

<sup>1</sup> Woody plant phenological responses are strongly associated  
<sup>2</sup> with key functional traits

<sup>3</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>4</sup> September 22, 2024

<sup>5</sup> <sup>1</sup> Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia,  
<sup>6</sup> 2424 Main Mall Vancouver, BC Canada V6T 1Z4.

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

<sup>10</sup> <sup>4</sup> Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts,  
<sup>11</sup> USA;

<sup>12</sup> <sup>5</sup> Department of Environmental Conservation, University of Massachusetts, Amherst, 160 Holdsworth  
<sup>13</sup> Way, Amherst, MA, USA

<sup>14</sup> <sup>6</sup> The Nature Conservancy, 334 Blackwell St, #300, Durham, NC, USA

<sup>15</sup> <sup>7</sup> The Nature Conservancy of Washington, 74 Wall Street, Seattle, WA USA

<sup>16</sup> <sup>8</sup> GloCEE—Global Change Ecology and Evolution Group, Department of Life Sciences, University of  
<sup>17</sup> Alcalá, Alcalá de Henares, Spain

<sup>18</sup> <sup>9</sup> Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

<sup>20</sup> Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca

<sup>21</sup> Running title: Budburst responses associated with traits

<sup>32</sup> **Summary**

<sup>33</sup> Species-level variation in phenology—the timing of recurring life history events—can vary seasonally  
<sup>34</sup> with changes in climatic risk, light, and nutrients. This favours acquisitive growth strategies early in  
<sup>35</sup> the spring season and conservative growth strategies under the more climatically benign, but compet-  
<sup>36</sup> itive, environment later in the season. This framework infers suites of traits that may co-vary with  
<sup>37</sup> phenologies, but high variability across environments makes this challenging to test. Here, we combine  
<sup>38</sup> a new joint modeling approach to accommodate this variability with global data on plant traits and  
<sup>39</sup> budburst responses in controlled environment experiments. We find that earlier species—which are  
<sup>40</sup> generally most responsive to anthropogenic warming—are generally shorter with denser, lower nitro-  
<sup>41</sup> gen leaves. These results suggest warming may reshape the trait structure of plant communities, and  
<sup>42</sup> could help improve predictions of how growth strategies and phenologies together shift with continued  
<sup>43</sup> climate change.

<sup>44</sup>  
<sup>45</sup> Key Words: Budburst, spring phenology, functional traits, trees, climate change, forest communities

<sup>46</sup> **Introduction**

<sup>47</sup> The timing of life history events—phenology—can shape both ecosystem services and community  
<sup>48</sup> dynamics. Spring phenology, for example, defines the start and overall length of the growing season—  
<sup>49</sup> shaping forest carbon storage and species interactions<sup>1–3</sup>. Shifts in phenology with climate change  
<sup>50</sup> across systems<sup>4,5</sup> have thus led to growing concerns over their possible impacts.

<sup>51</sup>  
<sup>52</sup> Predicting these changes requires understanding the drivers of phenology both at a proximate scale—  
<sup>53</sup> the environmental triggers of phenology each year, such as temperature and daylength—and at an  
<sup>54</sup> ultimate scale, where long-term environmental pressures may select for different phenologies across  
<sup>55</sup> species, e.g., certain species are early or late relative to other species each year<sup>6,7</sup>. At the proximate  
<sup>56</sup> level, environmental conditions throughout the winter and spring cause species to start growth at  
<sup>57</sup> different times. Similar environmental conditions appear to trigger spring phenological events across  
<sup>58</sup> taxa, including the start of growth in woody plants each year<sup>8,9</sup>, the timing of egg laying in birds<sup>10,11</sup>,  
<sup>59</sup> and the advance of spawning in amphibians<sup>12,13</sup>, but current work provides limited insights into the  
<sup>60</sup> drivers of species differences<sup>8,9,14</sup>.

<sup>61</sup>  
<sup>62</sup> At the ultimate level, species phenologies may vary due to changing pressures across the growing season.  
<sup>63</sup> Species that start growth early often risk high tissue loss—due to frost damage<sup>15,16</sup> or high herbivore  
<sup>64</sup> apparency<sup>17</sup>—but benefit from higher resource availability<sup>18,19</sup>. In contrast, later species face greater  
<sup>65</sup> biotic pressures, especially from high competition for resources<sup>20,21</sup>. For plants, this variation in early  
<sup>66</sup> to late season growth may mirror the stressors from early to late successional communities, and may  
<sup>67</sup> similarly shape phenology<sup>8</sup>.

<sup>68</sup>  
<sup>69</sup> Different pressures could shape a number of species attributes related to their growth strategies, includ-  
<sup>70</sup> ing phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced if  
<sup>71</sup> damaged<sup>22</sup>, while species with later phenology may benefit from investing in tissues that infer greater  
<sup>72</sup> resource retention<sup>23</sup>. Differences in traits, and trade-offs in allocation of resources to growth and tissue  
<sup>73</sup> quality, can be related to a broader framework of species growth strategies and functional traits<sup>21</sup> (Fig  
<sup>74</sup> 1), where species range from acquisitive (fast) to more conservative (slow) growth<sup>24,25</sup>.

<sup>75</sup>  
<sup>76</sup> Globally, gradients from acquisitive to conservative strategies appear common, and form the foundation  
<sup>77</sup> of the leaf economic and the wood economic spectra<sup>24–28</sup>, but they can make limited predictions of trait  
<sup>78</sup> variability<sup>29</sup>. As a result, highly variable traits like phenology are often excluded from trait studies,  
<sup>79</sup> leaving the relationships between broader trait syndromes and phenology largely unknown. Under-

80 standing these relationships is critical to forecasting community dynamics and responses to climate  
81 change. To date, studies have generally only examined the relationship between traits and phenology  
82 within a single site (as reviewed by Wolkovich and Cleland<sup>30</sup> and Wolkovich and Donahue<sup>7</sup>) where  
83 the problem of proximate drivers causing phenological variation can be more easily ignored. Adding  
84 phenology to broader trait frameworks becomes more complex when high levels of variation occurs  
85 across large spatial and temporal ranges.

86

87 Consistently defining early to late phenology is possible using the underlying cues that predict gra-  
88 dients in phenology, which do not generally vary strongly across space and time<sup>9,31,32</sup>. For many  
89 plants, early species generally have responses that are small in magnitude to all three major cues of  
90 spring leafout: warm spring temperatures (forcing), cool winter temperatures (chilling) and daylength  
91 (photoperiod). In contrast, later species have larger responses to chilling and/or photoperiod<sup>8,9</sup>, and  
92 likely larger forcing responses.

93

94 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-  
95 nology into functional trait research. In addition to how well we understand the environmental cues  
96 that trigger early versus late leafout, spring in many forests includes strong gradients in potential se-  
97 lective environments (Fig 1). Based on trade-offs between early and late spring phenologies, we predict  
98 acquisitive species to be shorter, with leaf traits favourable to higher light availability and tolerance  
99 to late spring frost (high specific leaf area, SLA, and leaf nitrogen content, LNC; Fig 1). Such species  
100 should exhibit early phenology, with small cue responses. Canopy species that budburst later via larger  
101 cue responses, when competition for soil resources is greater, would then have traits associated with  
102 conservative growth—taller with denser wood<sup>33</sup>—with leaf traits suited for more variable light (low  
103 SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to conservative con-  
104 tinuum, as acquisitive species produce smaller seeds and conservative species produce larger—better  
105 provisioned—seeds (Fig 1).

106

107 To test our predicted relationships between budburst responses to environmental cues and common  
108 functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases—  
109 BIEN<sup>34</sup> and TRY<sup>35</sup>—with budburst data from the OSPREE database of controlled environment stud-  
110 ies<sup>36</sup>. We developed a hierarchical Bayesian joint model that predicts phenological responses to forcing,  
111 chilling and photoperiod treatments based on species-level trait values, while allowing additional varia-  
112 tion due to species. This approach takes a step towards predicting variation via species traits instead of  
113 species identity (when traits explain a significant portion of the variation, species identity will explain  
114 only a small amount), which could help forecast species phenological responses based on trait values  
115 alone.

116

## 117 Methods

118 We merged three major databases for our analysis. We gathered phenological data from the OSPREE  
119 database<sup>36</sup>, which contains budburst data for woody, species from experiments of forcing, chilling and  
120 photoperiod. We updated this database since its initial publication, the methods of which are dis-  
121 cussed by Morales-Castilla et al.<sup>37</sup>. We gathered trait data from TRY and BIEN (v. 4.0)<sup>34,35</sup>, both  
122 of which are large trait databases that include plant trait data across many individuals, species, and  
123 studies (Table S1). We obtained data from both databases on 5 December, 2018, with an updated  
124 version of the TRY data obtained 10 April, 2019. We focused our search for trait data on the subset  
125 of 234 OSPREE species used in Morales-Castilla et al.<sup>37</sup>. Using the BIEN R package (v. 1.2.5)<sup>34</sup>, we  
126 downloaded trait data for the 94 species available, for which there were 13 traits. The TRY database  
127 included data for 10 traits for 96 of our focal species<sup>35</sup>. Given our focus on the phenology of adult  
128 trees, we included trait data from adult individuals with a minimum height of 1.38 m. We further

removed all data from experiments or from plants growing in non-natural habitats. We also grouped trait values where appropriate, for example categorizing trait values for “SLA”, “SLA with petioles”, and “SLA without petioles” as simply “SLA” in our analysis (see Table S1). Duplicated data in both the TRY and BIEN datasets were also removed ( $n = 434905$ ). Based on our selection criteria, our final dataset included data for 11 traits from 91 of the species also represented in the OSPREE database, with each species differing in the number and types of traits measured.

135

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

150

## 151 Joint model of trait and phenology

To understand connections between phenology and species traits, we developed and then parameterized a joint model for each trait: height, SLA, LNC, and seed mass. Our model is a joint model insofar as it involves two types of data—trait observations and phenological observations—that arise from shared latent processes. In particular, we assume that species “true” trait values determine observed trait values across different studies (trait sub-model), and separately, that the same “true” trait values interact with phenological cues (forcing, chilling, and photoperiod) to determine observed phenology, specifically the day of year of budburst (phenology sub-model). Below we describe the two sub-models, noting which parameters are shared across sub-models and which are independent.

### 160 Trait sub-model

The trait sub-model describes the processes that determine trait observations for 1 to  $n$  species across each of the 1 to  $m$  studies in our trait dataset (TRY and BIEN data). We use hierarchical modeling to partition trait variation by measurement error, species identity, and study identity. In particular, we assume that a trait observation for species  $i$  from study  $j$ ,  $Y_{\text{trait}_{i,j}}$ , has the following normal distribution:

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

with

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

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

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

166 The latent parameter  $\alpha_{\text{grand trait}}$  represents a trait value that is independent of study and species,  
 167  $\alpha_{\text{species},i}$  and  $\alpha_{\text{study},j}$  are species and study-level offsets from that trait value,  $\sigma_m^2$  is measurement error,  
 168 and  $\sigma_{\text{trait}}^2$  and  $\sigma_{\text{study}}^2$  represent species and study-level variances in trait values. Of these parameters,  
 169  $\alpha_{\text{trait}}$  are shared by the phenology sub-model.

## 170 Phenology sub-model

171 The phenology sub-model describes the processes that determine phenological observations for 1 to  
 172  $n$  species, specifically the timing (day of year) of budburst from the updated OSPREE dataset. We  
 173 assume that an observation of budburst day for species  $k$  under set  $g$  of chilling, forcing, and photope-  
 174 rioid treatments ( $c_g, f_g, p_g$ ),  $Y_{\text{pheno}_{k,g}}$  (which we  $z$ -scored to allow direct comparison of cues) has the  
 175 following normal distribution:

$$Y_{\text{pheno}_{k,g}} \sim \mathcal{N}(\mu_{k,g}, \sigma_d^2) \quad (4)$$

with

$$\mu_{k,g} = \alpha_{\text{pheno},k} + \beta_{\text{chill}_k} \cdot c_g + \beta_{\text{force}_k} \cdot f_g + \beta_{\text{photo}_k} \cdot p_g \quad (5)$$

and

$$\begin{aligned} \beta_{\text{chill}_k} &= \alpha_{\text{chill},k} + \beta_{\text{trait.chill}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{force}_k} &= \alpha_{\text{force},k} + \beta_{\text{trait.force}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{photo}_k} &= \alpha_{\text{photo},k} + \beta_{\text{trait.photo}} \cdot \alpha_{\text{trait},k} \end{aligned} \quad (6)$$

176 where  $\alpha_{\text{pheno}_k}$ ,  $\alpha_{\text{chill}_k}$ ,  $\alpha_{\text{force}_k}$ , and  $\alpha_{\text{photo}_k}$  are elements of the normal random vectors:

$$\begin{aligned} \boldsymbol{\alpha}_{\text{pheno}} &= \{\alpha_{\text{pheno}_1}, \dots, \alpha_{\text{pheno}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \mathcal{N}(\mu_{\text{pheno}}, \sigma_{\text{pheno}}^2) \\ \boldsymbol{\alpha}_{\text{chill}} &= \{\alpha_{\text{chill}_1}, \dots, \alpha_{\text{chill}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chill}} \sim \mathcal{N}(\mu_{\text{chill}}, \sigma_{\text{chill}}^2) \\ \boldsymbol{\alpha}_{\text{force}} &= \{\alpha_{\text{force}_1}, \dots, \alpha_{\text{force}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{force}} \sim \mathcal{N}(\mu_{\text{force}}, \sigma_{\text{force}}^2) \\ \boldsymbol{\alpha}_{\text{photo}} &= \{\alpha_{\text{photo}_1}, \dots, \alpha_{\text{photo}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photo}} \sim \mathcal{N}(\mu_{\text{photo}}, \sigma_{\text{photo}}^2) \end{aligned} \quad (7)$$

177 Parameter  $\alpha_{\text{pheno},k}$  represents the day of budburst for species  $k$  without the influence of chilling, forc-  
 178 ing, or photoperiod treatments. Average day of budburst (independent of treatments) is  $\mu_{\text{pheno}}$ , and  
 179  $\sigma_{\text{pheno}}^2$  is the variance across species. The parameters  $\alpha_{\text{chill},k}$ ,  $\alpha_{\text{force},k}$ , and  $\alpha_{\text{photo},k}$  represent the trait-  
 180 independent responses of species  $k$  to chilling, forcing, and photoperiod treatments respectively, each  
 181 with an associated mean ( $\mu_{\text{chill}}$ ,  $\mu_{\text{force}}$ ,  $\mu_{\text{photo}}$ ) and variance ( $\sigma_{\text{chill}}^2$ ,  $\sigma_{\text{force}}^2$ ,  $\sigma_{\text{photo}}^2$ ) across species. The  
 182 effect of the species trait value,  $\alpha_{\text{trait},k}$  (parameter shared with trait sub-model above), on its responses  
 183 to chilling, forcing, and photoperiod are described by parameters  $\beta_{\text{trait.chill}}$ ,  $\beta_{\text{trait.force}}$ ,  $\beta_{\text{trait.photo}}$ . Fi-  
 184 nally,  $\sigma_d^2$  is the variance arising from measurement error.

185  
 186 We chose weakly informative priors, and validated them using a series of prior predictive checks.  
 187 The model was coded in the Stan programming language, fit using the rstan package (v. 3.3.6)<sup>38</sup>,  
 188 with 1,000 iterations per chain across 4 chains (4,000 total sampling iterations), and all models met  
 189 basic diagnostic checks, including no divergences, high effective sample size ( $n_{\text{eff}}$ ), and  $\hat{R}$  close to 1,  
 190 fitting the data well (Fig S2). Here we present our model estimates as the means and 90% posterior  
 191 uncertainty intervals.

192 **Results**

193 Across traits, height, SLA, and LNC strongly related to chilling ( $\beta_{\text{chill}_k}$ ), forcing ( $\beta_{\text{force}_k}$ ), and photoperiod ( $\beta_{\text{photo}_k}$ ) treatments, Fig 2 a-f & j-l), but the direction of these relationships only showed  
194 consistent trends for LNC (Fig. 2 j-l). As we predicted, height was negatively related to chilling ( $\beta_{\text{chill}_k}$ )  
195 and photoperiod ( $\beta_{\text{photo}_k}$ ), with taller species having larger responses to cues (-0.5 m per standard-  
196 ized chilling; 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized photoperiod; 90%  
197 UI: -0.5, 0.0, Fig 2 a-c, Table S2). As illustrated for one characteristically acquisitive species, *Alnus*  
198 *incana*, and one characteristically conservative species, *Quercus rubra* (Fig S3), the cue relationships  
199 with height led to generally later budburst relative to estimates without trait effects ( $\mu_{k,g}$ ; Fig. 3). In  
200 contrast, seed mass had the smallest responses, with no relationship between seed mass and any cue  
201 (Fig. 2 g-i, Fig 3 d-f, & Table S3).

202  
203 Of our leaf traits, we found that species SLA related to photoperiod ( $\beta_{\text{photo}_k}$ , -0.2 mm<sup>2</sup>/mg per stan-  
204 dardized photoperiod; 90% UI: -0.4, 0.0, Fig. 2 f, Table S4), but did not strongly predict responses  
205 to chilling ( $\beta_{\text{chill}_k}$ ) or forcing treatments ( $\beta_{\text{force}_k}$ , Fig. 2 d and e). Thus, species with more acquisitive  
206 growth strategies (thin leaves and a lower investment in leaf mass that leads to large SLA values),  
207 had larger responses to photoperiod, contrary to our predictions (Fig. 2 f). For LNC, we found that  
208 species that produce leaves with high nitrogen content, which relates generally to high photosynthetic  
209 rates and acquisitive growth, show smaller responses to cues (Fig. 2 j-l). These findings are in line  
210 with our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g  
211 per standardized chilling; 90% UI: 0.3, 1.2, Table S5), but we also found high LNC species to be less  
212 responsive to photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0.0, 0.6) and to forcing  
213 (0.5 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig 2 j-l & Fig S3 d-f).

214  
215 We found species-level variation across traits ( $\sigma^2_{\text{trait}}$ ) were comparable to or greater than variation  
216 across studies ( $\sigma^2_{\text{study}}$ , Fig 4). The magnitude of study-level variation ( $\sigma^2_{\text{study}}$ ) that we found, however,  
217 suggests that models using large trait databases that fail to separate out study from species-level vari-  
218 ation ( $\sigma^2_{\text{trait}}$ ) may poorly estimate species traits. Variation across studies was greatest for height (with  
219  $\sigma^2_{\text{study}}$  of 7.5 m compared to 5.9 m for  $\sigma^2_{\text{trait}}$ , Fig 4a). For seed mass and LNC, study-level variation  
220 was less than that of the species-level variation, with estimates of 1 mg for study-level variation versus  
221 1.6 mg for species-level variation in seed mass and estimates of 3.6 mg g<sup>-1</sup> for study-level variation  
222 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  
223 variation in SLA was approximately half the value of the species-level variation (3.3 mm<sup>2</sup> mg<sup>-1</sup> versus  
224 7.8 mm<sup>2</sup> mg<sup>-1</sup> for  $\sigma^2_{\text{study}}$  and  $\sigma^2_{\text{trait}}$ , respectively, Fig 4b).

225  
226

227 **Discussion**

228 We found species traits influenced the timing of budburst in response to the three primary cues of  
229 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with ear-  
230 lier or later phenology following well-established gradients in growth strategies predicted by functional  
231 trait frameworks<sup>24-28</sup>: early species tended to have traits associated with fast and acquisitive strategies  
232 while later species had traits associated with conservative, slower strategies. We found the largest bud-  
233 burst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and  
234 height all showing large responses across our three cues. In contrast, our one reproductive trait—seed  
235 mass—showed a smaller response. Our results provide a major step forward in integrating phenology  
236 into broader trait syndromes that shape species growth strategies, and support previous findings from  
237 more local scales that found strong relationships between height and species phenology<sup>39-41</sup>. Our more  
238 global analysis is also in agreement with previous studies of plant phenological events, in which no  
239 relation is found between phenology and seed mass in woody plants<sup>42,43</sup>.

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

242 Our findings suggest the changing pressures across the early growing season may affect the temporal  
 243 assembly of communities. Strong abiotic pressures alongside weak competition early in the season were  
 244 associated with early-budbursting species with acquisitive traits (shorter heights and low LNC) that al-  
 245 low faster return on resource investments<sup>25,26,44</sup>. These traits should allow early species to more easily  
 246 replace tissue if lost to frost or other abiotic disturbances, and benefit from greater light availability in  
 247 the open canopy of many temperate forests in the early spring. In contrast, later-budbursting species  
 248 had traits associated with greater competitive abilities and slower growth<sup>25,26,44</sup> (Fig 2), which may  
 249 help them compete for soil and light resources when most other species are already growing. These  
 250 traits can be linked to other ecological processes and species characteristics, such as species succe-  
 251 sional position, as illustrated by the differences between early and late successional species (e.g., *Alnus*  
 252 *incana* and *Quercus rubra*; Fig 2).

253

254 The traits with cue responses that deviated from our expectations also offer novel insights into the  
 255 tradeoffs between traits and environmental cues. All of our traits are associated with multiple aspects  
 256 of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our  
 257 predictions, we found large responses to forcing for short trees, which could prevent frost damage or  
 258 xylem cavitation under a late spring frost<sup>45,46</sup> and influence annual cambial meristem growth<sup>47</sup>. Simi-  
 259 larly, the lack of a response to chilling or forcing by high SLA individuals could be driven by other trait  
 260 attributes and environmental cues—selecting for species relative growth rates or leaf longevity—and  
 261 not photosynthetic potential<sup>26,48</sup>. These findings highlight the complexity of determining the drivers  
 262 of species trait profiles, and further our understanding of how traits affect community dynamics under  
 263 variable environments.

264

## 265 Phenology-trait relationships under future climates

266 Incorporating phenology within broader trait syndromes could aid forecasting of species and commu-  
 267 nity responses to climate change. While decades of research have documented phenological shifts with  
 268 anthropogenic climate change, increasing research suggests a potential connection between phenolog-  
 269 ical responses to warming and performance with warming, where species that shift their phenology  
 270 more also perform better<sup>49,50</sup>.

271

272 Our results suggest this phenology-performance relationship could be driven in part by a suite of traits  
 273 that covary with phenological cues to determine how responsive species are to warming. Species with  
 274 smaller responses to all cues, especially chilling and photoperiod, would tend to advance more with  
 275 warming, which our results suggest would allow these species to also grow more quickly. These results  
 276 could further aid in predicting the potential for invasion, as communities with similar phenologies  
 277 and suites of traits, appear more susceptible to fast growing, phenologically more responsive invasive  
 278 species<sup>51–53</sup>.

279

280 Our analytical approach and results may be especially useful to help forecast changes in forest dy-  
 281 namics. Identifying the varying trait syndromes of forest communities over a spring season can aid  
 282 predictions of how climate change will alter species growth and productivity. For example, our results  
 283 suggest that, by favoring more phenologically responsive species (i.e., with small chilling and pho-  
 284 toperiod responses), warming may also favor species with acquisitive growth strategies. In contrast,  
 285 conservative species, which appear less phenologically responsive to changes in temperature (due to  
 286 larger chilling and photoperiod responses) could face greater abiotic and biotic stress<sup>54</sup>.

287

288 Our results could further help identify which species are most likely to be negatively impacted under  
289 future climates, and develop better strategies for climate change mitigation and conservation. Species  
290 that fail to advance phenologically with warming might experience more competition<sup>52,55</sup>, as species  
291 that begin growth increasingly earlier with warming have more time to deplete resources. In addition to  
292 altering the timing and interactions between species within a season, species trait syndromes have the  
293 potential to further redefine the environmental conditions under which growth occurs, and as a result,  
294 shape community assembly and productivity within ecological communities. By identifying the species  
295 most vulnerable to climate change impacts, we can develop more effective management practices that  
296 prevent the loss of critical ecosystem services and preserve community diversity under future conditions.  
297

## 298 **Acknowledgements**

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

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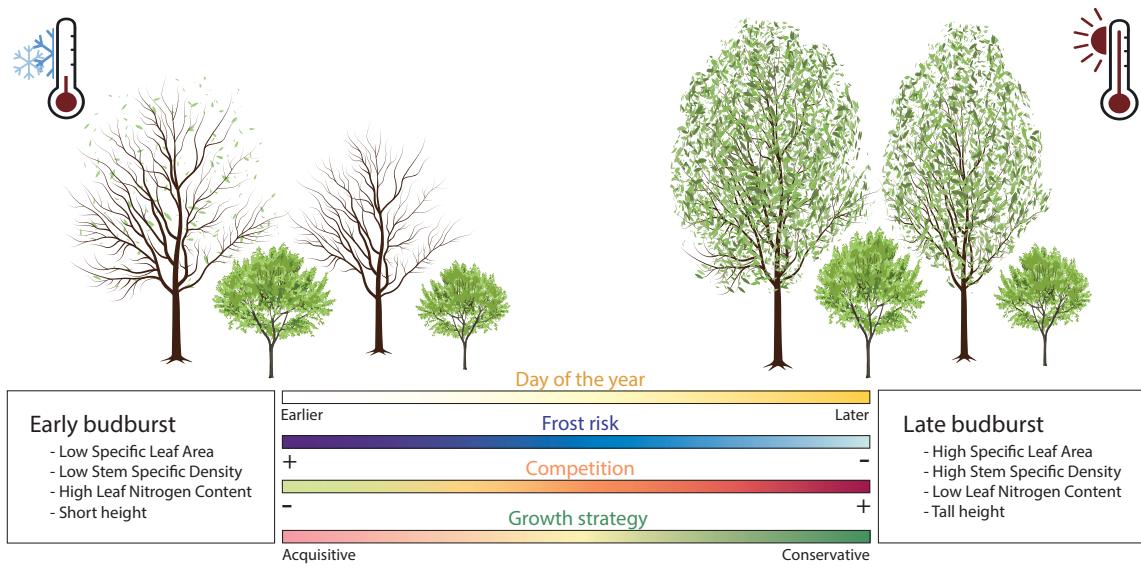


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost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

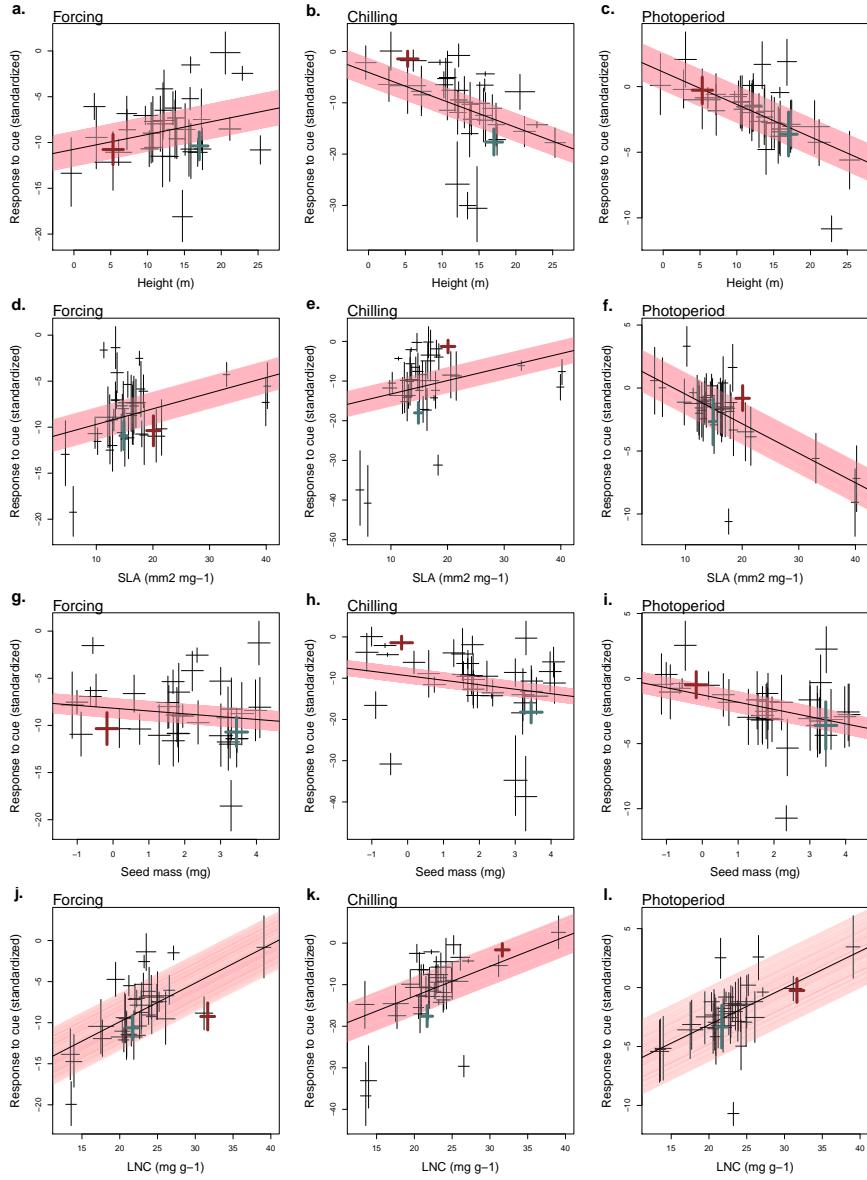


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third 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 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.

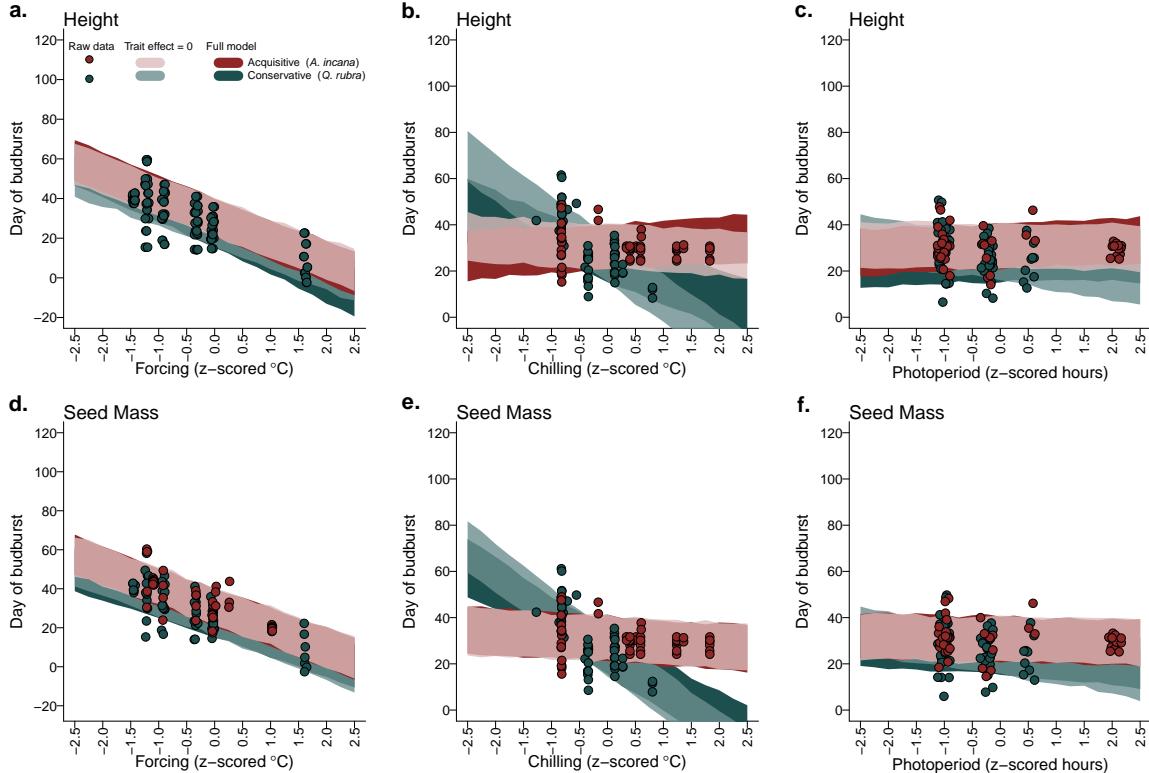


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with 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.

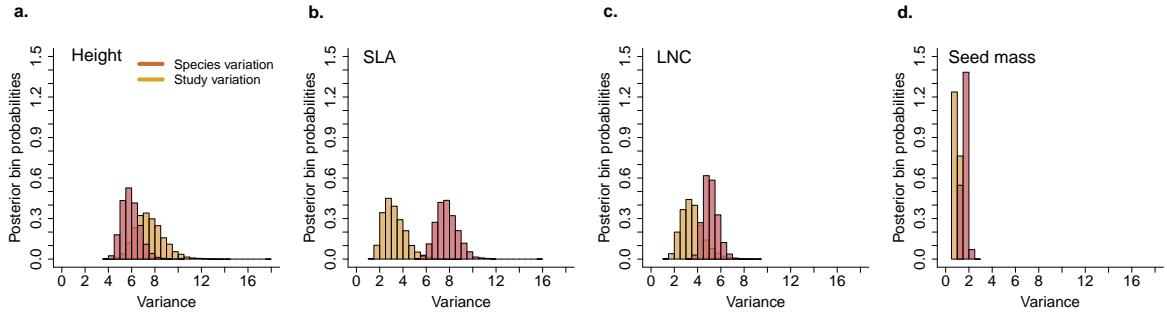


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation, with only **a**, the height model estimating greater study-level variation than species-level, while our **b**, specific leaf area, **c**, leaf nitrogen content, and **d**, seed mass models all estimated 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.