 conditions (-0.5 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per  
233 standardized photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). We found height to have a strong  
234 relationship with the timing of budburst (as estimated by  $\mu_{k,g}$ ), with later budburst estimated for  
235 taller trees under increasing chilling and photoperiods (Fig. S5). In contrast, seed mass had a negligi-  
236 ble relationship with budburst and all three cues (Fig. 2 g-i & Table S4).

237

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

250

251 To illustrate the relationship between traits and the three phenological cues we selected two example  
252 species that differ greatly in their architecture and life history—*Alnus incana*—a shorter, shrubby tree  
253 species with a growth strategy characteristic of an acquisitive species—and *Quercus rubra*—a taller  
254 and characteristically conservative species (Fig 2 and S5). Interestingly the observed trait values for  
255 these two species did differ substantially for most traits, with the exception of SLA, for which the  
256 observed trait values were quite similar (as depicted by the colored crosses in Fig. 2). Using the  
257 posterior estimates for each trait model individually, we visualized the relative effect of including traits  
258 in our estimates of budburst in Fig. S5, using the estimated the day of budburst generated from the  
259 posteriors of our two example species and either with the effects of traits included (denoted as the  
260 full model), or without trait effects (with the parameter for the trait effect was set to zero). The  
261 largest differences 50% uncertainty intervals with our without the trait effects reflect the strength of  
262 the relationship between a trait and the cues shaping budburst. As supported by our overall model  
263 estimates, strong trait effects were observed between height and chilling and photoperiod for both  
264 species (Fig. S5 b and c), and all cues and LNC (Fig. S5 j to l). But the weak relationships between  
265 seed mass and phenological cues produced relatively small differences between estimates of budburst  
266 when the effects of seed mass are included in estimates or not (Fig S5 d-f & Table S4).

267 In partitioning the measurement error in the trait values from variation from species and study-level  
268 effects, we found that the species-level variation across traits ( $\sigma_{\text{trait}}^2$ ) were comparable to, or greater  
269 than variation across studies ( $\sigma_{\text{study}}^2$ ; Fig 3). In particular, variation across studies was greatest for  
270 height, with an estimated study level variation ( $\sigma_{\text{study}}^2$ ) of 7.5 m (90% UI: 5.8, 9.7), than caused by  
271 species-level variation ( $\sigma_{\text{trait}}^2$ ), with an estimate of 5.9 m (90% UI: 4.8, 7.3, Fig 3a). For seed mass  
272 and LNC, study-level variation was less than that of the species-level variation, with variation in seed

273 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 species-  
274 level variation respectively and for LNC 3.6 mg g<sup>-1</sup> (90% UI: 2.2, 5.3) for study-level variation and  
275 5.1 mg g<sup>-1</sup> for the species-level variation (90% UI: 2.2, 5.3, Fig 3c and d). Study-level variation was  
276 smallest for SLA, with the estimate of 3.3 mm<sup>2</sup> mg<sup>-1</sup> (90% UI: 2, 5.1) for study-level variations being  
277 approximately half that of the estimated species-level variation of 7.8 mm<sup>2</sup> mg<sup>-1</sup> (90% UI: 6.4, 9.4, Fig  
278 3b). Across all traits, study-level variation ( $\sigma_{\text{study}}^2$ ) made a considerable contribution to the overall  
279 variation observed in our trait values and suggests that models using large trait databases that fail to  
280 separate out study from species-level variation ( $\sigma_{\text{trait}}^2$ ) may poorly estimate species traits.

281

## 282 Discussion

283 We found several species traits influenced the timing of budburst in response to one or more of the  
284 three primary cues of spring phenology: chilling, forcing and photoperiod. While the relationships be-  
285 tween SLA and seed mass with phenological cues differed from our predictions, the trait effects of height  
286 and LNC were associated with earlier or later phenology, following well-established gradients in growth  
287 strategies predicted by functional trait frameworks (Chave *et al.*, 2009; Díaz *et al.*, 2016; Westoby, 1998;  
288 Westoby & Wright, 2006; Wright *et al.*, 2004). Early species—known to budburst under weak forcing,  
289 chilling, and photoperiod cues—exhibited relationships with several traits associated with fast and  
290 acquisitive growth strategies, while later budbursting species—that require stronger forcing, chilling,  
291 and photoperiod cues to initiate growth—did exhibit traits indicative of conservative, slower growth  
292 strategies. We found the largest budburst responses occurred for traits related to resource acquisition  
293 and structure, with SLA, LNC, and height all showing large responses to at least one of our three  
294 cues. In contrast, our one reproductive trait—seed mass—showed the smallest response. Our results  
295 provide a major step forward in integrating phenology into broader trait syndromes that shape species  
296 growth strategies, and support previous findings from more local scales that found strong relationships  
297 between height and species phenology (Osada & Hiura, 2019; Seiwa, 1999). Our more global analysis  
298 is also in agreement with previous studies of plant phenological events, in which no relation is found  
299 between phenology and seed mass in woody plants (Bolmgren & D. Cowan, 2008; Ettinger *et al.*, 2018).

300

301 In addition to identifying trait-phenology relationships shaping the timing of spring budburst, our  
302 results also provide important insight into the use of data from large databases to estimate ecological  
303 processes. By partitioning the different sources of variation that contribute to the observed trait values,  
304 we were able to demonstrate the considerable effects study-level variation can have on trait values,  
305 which for some traits even exceeded the species-level variation. This variation is the result of a myriad

306 of factors, including observer error or differences in methodologies, and are present in any dataset that  
307 pools data from diverse sources. To the best of our knowledge, our results provide some of the strongest  
308 evidence for why it is important for analyses using data from aggregate databases to account for the  
309 effects of this and other sources of variation in their analyses if they are to make accurate predictions  
310 of trait effects.

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

312 Our findings suggest the changing pressures across the early growing season may affect the tempo-  
313 ral assembly of communities. Species with weak cue responses, an indication of earlier budburst,  
314 had some traits indicative of acquisitive growth strategies (shorter heights and high LNC) that allow  
315 faster return on resource investments (Chave *et al.*, 2009; Grime, 1977; Westoby, 1998). These traits  
316 should allow early species to benefit from greater light availability in the open forest canopy in the  
317 early spring and withstand the low light conditions later in the season. In contrast, later-budbursting  
318 species had traits associated with slower, more conservative, growth (Chave *et al.*, 2009; Grime, 1977;  
319 Westoby, 1998), which may help them compete for the more limited soil and light resources later in  
320 the growing season. Similar trait-phenology relationships have also been linked to other ecological  
321 processes and species characteristics that define community structure and diversity, such as species  
322 successional position (Laube *et al.*, 2014b), and are in agreement with the differences we observed for  
323 height and LNC in our example comparing *Alnus incana* (a pioneer species) and *Quercus rubra* (a  
324 later successional species); Fig 2).

325  
326 The traits with cue responses that deviated from our expectations also offer novel insights into the  
327 tradeoffs between traits and environmental cues. All of our traits are associated with multiple aspects  
328 of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our  
329 predictions, we found large responses to forcing for short trees, which could prevent frost damage or  
330 xylem cavitation under a late spring frost (Clements *et al.*, 1972; Marquis *et al.*, 2020) and influence  
331 annual cambial meristem growth (Lenz *et al.*, 2016). Similarly, the lack of a relationship between SLA  
332 and chilling and forcing could be driven by other physiological constraints or tradeoffs with selection  
333 by other cues—as variation in SLA also reflects differences in species relative growth rates or leaf  
334 longevity—and not just photosynthetic potential (Reich, 2014; Westoby, 1998). These findings high-  
335 light the complexity of determining the drivers of species trait profiles, and further our understanding  
336 of how traits affect community dynamics under variable environments.

337

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

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

345

346 Our results suggest this phenology-performance relationship could be driven in part by a suite of traits  
347 that covary with phenological cues to determine how responsive species are to warming. Species with  
348 smaller responses to all cues, especially chilling and photoperiod, would tend to advance more with  
349 warming (Guy, 2014). Our results suggest that these same species are likely to have acquisitive traits,  
350 such as short heights and high LNC that allow them to grow quickly and benefit from the greater  
351 availability of nutrients in the early spring. Understanding these trait-phenology relationships may  
352 provide insight into how climate change may alter species coexistence (Rudolf, 2019). A greater un-  
353 derstanding of trait-phenology relationships may also improve our ability to manage species invasions,  
354 as invasive species to have earlier phenologies (Alexander & Levine, 2019; Polgar *et al.*, 2014; Zettle-  
355 moyer *et al.*, 2019), but possibly a unique suite of traits that facilitate fast growth (Fridley *et al.*, 2022)..

356

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

364

365 Our results could further help identify which species are most likely to be negatively impacted under  
366 future climates, and develop better strategies for climate change mitigation and conservation. Species  
367 that fail to advance phenologically with warming might experience more competition (Alexander &  
368 Levine, 2019; Carter *et al.*, 2018), as species that begin growth increasingly earlier with warming have  
369 more time to deplete resources. In addition to altering the timing and interactions between species  
370 within a season, species trait syndromes have the potential to further redefine the environmental condi-  
371 tions under which growth occurs, and as a result, shape community assembly and productivity within

<sup>372</sup> ecological communities (Rudolf, 2019). By identifying the species most vulnerable to climate change  
<sup>373</sup> impacts, we can develop more effective management practices that prevent the loss of critical ecosys-  
<sup>374</sup> tem services and preserve community diversity under future conditions.

<sup>375</sup>

## <sup>376</sup> Acknowledgements

<sup>377</sup> We thank the researchers who measured the traits and conducted the experiments producing the data  
<sup>378</sup> used in this manuscript.

## <sup>379</sup> Author Contributions Statement

<sup>380</sup> DL, FAMJ, GL, MG, DS, and EMW planned and designed the study. All authors conducted the  
<sup>381</sup> literature review and cleaned the database. DL, FAMJ, GL, and EMW performed the data analysis  
<sup>382</sup> and contributed code. DL, FAMJ, and GL created the figures. DL and EMW wrote the initial draft  
<sup>383</sup> and all authors reviewed and revised the manuscript.

## <sup>384</sup> Competing Interests Statement

<sup>385</sup> The authors declare no competing interests.

## <sup>386</sup> Data availability statement

<sup>387</sup> The phenological data used for this manuscript is a subset of the existing OSPREE dataset (doi:10.5063/F1CZ35KB)  
<sup>388</sup> and the trait data a subset of the TRY database (doi:10.1111/gcb.14904) and the BIEN database  
<sup>389</sup> (doi: 10.1111/2041-210X.1286).

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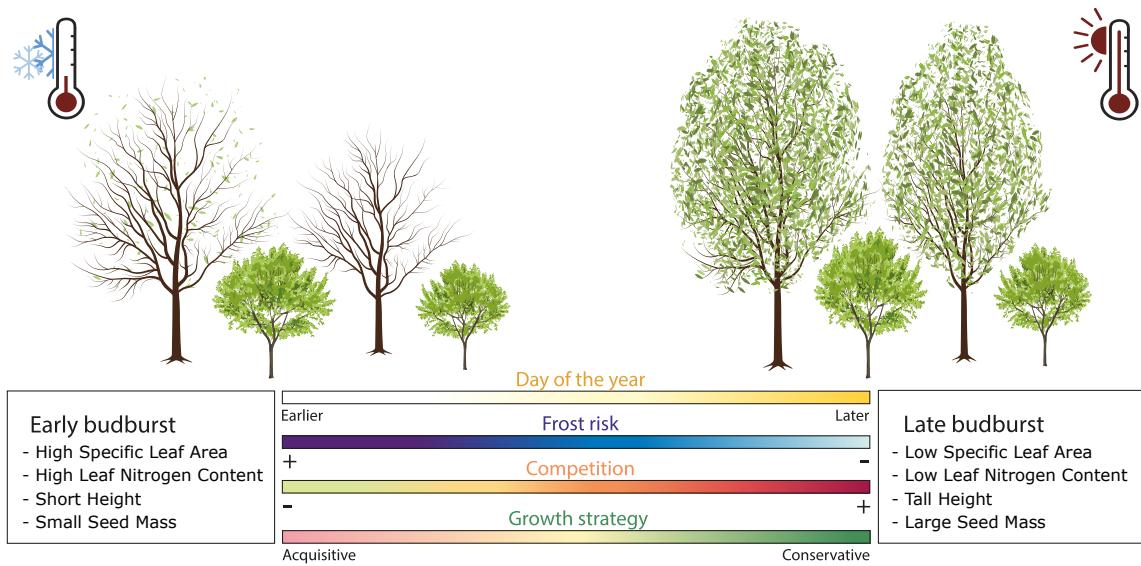


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater abiotic and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

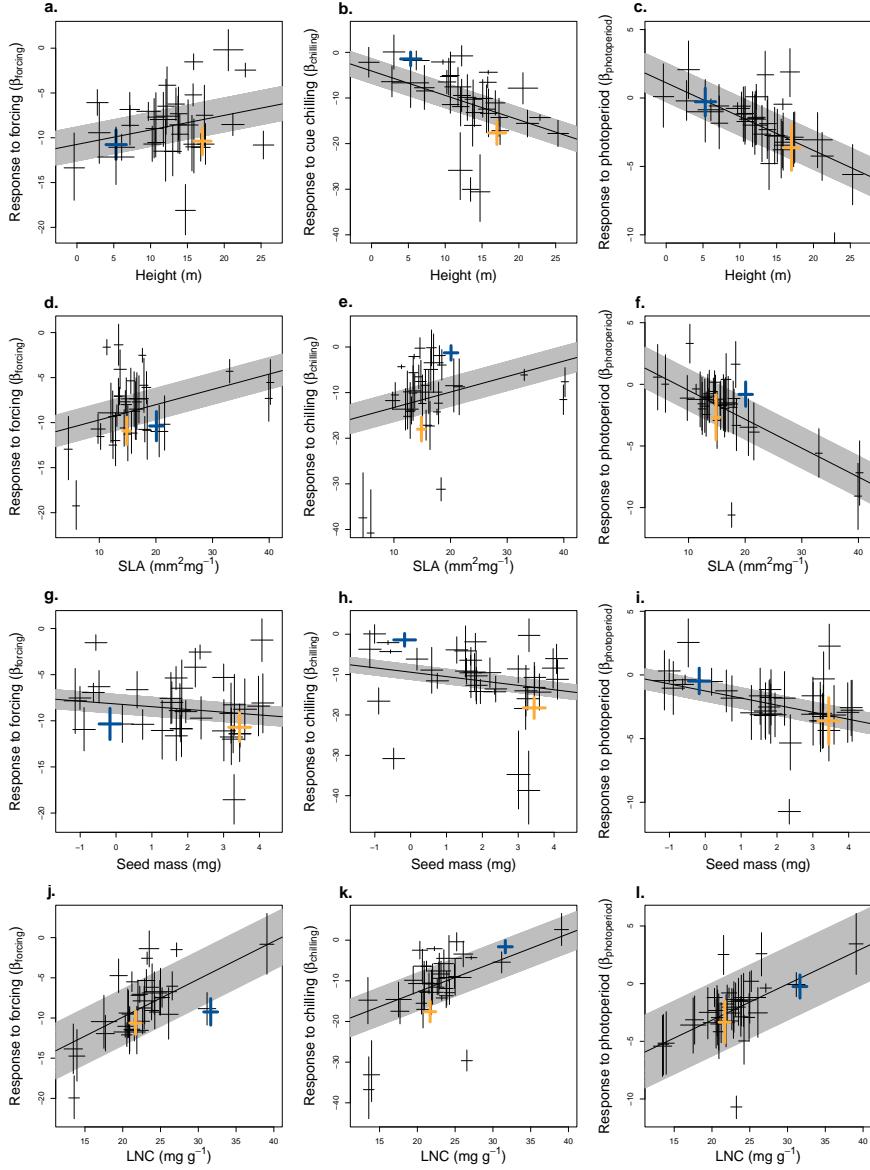


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third row: g-i), and LNC (fourth row: j-l). We estimated parameters using a joint trait-phenology model, with the black line depicting the mean linear relationship between estimated trait effects and the slope of the cue response (either  $\beta_{\text{chilling}}$ ,  $\beta_{\text{forcing}}$ ,  $\beta_{\text{photoperiod}}$  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. The two example species depicted in Fig S5 are colored in each panel, with the acquisitive species (*Alnus incana*) shown in blue, and the conservative species (*Quercus rubra*) shown in yellow.

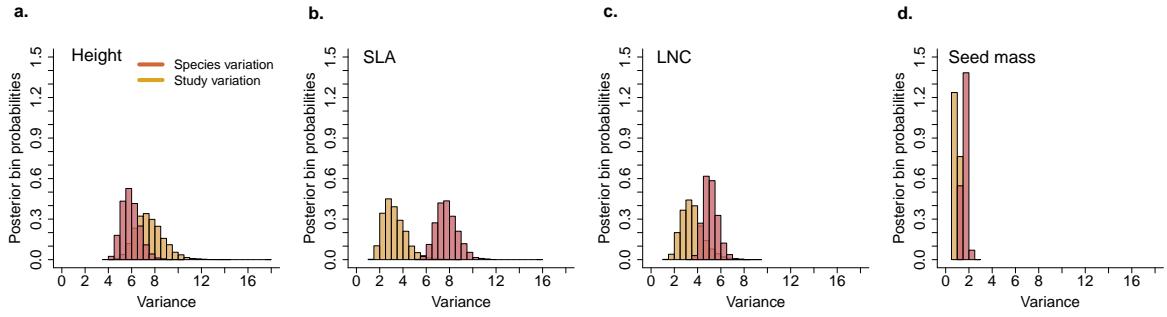


Figure 3: Traits differed in the relative magnitude of their species-level and study-level variation ( $\sigma_{\text{species}}^2$  and  $\sigma_{\text{study}}^2$  respectively), with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf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