

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

<sup>2</sup> Deirdre Loughnan<sup>1</sup>, Faith A M Jones<sup>1,2</sup>, Geoffrey Legault<sup>1</sup>, Daniel Buonaiuto<sup>3,4,5</sup>,  
Catherine Chamberlain<sup>3,4,6</sup>, Ailene Ettinger<sup>7</sup>, Mira Garner<sup>1</sup>, Ignacio Morales-Castilla<sup>8,9</sup>,  
Darwin Sodhi<sup>1</sup> and E M Wolkovich<sup>1,3,4</sup>

<sup>3</sup> December 5, 2024

<sup>4</sup> <sup>1</sup> Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia,  
<sup>5</sup> 2424 Main Mall Vancouver, BC Canada V6T 1Z4.

<sup>6</sup>  
<sup>7</sup> <sup>2</sup> Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sci-  
<sup>8</sup> ences, 901 83 Umeå, Sweden

<sup>9</sup>  
<sup>10</sup> <sup>3</sup> Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

<sup>11</sup>  
<sup>12</sup> <sup>4</sup> Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts,  
<sup>13</sup> USA;

<sup>14</sup>  
<sup>15</sup> <sup>5</sup> Department of Environmental Conservation, University of Massachusetts, Amherst, 160 Holdsworth  
<sup>16</sup> Way, Amherst, MA, USA

<sup>17</sup>  
<sup>18</sup> <sup>6</sup> The Nature Conservancy, 334 Blackwell St, #300, Durham, NC, USA

<sup>19</sup>  
<sup>20</sup> <sup>7</sup> The Nature Conservancy of Washington, 74 Wall Street, Seattle, WA USA

<sup>21</sup>  
<sup>22</sup> <sup>8</sup> GloCEE—Global Change Ecology and Evolution Group, Department of Life Sciences, University of  
<sup>23</sup> Alcalá, Alcalá de Henares, Spain

<sup>24</sup>  
<sup>25</sup> <sup>9</sup> Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

<sup>27</sup> Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca

<sup>28</sup>

<sup>29</sup> Running title: Budburst responses associated with traits

<sup>30</sup> **Summary**

- <sup>31</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 early (spring) growing season: from the early season, where higher abiotic risks and greater availability of nutrients and light favour acquisitive growth strategies, to later when a more benign environment and greater competition 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>41</sup> 2. Using a modelling framework that accommodates this variability we performed a meta-analysis using phenological data from controlled environment experiments and plant traits to test the relationships between traits and cues for tree budburst (forcing, chilling, and photoperiod).
- <sup>44</sup> 3. We found that earlier species are shorter with denser, lower nitrogen leaves, while later-active species were taller with low nitrogen leaves. How budburst timing related to leaf density, however, was less in line with our predictions, as species with denser leaves had large responses to only some cues.
- <sup>47</sup> 4. Synthesis: Our findings show how spring leafout phenology fits within a functional trait framework of acquisitive to conservative growth strategies, and better predicts how communities may shift in their growth strategies alongside changing phenology with climate change.

<sup>50</sup>

<sup>51</sup> Key Words: Budburst, spring phenology, traits, trees, climate change, forest communities

<sup>52</sup> **Introduction**

<sup>53</sup> The timing of life history events—phenology—can shape both ecosystem services and community dynamics. Spring phenology, for example, defines the start and overall length of the growing season—shaping forest carbon storage and species interactions (Beard et al., 2019; Cleland et al., 2007; Gu et al., 2022). Shifts in phenology with climate change across systems (Menzel et al., 2006; Vitasse et al., 2021) have thus led to growing concerns over their possible impacts.

58

59 Predicting these changes requires understanding the drivers of phenology both at a proximate scale—  
60 the environmental triggers of phenology each year, such as temperature and daylength—and at an  
61 ultimate scale, where long-term environmental pressures may select for different phenologies across  
62 species, (e.g., certain species are early or late relative to other species each year Ovaskainen et al.,  
63 2013; Wolkovich and Donahue, 2021). At the proximate level, environmental conditions throughout  
64 the winter and spring cause species to start growth at different times. Similar environmental conditions  
65 appear to trigger spring phenological events across taxa, including the start of growth in woody plants  
66 each year (Flynn and Wolkovich, 2018; Laube et al., 2014), the timing of egg laying in birds (Crick  
67 et al., 1997; D’Alba et al., 2010), and the advance of spawning in amphibians (Kusano and Inoue,  
68 2008; Tryjanowski et al., 2003), but current work provides limited insights into the drivers of species  
69 differences (Chuine et al., 2016; Flynn and Wolkovich, 2018; Laube et al., 2014).

70

71 At the ultimate level, species phenologies may vary due to changing pressures across the growing sea-  
72 son. Species that start growth early often risk high tissue loss—due to frost damage (Augspurger,  
73 2009; Sakai and Larcher, 1987) or high herbivore apparencty (Wainwright et al., 2012)—but benefit  
74 from higher resource availability (Hufkens et al., 2012; Rathcke and Lacey, 1985). In contrast, later  
75 species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008;  
76 Wolkovich and Ettinger, 2014). For plants, this variation in early to late season growth may mirror  
77 the stressors from early to late successional communities, and may similarly shape phenology (Laube  
78 et al., 2014).

79

80 Different pressures could shape a number of species attributes related to their growth strategies, in-  
81 cluding phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced  
82 if damaged (Reich et al., 1999), while species with later phenology may benefit from investing in tis-  
83 sues that infer greater resource retention (Gorné et al., 2020). Differences in traits, and trade-offs in  
84 allocation of resources to growth and tissue quality, can be related to a broader framework of species  
85 growth strategies and functional traits (Wolkovich and Ettinger, 2014) (Fig 1), where species range  
86 from acquisitive (fast) to more conservative (slow) growth (Chave et al., 2009; Wright et al., 2004).

87

88 Globally, gradients from acquisitive to conservative strategies appear common, and form the foun-  
89 dation of the leaf economic and the wood economic spectra (Chave et al., 2009; Díaz et al., 2016;  
90 Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004), but they can make limited predictions  
91 of trait variability (Violle et al., 2012). As a result, highly variable traits like phenology are often  
92 excluded from trait studies, leaving the relationships between broader trait syndromes and phenology

93 largely unknown. Understanding these relationships is critical to forecasting community dynamics and  
94 responses to climate change. To date, studies have generally only examined the relationship between  
95 traits and phenology within a single site (as reviewed by Wolkovich and Cleland (2014) and Wolkovich  
96 and Donahue (2021)) where the problem of proximate drivers causing phenological variation can be  
97 more easily ignored. Adding phenology to broader trait frameworks becomes more complex when high  
98 levels of variation occurs across large spatial and temporal ranges.

99

100 Consistently defining early to late phenology is possible using the underlying cues that predict gradi-  
101 ents in phenology, (which do not generally vary strongly across space and time Chuine and Cour, 1999;  
102 Flynn and Wolkovich, 2018; Harrington and Gould, 2015). For many plants, early species generally  
103 have responses that are small in magnitude to all three major cues of spring leafout: warm spring  
104 temperatures (forcing), cool winter temperatures (chilling) and daylength (photoperiod). In contrast,  
105 later species have larger responses to chilling and/or photoperiod (Flynn and Wolkovich, 2018; Laube  
106 et al., 2014), and likely larger forcing responses.

107

108 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-  
109 nology into functional trait research. In addition to how well we understand the environmental cues  
110 that trigger early versus late leafout, spring in many forests includes strong gradients in potential se-  
111 lective environments (Fig 1). Based on trade-offs between early and late spring phenologies, we predict  
112 acquisitive species to be shorter, with leaf traits favourable to higher light availability and tolerance  
113 to late spring frost (high specific leaf area, SLA, and leaf nitrogen content, LNC; Fig 1). Such species  
114 should exhibit early phenology, with small cue responses. Canopy species that budburst later via larger  
115 cue responses, when competition for soil resources is greater, would then have traits associated with  
116 conservative growth—taller with denser wood (Laughlin et al., 2010)—with leaf traits suited for more  
117 variable light (low SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to  
118 conservative continuum, as acquisitive species produce smaller seeds and conservative species produce  
119 larger—better provisioned—seeds (Fig 1).

120

121 To test our predicted relationships between budburst responses to environmental cues and common  
122 functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases—  
123 BIEN (Maitner et al., 2018) and TRY (Kattge et al., 2020)—with budburst data from the OSPREE  
124 database of controlled environment studies (Ettinger et al., 2020). We developed a hierarchical Bayesian  
125 joint model that predicts phenological responses to forcing, chilling and photoperiod treatments based  
126 on species-level trait values, while allowing additional variation due to species. This approach takes  
127 a step towards predicting variation via species traits instead of species identity (when traits explain

<sup>128</sup> a significant portion of the variation, species identity will explain only a small amount), which could  
<sup>129</sup> help forecast species phenological responses based on trait values alone.

<sup>130</sup>

## <sup>131</sup> Methods

<sup>132</sup> We merged three major databases for our analysis. We gathered phenological data from the OSPREE  
<sup>133</sup> database (Ettinger et al., 2020), which contains budburst data for woody, species from experiments of  
<sup>134</sup> forcing, chilling and photoperiod. We constructed the OSPREE database by performing a systematic  
<sup>135</sup> review of the literature, and searched both ISI Web of Science and Google Scholar using the following  
<sup>136</sup> two search terms:

<sup>137</sup>

- <sup>138</sup> 1. TOPIC = (budburst OR leafout) AND (photoperiod or daylength) AND temperature\*
- <sup>139</sup> 2. TOPIC = (budburst OR leafout) AND dorman\*

<sup>140</sup>

<sup>141</sup> We then scraped the data from all articles of woody species that experimentally manipulated both  
<sup>142</sup> photoperiod and/or temperature cues of budburst, leafout, or flowering phenology, and for which there  
<sup>143</sup> was a quantifiable response to each cue. We updated this database in July 2019 reviewing all new  
<sup>144</sup> articles found using the previous search terms. Additional details on the methods used to assemble,  
<sup>145</sup> clean, and update this database are discussed by Ettinger et al. (2020) and Morales-Castilla et al.  
<sup>146</sup> (2024). For the purpose of this study, we used a subset of the OSPREE database, using data only for  
<sup>147</sup> budburst phenology and for the subset of 234 species used in Morales-Castilla et al. (2024).

<sup>148</sup>

<sup>149</sup> We gathered trait data from the TRY and BIEN (v. 4.0) databases (Kattge et al., 2020; Maitner et al.,  
<sup>150</sup> 2018), both of which are large trait databases that include plant trait data across many individuals,  
<sup>151</sup> species, and studies (Table S1). We obtained data from both databases on 5 December, 2018, and  
<sup>152</sup> requested an updated version of the TRY data on 10 April, 2019. We again focused our search for trait  
<sup>153</sup> data on the subset of 234 OSPREE species used in Morales-Castilla et al. (2024). Using the BIEN  
<sup>154</sup> R package (v. 1.2.5) (Maitner et al., 2018), we downloaded all available trait data for the 94 species  
<sup>155</sup> available, for which there were 13 unique traits. From the TRY database we received data for 10  
<sup>156</sup> unique traits for 96 of our focal species (Kattge et al., 2020). Given our focus on the phenology of  
<sup>157</sup> adult trees, we subset the available data to only include traits measured from adult individuals with  
<sup>158</sup> a minimum height of 1.38 m. We further removed all data from manipulative experiments or from  
<sup>159</sup> plants growing in non-natural habitats. We also grouped trait values where appropriate, for example  
<sup>160</sup> pooling trait values for specific leaf area (SLA) with those denoted as “SLA with petioles”, and “SLA

161 without petioles” in our analysis (see Table S1). We also removed data that was duplicated in both  
162 the TRY and BIEN datasets ( $n = 434905$ ).

163

164 For our analysis, we only include species for which we had a complete trait profile (i.e., all traits mea-  
165 sured for all species). We initially considered six commonly measured traits—SLA, leaf dry matter  
166 content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species had  
167 at least one trait measurement for each trait. We then used a principle component analysis (PCA) to  
168 understand trait correlations and adjusted which traits we included. The PCA of our six initial traits  
169 identified high correlations between SLA and LDMC, and between height and SSD. The first principal  
170 component explained 32% of variation while the second explained 24.2% of the variation (Fig. S1).  
171 By excluding one trait from each of these highly correlated trait pairs (specifically LDMC and SSD)  
172 we increased the number of species in our dataset from the 26 species with six traits, to 37 species for  
173 which we had complete datasets for four traits. The data for these 37 species were from 24 unique  
174 studies (samples sizes: height  $n = 47781$ , seed mass  $n = 281$ , LNC  $n = 3853$ , SLA  $n = 7656$ ). We  
175 also subsampled height measurements to reduce the influence of the 13 most frequently measured tree  
176 species on our height model. Since these 13 species were measured 19 times more frequently than other  
177 species, we randomly sampled 3000 height measurements for each species.

178

## 179 Joint model of trait and phenology

180 To understand connections between phenology and species traits, we developed and then parameterized  
181 a joint model for each trait: height, SLA, LNC, and seed mass. Our model is a joint model insofar as  
182 it involves two sub-models—one that models trait observations and a second that uses shared latent  
183 processes to model phenological observations. In particular, we assume that trait values are the result  
184 of multiple sources of variation, include species and study-level variation, combining into one trait  
185 value that we observe (trait sub-model). This trait value ( $\alpha_{\text{trait}}$ ) has a separate interaction with the  
186 environmental cues (forcing, chilling, and photoperiod) that determine phenology—specifically the  
187 day of year of budburst (phenology sub-model). Below we describe the two sub-models, noting which  
188 parameters are shared across sub-models and which are independent.

## 189 Trait sub-model

190 Our trait sub-model describes the processes that determine trait observations for 1 to  $n$  species across  
191 each of the 1 to  $m$  studies in our trait dataset. We use hierarchical modeling to partition trait values  
192 by measurement error ( $\sigma_m^2$ ), species identity  $\alpha_{\text{species}_i}$ , and study  $\alpha_{\text{study}_j}$ . In particular, we assume that

<sup>193</sup> a trait observation for species  $i$  from study  $j$ ,  $Y_{\text{trait}_{i,j}}$ , has the following normal distribution:

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

with

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

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

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

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

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

## <sup>199</sup> Phenology sub-model

<sup>200</sup> Our phenology sub-model describes the processes that determine the relationships between traits and  
<sup>201</sup> environment cues and their effects on phenological observations for 1 to  $n$  species, specifically the  
<sup>202</sup> timing (day of year) of budburst from the updated OSPREE dataset. We assume that an observation  
<sup>203</sup> of budburst for species  $k$  under  $g$  treatments levels of chilling, forcing, and photoperiod ( $c_g, f_g, p_g$ ),  
<sup>204</sup> parameter  $Y_{\text{pheno}_{k,g}}$  representing the observed day of budburst (which we  $z$ -scored to allow direct  
<sup>205</sup> comparison of cues) has the following normal distribution:

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

with

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

and

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

206 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:

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

207 Parameter  $\alpha_{\text{pheno},k}$  represents the overall mean day of budburst for species  $k$  without the influence  
208 of chilling, forcing, or photoperiod treatments. The species average day of budburst (independent of  
209 treatments) is  $\mu_{\text{pheno}}$ , and  $\sigma_{\text{pheno}}^2$  is the variance across species. The parameters  $\alpha_{\text{chilling},k}$ ,  $\alpha_{\text{forcing},k}$ ,  
210 and  $\alpha_{\text{photoperiod},k}$  represent the trait-independent responses of species  $k$  to chilling, forcing, and photo-  
211 peroid treatments respectively, each with an associated mean ( $\mu_{\text{chilling}}$ ,  $\mu_{\text{forcing}}$ ,  $\mu_{\text{photoperiod}}$ ) and  
212 variance ( $\sigma_{\text{chilling}}^2$ ,  $\sigma_{\text{forcing}}^2$ ,  $\sigma_{\text{photoperiod}}^2$ ) across species. The effect of the species trait value,  $\alpha_{\text{trait},k}$ —  
213 the parameter shared with trait sub-model above—on its responses to chilling, forcing, and photoperiod  
214 are described by parameters  $\beta_{\text{trait.chilling}}$ ,  $\beta_{\text{trait.forcing}}$ ,  $\beta_{\text{trait.photoperiod}}$ . Finally,  $\sigma_d^2$  is the variance arising  
215 from measurement error.

216

217 We chose weakly informative priors, and validated them using a series of prior predictive checks.  
218 The model was coded in the Stan programming language, fit using the rstan package (v. 3.3.6)  
219 (Stan Development Team, 2018), with 1,000 iterations per chain across 4 chains (4,000 total sampling  
220 iterations), and all models met basic diagnostic checks, including no divergences, high effective sample  
221 size ( $n_{\text{eff}}$ ), and  $\hat{R}$  close to 1, fitting the data well (Fig S2). Here we present our model estimates as  
222 the means and 90% posterior uncertainty intervals.

## 223 Results

224 Across traits, height, SLA, and LNC strongly related to chilling ( $\beta_{\text{chilling}_k}$ ), forcing ( $\beta_{\text{forcing}_k}$ ), and  
225 photoperiod ( $\beta_{\text{photoperiod}_k}$ ) treatments, Fig 2 a-f & j-l), but the direction of these relationships only  
226 showed consistent trends for LNC (Fig. 2 j-l). As we predicted, height was negatively related to

227 chilling ( $\beta_{\text{chilling}_k}$ ) and photoperiod ( $\beta_{\text{photoperiod}_k}$ ), with taller species having larger responses to cues  
228 (-0.5 m per standardized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized  
229 photoperiod; 90% UI: -0.5, 0.0, Fig 2 a-c, Table S2). As illustrated for one characteristically acquisitive  
230 species, *Alnus incana*, and one characteristically conservative species, *Quercus rubra* (Fig S3), the cue  
231 relationships with height led to generally later budburst relative to estimates without trait effects ( $\mu_{k,g}$ ;  
232 Fig. 3). In contrast, seed mass had the smallest responses, with no relationship between seed mass  
233 and any cue (Fig. 2 g-i, Fig 3 d-f, & Table S3).

234

235 Of our leaf traits, we found that species SLA related to photoperiod ( $\beta_{\text{photoperiod}_k}$ , -0.2 mm<sup>2</sup>/mg per  
236 standardized photoperiod; 90% UI: -0.4, 0.0, Fig. 2 f, Table S4), but did not strongly predict responses  
237 to chilling ( $\beta_{\text{chilling}_k}$ ) or forcing treatments ( $\beta_{\text{forcing}_k}$ , Fig. 2 d and e). Thus, species with more acquisi-  
238 tive growth strategies (thin leaves and a lower investment in leaf mass that leads to large SLA values),  
239 had larger responses to photoperiod, contrary to our predictions (Fig. 2 f). For LNC, we found that  
240 species that produce leaves with high nitrogen content, which relates generally to high photosynthetic  
241 rates and acquisitive growth, show smaller responses to cues (Fig. 2 j-l). These findings are in line  
242 with our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g  
243 per standardized chilling; 90% UI: 0.3, 1.2, Table S5), but we also found high LNC species to be less  
244 responsive to photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6) and to forcing  
245 (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig 2 j-l & Fig S3 d-f).

246

247 We found species-level variation across traits ( $\sigma_{\text{trait}}^2$ ) were comparable to or greater than variation  
248 across studies ( $\sigma_{\text{study}}^2$ , Fig 4). The magnitude of study-level variation ( $\sigma_{\text{study}}^2$ ) that we found, however,  
249 suggests that models using large trait databases that fail to separate out study from species-level vari-  
250 ation ( $\sigma_{\text{trait}}^2$ ) may poorly estimate species traits. Variation across studies was greatest for height (with  
251  $\sigma_{\text{study}}^2$  of 7.5 m compared to 5.9 m for  $\sigma_{\text{trait}}^2$ , Fig 4a). For seed mass and LNC, study-level variation  
252 was less than that of the species-level variation, with estimates of 1 mg for study-level variation versus  
253 1.6 mg for species-level variation in seed mass and estimates of 3.6 mg g<sup>-1</sup> for study-level variation  
254 and 5.1 mg g<sup>-1</sup> for the species-level variation in LNC (Fig 4c and d). At the lowest end, study-level  
255 variation in SLA was approximately half the value of the species-level variation (3.3 mm<sup>2</sup> mg<sup>-1</sup> versus  
256 7.8 mm<sup>2</sup> mg<sup>-1</sup> for  $\sigma_{\text{study}}^2$  and  $\sigma_{\text{trait}}^2$ , respectively, Fig 4b).

257

258 **Discussion**

259 We found species traits influenced the timing of budburst in response to the three primary cues of  
260 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or  
261 later phenology following well-established gradients in growth strategies predicted by functional trait  
262 frameworks (Chave et al., 2009; Díaz et al., 2016; Westoby, 1998; Westoby and Wright, 2006; Wright  
263 et al., 2004): early species tended to have traits associated with fast and acquisitive strategies while  
264 later species had traits associated with conservative, slower strategies. We found the largest bud-  
265 burst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and  
266 height all showing large responses across our three cues. In contrast, our one reproductive trait—seed  
267 mass—showed a smaller response. Our results provide a major step forward in integrating phenology  
268 into broader trait syndromes that shape species growth strategies, and support previous findings from  
269 more local scales that found strong relationships between height and species phenology (Segrestin et al.,  
270 2020; Sporbert et al., 2022; Sun and Frelich, 2011). Our more global analysis is also in agreement with  
271 previous studies of plant phenological events, in which no relation is found between phenology and  
272 seed mass in woody plants (Bolmgren and Cowan, 2008; Ettinger et al., 2018).

273

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

275 Our findings suggest the changing pressures across the early growing season may affect the temporal  
276 assembly of communities. Strong abiotic pressures alongside weak competition early in the season were  
277 associated with early-budbursting species with acquisitive traits (shorter heights and low LNC) that  
278 allow faster return on resource investments (Chave et al., 2009; Grime, 1977; Westoby, 1998). These  
279 traits should allow early species to more easily replace tissue if lost to frost or other abiotic distur-  
280 bances, and benefit from greater light availability in the open canopy of many temperate forests in  
281 the early spring. In contrast, later-budbursting species had traits associated with greater competitive  
282 abilities and slower growth (Chave et al., 2009; Grime, 1977; Westoby, 1998) (Fig 2), which may help  
283 them compete for soil and light resources when most other species are already growing. These traits  
284 can be linked to other ecological processes and species characteristics, such as species successional po-  
285 sition, as illustrated by the differences between early and late successional species (e.g., *Alnus incana*  
286 and *Quercus rubra*; Fig 2).

287

288 The traits with cue responses that deviated from our expectations also offer novel insights into the  
289 tradeoffs between traits and environmental cues. All of our traits are associated with multiple aspects  
290 of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our

291 predictions, we found large responses to forcing for short trees, which could prevent frost damage or  
292 xylem cavitation under a late spring frost (Clements et al., 1972; Marquis et al., 2020) and influence  
293 annual cambial meristem growth (Lenz et al., 2016). Similarly, the lack of a response to chilling or  
294 forcing by high SLA individuals could be driven by other trait attributes and environmental cues—  
295 selecting for species relative growth rates or leaf longevity—and not photosynthetic potential (Reich,  
296 2014; Westoby, 1998). These findings highlight the complexity of determining the drivers of species  
297 trait profiles, and further our understanding of how traits affect community dynamics under variable  
298 environments.

299

### 300 **Phenology-trait relationships under future climates**

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

306

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

314

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

322

323 Our results could further help identify which species are most likely to be negatively impacted under

324 future climates, and develop better strategies for climate change mitigation and conservation. Species  
325 that fail to advance phenologically with warming might experience more competition (Alexander and  
326 Levine, 2019; Carter et al., 2018), as species that begin growth increasingly earlier with warming have  
327 more time to deplete resources. In addition to altering the timing and interactions between species  
328 within a season, species trait syndromes have the potential to further redefine the environmental condi-  
329 tions under which growth occurs, and as a result, shape community assembly and productivity within  
330 ecological communities. By identifying the species most vulnerable to climate change impacts, we can  
331 develop more effective management practices that prevent the loss of critical ecosystem services and  
332 preserve community diversity under future conditions.

333

## 334 **Acknowledgements**

335 We thank the researchers who measured the traits and conducted the experiments producing the data  
336 used in this manuscript.

## 337 **Author Contributions Statement**

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

## 342 **Competing Interests Statement**

343 The authors declare no competing interests.

## 344 **Data availability statement**

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

## 348 References

- 349 Alexander, J. M., and J. M. Levine. 2019. Earlier phenology of a nonnative plant increases impacts  
350 on native competitors. *PNAS* 116:6199–6204.
- 351 Augspurger, C. K. 2009. Spring 2007 warmth and frost : phenology , damage and refoliation in a  
352 temperate deciduous forest. *Functional Ecology* 23:1031–1039.
- 353 Beard, K. H., K. C. Kelsey, A. J. Leffler, and J. M. Welker. 2019. The Missing Angle : Ecosystem  
354 Consequences of Phenological Mismatch. *Trends in Ecology and Evolution* 34:885–888.
- 355 Bolmgren, K., and P. D. Cowan. 2008. Time-size tradeoffs: a phylogenetic comparative study of  
356 flowering time, plant height, and seed mass in a north-temperate flora. *Oikos* 117:424–429.
- 357 Carter, S. K., D. Saenz, and V. H. Rudolf. 2018. Shifts in phenological distributions reshape interaction  
358 potential in natural communities. *Ecology Letters* 21:1143–1151.
- 359 Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a  
360 worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- 361 Chuine, I., M. Bonhomme, J. M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and  
362 T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The  
363 unrevealed hurdle of endodormancy break. *Global change biology* 22:3444–3460.
- 364 Chuine, I., and P. Cour. 1999. Climatic determinants of budburst seasonality in four temperate-zone  
365 tree species. *New Phytologist* 143:339–349.
- 366 Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta,  
367 and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate  
368 change.pdf. *Ecology* 93:1765–1771.
- 369 Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology  
370 in response to global change. *Trends in Ecology and Evolution* 22:357–365.
- 371 Clements, J. R., W. Fraser, J, and C. W. Yeatman. 1972. Frost Damage to White Spruce Buds.  
372 *Canadian Journal of Forest Research* 2:62–63.
- 373 Crick, H., C. Dudley, D. E. Glue, and D. L. Thomson. 1997. UK birds are laying eggs earlier. *Nature*  
374 388:526–527.
- 375 D'Alba, L., P. Monaghan, and R. G. Nager. 2010. Advances in laying date and increasing population  
376 size suggest positive responses to climate change in Common Eiders Somateria mollissima in Iceland.  
377 *International Journal of Avian Science* 152:19–28.

- 378 Díaz, S., J. Kattge, J. H. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth,  
379 I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie,  
380 A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet Ev, H. Jactel, C. Baraloto,  
381 B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falczuk,  
382 N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function.  
383 *Nature* 529:167–171.
- 384 Ettinger, A. K., C. J. Chamberlain, I. Morales-Castilla, D. M. Buonaiuto, D. F. Flynn, T. Savas,  
385 J. A. Samaha, and E. M. Wolkovich. 2020. Winter temperatures predominate in spring phenological  
386 responses to warming. *Nature Climate Change* 10:1137–1142.
- 387 Ettinger, A. K., S. Gee, and E. M. Wolkovich. 2018. Phenological sequences: how early-season events  
388 define those that follow. *American Journal of Botany* 105:1771–1780.
- 389 Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology  
390 across all species in a temperate forest community. *New Phytologist* 219:1353–1362.
- 391 Gorné, L. D., S. Díaz, V. Minden, Y. Onoda, K. Kramer, C. Muir, S. T. Michaletz, S. Lavorel,  
392 J. Sharpe, S. Jansen, M. Slot, E. Chacon, and G. Boenisch. 2020. The acquisitive–conservative axis  
393 of leaf trait variation emerges even in homogeneous environments. *Annals of Botany* 129:709–722.
- 394 Grime, J. P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance  
395 to Ecological and Evolutionary Theory. *The American Naturalist* 111:1169–1194.
- 396 Gu, H., Y. Qiao, Z. Xi, S. Rossi, N. G. Smith, J. Liu, and L. Chen. 2022. Warming-induced increase  
397 in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. *Nature  
398 Communications* 13:1–8.
- 399 Guy, R. D. 2014. The early bud gets to warm. *New Phytologist* 202:7–9.
- 400 Harrington, C. A., and P. J. Gould. 2015. Tradeoffs between chilling and forcing in satisfying dormancy  
401 requirements for Pacific Northwest tree species. *Frontiers in Plant Science* 6:1–12.
- 402 Hufkens, K., M. A. Friedl, T. F. Keenan, O. Sonnentag, A. Bailey, J. O’keefe, and A. D. Richardson.  
403 2012. Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change  
404 Biology* 18:2365–2377.
- 405 Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I. C. Prentice, and et al. 2020. TRY plant trait database  
406 – enhanced coverage and open access. *Global Change Biology* 26:119–188.
- 407 Kusano, T., and M. Inoue. 2008. Long-Term Trends toward Earlier Breeding of Japanese Amphibians.  
408 *Journal of Herpetology* 42:608–614.

- 409 Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs  
410 photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- 411 Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf-  
412 height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*  
413 24:493–501.
- 414 Lenz, A., G. Hoch, C. Körner, and Y. Vitasse. 2016. Convergence of leaf-out towards minimum risk  
415 of freezing damage in temperate trees. *Functional Ecology* 30:1480–1490.
- 416 Lopez, O. R., K. Farris-Lopez, R. A. Montgomery, and T. J. Givnish. 2008. Leaf phenology in relation  
417 to canopy closure in southern Appalachian trees. *American Journal of Botany* 95:1395–1407.
- 418 Macgregor, C. J., C. D. Thomas, D. B. Roy, M. A. Beaumont, J. R. Bell, T. Brereton, J. R. Bridle,  
419 C. Dytham, R. Fox, K. Gotthard, A. A. Hoffmann, G. Martin, I. Middlebrook, S. Nylin, P. J.  
420 Platts, R. Rasteiro, I. J. Saccheri, R. Villoutreix, C. W. Wheat, and J. K. Hill. 2019. Climate-  
421 induced phenology shifts linked to range expansions in species with multiple reproductive cycles per  
422 year. *Nature Communications* 10:1–10.
- 423 Maitner, B. S., B. Boyle, N. Casler, R. Condit, J. Donoghue, S. M. Durán, D. Guaderrama, C. E.  
424 Hinchliff, P. M. Jørgensen, N. J. Kraft, B. McGill, C. Merow, N. Morueta-Holme, R. K. Peet,  
425 B. Sandel, M. Schildhauer, S. A. Smith, J. C. Svenning, B. Thiers, C. Violette, S. Wiser, and B. J.  
426 Enquist. 2018. The bien r package: A tool to access the Botanical Information and Ecology Network  
427 (BIEN) database. *Methods in Ecology and Evolution* 9:373–379.
- 428 Marquis, B., Y. Bergeron, M. Simard, and F. Tremblay. 2020. Growing-season frost is a better predictor  
429 of tree growth than mean annual temperature in boreal mixedwood forest plantations. *Global Change  
430 Biology* 26:6537–6554.
- 431 Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kübler, P. Bissolli,  
432 O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Don-  
433 nnelly, Y. Filella, K. Jatczak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová,  
434 H. Scheifinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Zust. 2006.  
435 European phenological response to climate change matches the warming pattern. *Global Change  
436 Biology* 12:1969–1976.
- 437 Morales-Castilla, I., T. J. Davies, G. Legault, D. M. Buonaiuto, C. J. Chamberlain, A. K. Ettinger,  
438 M. Garner, F. A. M. Jones, D. Loughnan, W. D. Pearse, D. Sodhi, and E. M. Wolkovich. 2024.  
439 Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate  
440 Change* 14:989–995.

- 441 Ovaskainen, O., S. Skorokhodova, M. Yakovleva, A. Sukhov, A. Kutenkov, N. Kutenkova,  
442 A. Shcherbakov, E. Meyke, and M. del Mar Delgado. 2013. Community-level phenological response  
443 to climate change. PNAS 110:13434–13439.
- 444 Rathcke, B., and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. Annual Review of  
445 Ecology and Systematics 16:179–214.
- 446 Reich, P. B. 2014. The world-wide ‘fast – slow’ plant economics spectrum : a traits manifesto. Journal  
447 of Ecology 102:275–301.
- 448 Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman.  
449 1999. Generality of leaf trait relationships: A test across six biomes. Ecology 80:1955–1969.
- 450 Sakai, A., and W. Larcher. 1987. Frost Survival of Plants: Responses and adaptation to freezing stress.  
451 Springer-Verlag, Berlin, Heidelberg.
- 452 Schuster, M. J., P. D. Wragg, and P. B. Reich. 2021. Phenological niche overlap between invasive  
453 buckthorn (*Rhamnus cathartica*) and native woody species. Forest Ecology and Management 498:1–  
454 7.
- 455 Segrestin, J., M.-l. Navas, and E. Garnier. 2020. Reproductive phenology as a dimension of the  
456 phenotypic space in 139 plant species from the Mediterranean. New Phytologist 225:740–753.
- 457 Sporbert, M., D. Jakubka, S. F. Bucher, I. Hensen, M. Freiberg, K. Heubach, A. Konig, B. Nordt,  
458 C. Plos, I. Blinova, A. Bonn, B. Knickmann, T. Koubek, A. Linstadter, T. Maskova, R. Primack,  
459 C. Rosche, M. A. Shah, A.-D. Stevens, K. Teilborger, S. Trager, C. Wirth, and C. Romermann.  
460 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-  
461 botanical garden study. New Phytologist 235:2199–2210.
- 462 Stan Development Team. 2018. RStan: the R interface to Stan. R package version 2.17.3.
- 463 Sun, S., and L. E. Frelich. 2011. Flowering phenology and height growth pattern are associated with  
464 maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland  
465 species. Journal of Ecology 99:991–1000.
- 466 Tryjanowski, P., M. Rybacki, and T. Sparks. 2003. Changes in the first spawning dates of common  
467 frogs and common toads in western Poland in 1978-2002. Annales Zoologici Fennici 40:459–464.
- 468 Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier.  
469 2012. The return of the variance: Intraspecific variability in community ecology. Trends in Ecology  
470 and Evolution 27:244–252.

- 471 Vitasse, Y., S. Ursenbacher, G. Klein, T. Bohnenstengel, Y. Chittaro, A. Delestrade, C. Monnerat,  
472 M. Rebetez, C. Rixen, N. Strelbel, B. R. Schmidt, S. Wipf, T. Wohlgemuth, N. G. Yoccoz, and  
473 J. Lenoir. 2021. Phenological and elevational shifts of plants , animals and fungi under climate  
474 change in the European Alps. *Biological Reviews* 96:1816–1835.
- 475 Wainwright, C. E., E. M. Wolkovich, and E. E. Cleland. 2012. Seasonal priority effects : implications  
476 for invasion and restoration in a semi-arid system. *Journal of Applied Ecology* 49:234–241.
- 477 Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- 478 Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in  
479 Ecology and Evolution* 21:261–268.
- 480 Wolkovich, E. M., and E. E. Cleland. 2011. The phenology of plant invasions: A community ecology  
481 perspective. *Frontiers in Ecology and the Environment* 9:287–294.
- 482 ———. 2014. Phenological niches and the future of invaded ecosystems with climate change. *AoB  
483 PLANTS* 6:1–16.
- 484 Wolkovich, E. M., and M. J. Donahue. 2021. How phenological tracking shapes species and communities  
485 in non-stationary environments. *Biological Reviews* 96:2810–2827.
- 486 Wolkovich, E. M., and A. K. Ettinger. 2014. Back to the future for plant phenology research. *New  
487 Phytologist* 203:1021–1024.
- 488 Wright, I. J., M. Westoby, P. B. Reich, J. Oleksyn, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-  
489 Bares, T. Chapin, J. H. C. Cornellissen, M. Diemer, J. Flexas, J. Gulias, E. Garnier, M. L. Navas,  
490 C. Roumet, P. K. Groom, B. B. Lamont, K. Hikosaka, T. Lee, W. Lee, C. Lusk, J. J. Midgley,  
491 Ü. Niinemets, H. Osada, H. Poorter, P. Pool, E. J. Veneklaas, L. Prior, V. I. Pyankov, S. C. Thomas,  
492 M. G. Tjoelker, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.

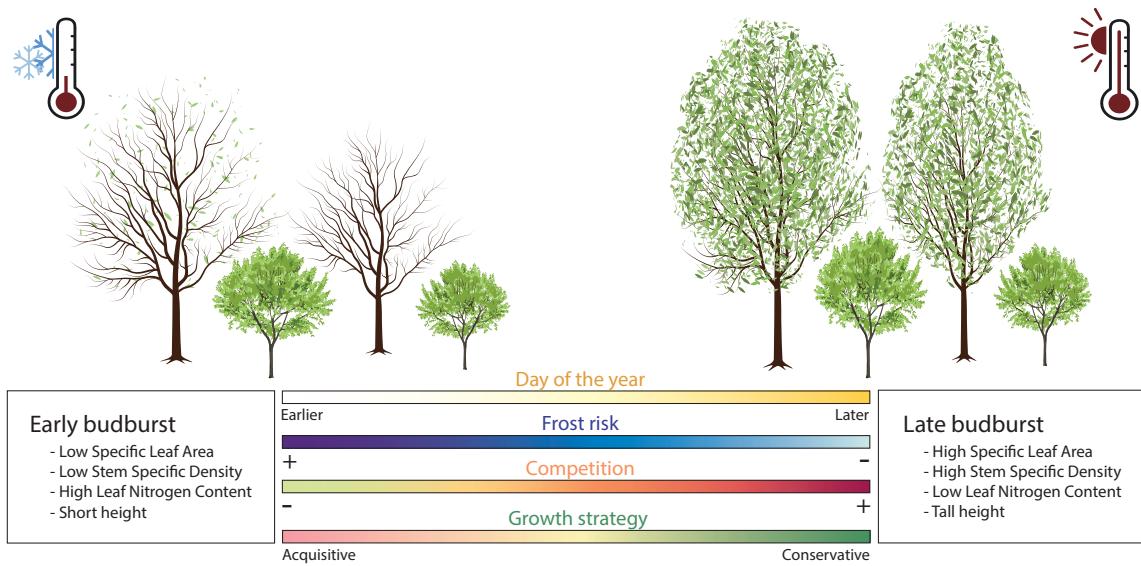


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost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

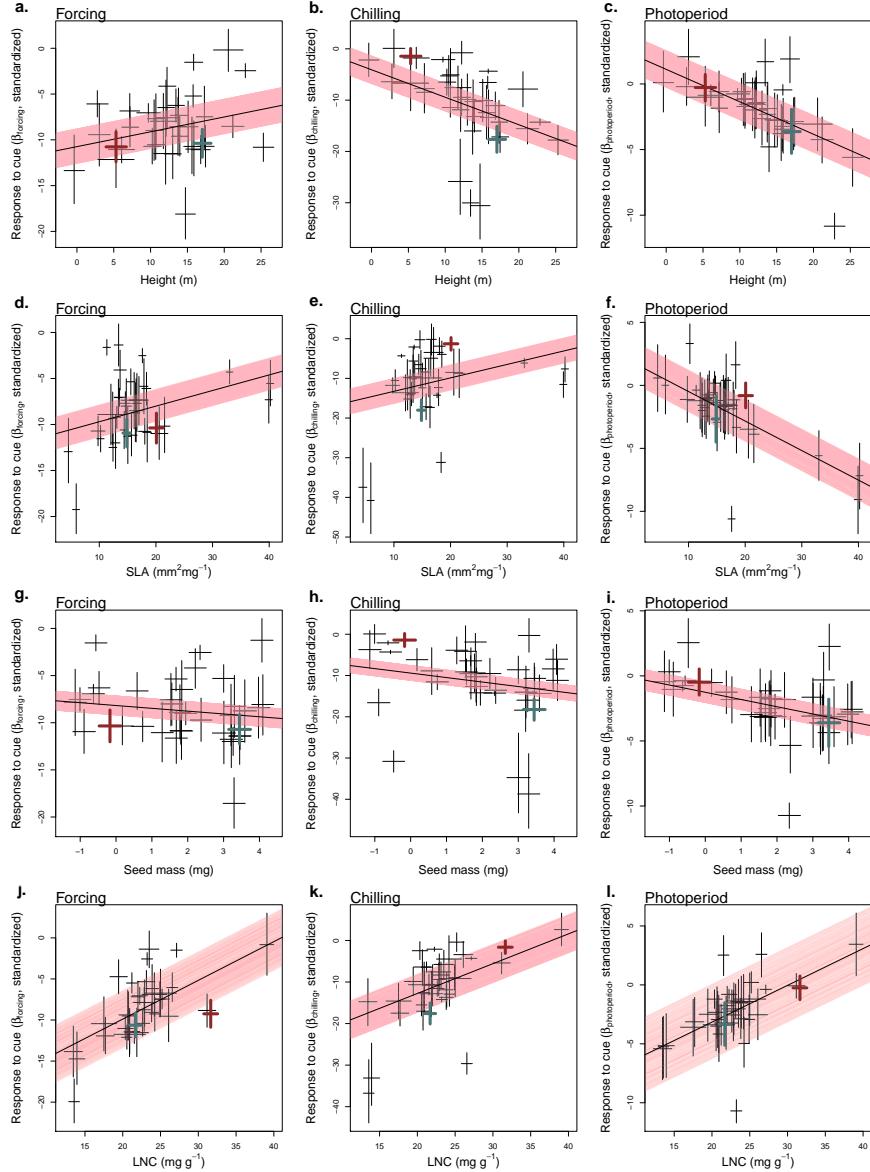


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third 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 cues) and the pink band the 50% uncertainty interval. Each set of crossed lines represents one species (with each line spanning the 50% uncertainty interval), with the species depicted in Fig 3 colored in each panel, with the acquisitive species (*Alnus incana*) shown in red, and the conservative species (*Quercus rubra*) shown in blue.

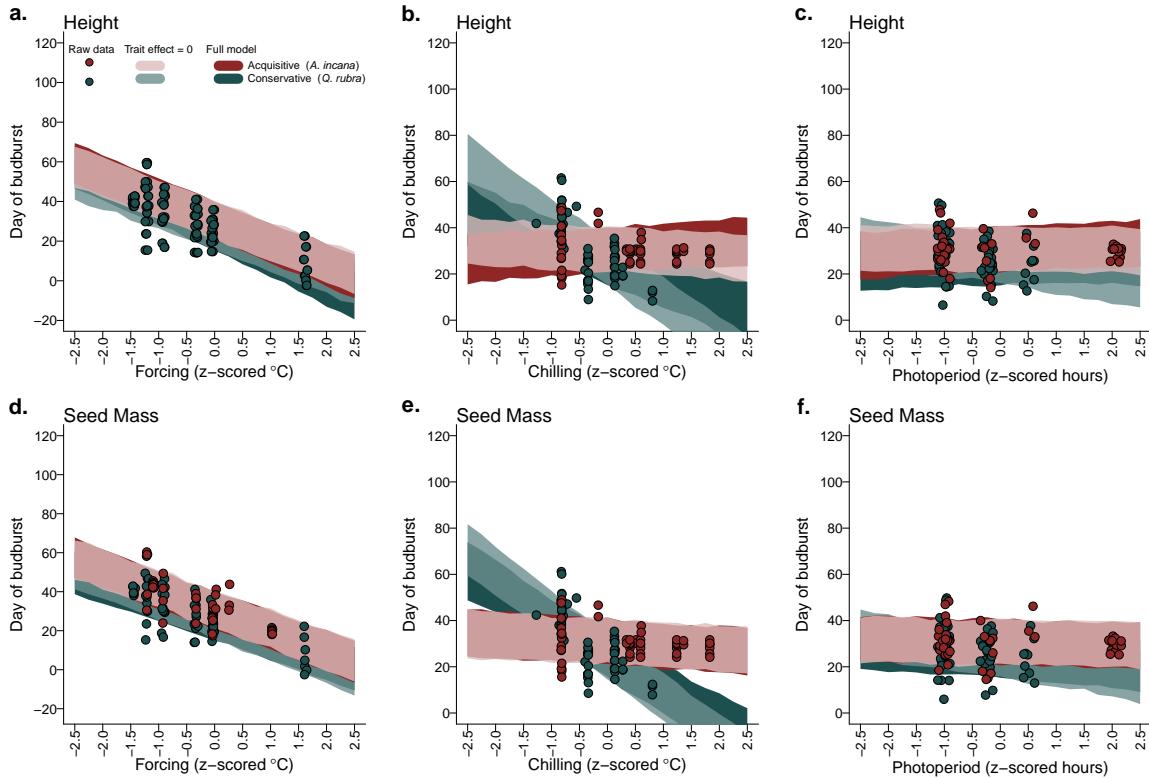


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with height (**a-c**) and seed mass (**d-f**) for an acquisitive species, *Alnus incana* shown in red, and a conservative species, *Quercus rubra*, shown in blue. **a**, The effect of height on budburst timing was smaller in response to forcing cues, but larger in response to both **b**, chilling and **c**, photoperiod. In contrast, seed mass had a negligible effect on **d**, forcing and **f**, photoperiod responses, **e**, but a greater response to chilling. Points represent the raw data and the coloured bands the 50% uncertainty intervals of the model estimates and points individual trait measurements.

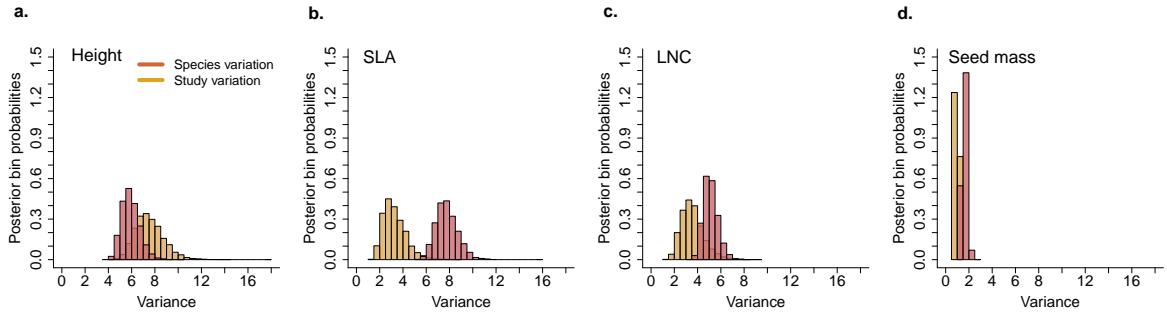


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation ( $\sigma_{\text{species}}^2$  and  $\sigma_{\text{study}}^2$  respectively), with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf 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.