

<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> August 14, 2024

<sup>5</sup> <sup>1</sup> Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, 2424  
<sup>6</sup> 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 Ste 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 trait variability across environments makes this challenging to test. Here, we  
<sup>38</sup> combine a new joint modeling approach to accommodate this variability with global data on plant traits  
<sup>39</sup> and budburst responses in controlled environment experiments. We find that earlier species—which  
<sup>40</sup> are generally most responsive to anthropogenic warming—are generally shorter with denser, lower  
<sup>41</sup> nitrogen leaves. These results suggest warming may reshape the trait structure of plant communities,  
<sup>42</sup> and could help improve predictions of how growth strategies and phenologies together may shift with  
<sup>43</sup> continued 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 (Cleland et al., 2007; Beard et al., 2019; Gu  
<sup>50</sup> et al., 2022). Shifts in phenology with climate change across systems (Menzel et al., 2006; Vitasse  
<sup>51</sup> et al., 2021) have thus led to growing concerns over their possible impacts.

<sup>52</sup>

<sup>53</sup> Predicting these changes requires understanding the drivers of phenology both at a proximate scale—  
<sup>54</sup> the environmental triggers of phenology each year, such as temperature and daylength—and at an  
<sup>55</sup> ultimate scale, where long-term environmental pressures may select for different phenologies across  
<sup>56</sup> species (e.g., certain species are early or late relative to other species each year, Ovaskainen et al.,  
<sup>57</sup> 2013; Wolkovich and Donahue, 2021). At the proximate level, environmental conditions throughout  
<sup>58</sup> the winter and spring cause species to start growth at different times. This is well documented for the  
<sup>59</sup> start of growth in woody plants each year (Laube et al., 2014; Flynn and Wolkovich, 2018). Similar  
<sup>60</sup> environmental conditions appear to trigger spring phenological events across taxa, including in the  
<sup>61</sup> timing of egg laying in birds (Crick et al., 1997; D'Alba et al., 2010) and the advance of spawning  
<sup>62</sup> in amphibians (Tryjanowski et al., 2003; Kusano and Inoue, 2008), but current work provides lim-  
<sup>63</sup> ited insights into the drivers of species differences (Laube et al., 2014; Chuine et al., 2016; Flynn and  
<sup>64</sup> Wolkovich, 2018).

<sup>65</sup>

<sup>66</sup> At the ultimate level, species phenologies may vary due to changing pressures across the growing  
<sup>67</sup> season. Species that start growth early often risk high tissue loss—due to frost damage (Sakai and  
<sup>68</sup> Larcher, 1987; Augspurger, 2009) or high herbivore apperency (Wainwright et al., 2012)—but benefit  
<sup>69</sup> from higher resource availability (Rathcke and Lacey, 1985; Hufkens et al., 2012). In contrast, later  
<sup>70</sup> species face greater biotic pressures, especially from high competition for resources (Lopez et al., 2008;  
<sup>71</sup> Wolkovich and Ettinger, 2014). For plants, this variation in early to late season growth, may mirror  
<sup>72</sup> the stressors from early to late successional communities, and may similarly shape phenology (Laube  
<sup>73</sup> et al., 2014).

<sup>74</sup>

<sup>75</sup> Different pressures could shape a number of species attributes related to their growth strategies, in-  
<sup>76</sup> cluding phenology. Species with earlier phenology may produce cheaper tissues that are easily replaced  
<sup>77</sup> if damaged (Reich et al., 1999), while species with later phenology may benefit from investing in tis-  
<sup>78</sup> sures that infer greater resource retention (Gorné et al., 2020). Differences in traits, and trade-offs in  
<sup>79</sup> allocation of resources to growth and tissue quality, can be related to a broader framework of species

80 growth strategies and functional traits (Fig. 1, Wolkovich and Ettinger, 2014), where species range  
 81 from acquisitive (fast) to more conservative (slow) growth (Wright et al., 2004; Chave et al., 2009).

82  
 83 Globally, gradients from acquisitive to conservative strategies appear common, and form the founda-  
 84 tion of the leaf economic and the wood economic spectra (Westoby, 1998; Westoby and Wright, 2006;  
 85 Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016), but they can make limited predictions of  
 86 trait variability (Violle et al., 2012). As a result, highly variable traits like phenology are often ex-  
 87 cluded from trait studies, leaving the relationships between broader trait syndromes and phenology  
 88 largely unknown. Understanding these relationships is critical to forecasting community dynamics and  
 89 responses to climate change. To date, studies have generally only examined the relationship between  
 90 traits and phenology within a single site (reviewed in Wolkovich and Cleland, 2014; Wolkovich and  
 91 Donahue, 2021), where the problem of proximate drivers causing phenological variation can be more  
 92 easily ignored. Adding phenology to broader trait frameworks becomes more complex when high levels  
 93 of variation occurs across large spatial and temporal ranges.

94  
 95 Consistently defining early to late phenology is possible using the underlying cues that predict gradi-  
 96 ents in phenology (which do not generally vary strongly across space and time, Chuine and Cour, 1999;  
 97 Harrington and Gould, 2015; Flynn and Wolkovich, 2018). For many plants, early species generally  
 98 have small in magnitude responses to all three major cues of spring leafout: warm spring temperatures  
 99 (forcing), cool winter temperatures (chilling) and daylength (photoperiod). In contrast, later species  
 100 have larger responses to chilling and/or photoperiod (Laube et al., 2014; Flynn and Wolkovich, 2018),  
 101 and likely larger forcing responses.

102  
 103 Studies of spring phenology in temperate forests may provide the best opportunity to integrate phe-  
 104 nology into functional trait research. In addition to how well we understand the environmental cues  
 105 that trigger early versus late leafout, spring in many forests includes strong gradients in potential se-  
 106 lective environments (Fig 1). Based on trade-offs between early and late spring phenologies, we predict  
 107 acquisitive species to be shorter, with leaf traits favourable to higher light availability and tolerance  
 108 of late spring frost (high specific leaf area, SLA, and leaf nitrogen content, LNC; Fig 1). Such species  
 109 should exhibit early phenology, with small cue responses. Canopy species that budburst later via larger  
 110 cue responses, when competition for soil resources is greater, would then have traits associated with  
 111 conservative growth—taller with denser wood (Laughlin et al., 2010)—with leaf traits suited for more  
 112 variable light (low SLA and LNC, Fig 1). Seed size may similarly be predicted from this acquisitive to  
 113 conservative continuum, as acquisitive species produce smaller seeds and conservative species produce  
 114 larger—better provisioned—seeds (Fig 1).

115  
 116 To test our predicted relationships between budburst responses to environmental cues and common  
 117 functional traits (height, SLA, seed mass, and LNC), we merged available data from trait databases—  
 118 BIEN (Maitner et al., 2018) and TRY (Kattge et al., 2020)—with budburst data from the OSPREE  
 119 database of controlled environment studies (Ettinger et al., 2020). We developed a hierarchical Bayesian  
 120 joint model that predicts phenological responses to forcing, chilling and photoperiod treatments based  
 121 on species-level trait values, while allowing additional variation due to species. This approach takes  
 122 a step towards predicting variation via species traits instead of species identity (when traits explain  
 123 a significant portion of the variation, species identity will explain only a small amount), which could  
 124 help forecast species phenological responses based on trait values alone.

125

## 126 Methods

127 We merged three major databases for our analysis. We gathered phenological data from the OSPREE  
 128 database (Ettinger et al., 2020), which contains budburst data for woody, deciduous species from ex-

129 periments of forcing, chilling and photoperiod. We updated this database since its initial publication,  
 130 the methods of which are discussed by Morales-Castilla et al. (2024). We gathered trait data from  
 131 TRY and BIEN (Maitner et al., 2018; Kattge et al., 2020), both of which are large trait databases  
 132 that include plant trait data across many individuals, species, and studies (Table S1). We obtained  
 133 data from both databases on 5 December, 2018, with an updated version of the TRY data obtained  
 134 10 April, 2019. We focused our search for trait data on the subset of 234 OSPREE species used in  
 135 Morales-Castilla et al. (2024). Using the BIEN R package, version 1.2.5 (Maitner et al., 2018), we  
 136 downloaded trait data for the 94 species available, for which there were 13 traits. The TRY database  
 137 included data for 10 traits for 96 of our focal species (Kattge et al., 2020). Given our focus on phenol-  
 138 ogy of adult trees, we included trait data from adult individuals with a minimum height of 1.38 m. We  
 139 further removed all data from experiments or from plants growing in non-natural habitats. We also  
 140 grouped trait values where appropriate, for example categorizing trait values for “SLA”, “SLA with  
 141 petioles”, and “SLA without petioles” as simply “SLA” in our analysis (see Table S1). Duplicated data  
 142 in both the TRY and BIEN datasets were also removed ( $n = 434905$ ). Based on our selection criteria,  
 143 our final dataset included data for 11 traits from 91 of the species also represented in the OSPREE  
 144 database, with each species differing in the number and types of traits measured.

145  
 146 For our analysis, we only include species for which we had a complete trait profile (i.e., all traits mea-  
 147 sured for all species). We initially considered six commonly measured traits—SLA, leaf dry matter  
 148 content (LDMC), height, seed mass, stem specific density (SSD), and LNC—for which 26 species had at  
 149 least one trait measurement for each trait. We then used a principle component analysis to understand  
 150 trait correlations and adjusted which traits we included. A PCA of our six initial traits identified high  
 151 correlations between SLA and LDMC, and between height and SSD (see Supplementary material).  
 152 The first principal component explained 32% of variation while the second explained 24.2% of the  
 153 variation (Fig. S1). By excluding one trait from each of these highly correlated trait pairs (specifically  
 154 LDMC and SSD) we increased the number of species in our dataset from the 26 species with six traits,  
 155 to 37 species for which we had complete datasets for four traits. The data for these 37 species were  
 156 from 24 unique studies (height  $n = 47781$ , seed mass  $n = 281$ , LNC  $n = 3853$ , SLA  $n = 7656$ ). We  
 157 subsampled height measurements to reduce the influence the 13 most frequently measured tree species  
 158 had on our height model. Since these 13 species were measured 19 times more frequently than other  
 159 species, for each species, we randomly sampled 3000 height measurements.  
 160

## 161 Joint model of trait and phenology

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

## 170 Trait sub-model

171 The trait sub-model describes the processes that determine trait observations for 1 to  $n$  species across  
 172 each of the 1 to  $m$  studies in our trait dataset (TRY and BIEN data). We use hierarchical modeling to  
 173 partitions trait variation by measurement error, species identity, and study identity. In particular, we  
 174 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:

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

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

## Phenology sub-model

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

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

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:

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

Parameter  $\alpha_{\text{pheno},k}$  represents the day of budburst for species  $k$  without the influence of chilling, forcing, or photoperiod treatments. Average day of budburst (independent of treatments) is  $\mu_{\text{pheno}}$ , and  $\sigma_{\text{pheno}}^2$  is the variance across species. The parameters  $\alpha_{\text{chill},k}$ ,  $\alpha_{\text{force},k}$ , and  $\alpha_{\text{photo},k}$  represent the trait-independent responses of species  $k$  to chilling, forcing, and photoperiod treatments respectively, each 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

192 effect of the species trait value,  $\alpha_{\text{trait},k}$  (parameter shared with trait sub-model above), on its responses  
 193 to chilling, forcing, and photoperiod are described by parameters  $\beta_{\text{trait.chill}}$ ,  $\beta_{\text{trait.force}}$ ,  $\beta_{\text{trait.photo}}$ . Finally,  
 194  $\sigma_d^2$  is the variance arising from measurement error.

195

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

## 202 Results

203 Across traits, height, SLA, and LNC strongly related to chilling, forcing and photoperiod treatments  
 204 ( $\beta_{\text{chill}_k}$ ,  $\beta_{\text{force}_k}$ , and  $\beta_{\text{photo}_k}$ , Fig 2 a-f & j-l), but the direction of these relationships only showed  
 205 consistent trends for LNC (Fig. 2 j-l). As we predicted, height was related to chilling ( $\beta_{\text{chill}_k}$ ) and photo-  
 206 period ( $\beta_{\text{photo}_k}$ ), with taller species having larger responses to cues (-0.5 m per standardized chilling;  
 207 90% uncertainty interval (UI): -1.0, -0.1 and -0.2 m per standardized photoperiod; 90% UI: -0.5, 0.0,  
 208 Fig 2 a-c, Table S2). As illustrated for one characteristically acquisitive species, *Alnus incana*, and  
 209 one characteristically conservative species, *Quercus rubra* (Fig S3), the cue relationships with height  
 210 led to generally later budburst ( $\mu_{k,g}$ ; Fig. 3). In contrast, seed mass had the smallest responses, with  
 211 no relationship between seed mass and any cue (Fig. 2 g-i, Fig 3 d-f, & Table S3).

212

213 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-  
 214 dardized photoperiod; 90% UI: -0.4, 0.0, Fig. 2 f, Table S4), but did not strongly predict responses  
 215 to chilling ( $\beta_{\text{chill}_k}$ ) or forcing treatments ( $\beta_{\text{force}_k}$ , Fig. 2 d and e). Thus, species with more acquisitive  
 216 growth strategies (thin leaves and a lower investment in leaf mass that leads to large SLA values),  
 217 had larger responses to photoperiod, contrary to our predictions (Fig. 2 f). For LNC, we found that  
 218 species that produce leaves with high nitrogen content, which relates generally to high photosynthetic  
 219 rates and acquisitive growth, show smaller responses to cues (Fig. 2 j-l). These findings are in line  
 220 with our predictions that high LNC species (acquisitive) would be less responsive to chilling (0.7 mg/g  
 221 per standardized chilling; 90% UI: 0.3, 1.2, Table S5), but we also found high LNC species to be less  
 222 responsive to photoperiod (0.3 mg/g per standardized photoperiod; 90% UI: 0, 0.6) and to forcing (0.5  
 223 mg/g per standardized forcing; 90% UI: 0.1, 0.9, Fig 2 j-l & Fig S3 d-f).

224

225 Across our models, we found species-level variation across traits ( $\sigma_{\text{trait}}^2$ ) were comparable to or greater  
 226 than variation across studies ( $\sigma_{\text{study}}^2$ , Fig 4). The magnitude of study-level variation ( $\sigma_{\text{study}}^2$ ) that we  
 227 found, however, suggests that models using large trait databases that fail to separate out study from  
 228 species-level variation ( $\sigma_{\text{trait}}^2$ ) may poorly estimate species traits. Variation across studies was greatest  
 229 for height (with  $\sigma_{\text{study}}^2$  of 7.5 m compared to 5.9 m for  $\sigma_{\text{trait}}^2$ , Fig 4a). For seed mass and LNC study-  
 230 level variation was less than that of the species-level variation, with estimates of 1 mg for study-level  
 231 variation versus 1.6 for species-level variation in seed mass and estimates of 3.6 mg g<sup>-1</sup> for study-level  
 232 variation and 5.1 mg g<sup>-1</sup> for the species-level variation in LNC (Fig 4c and d). At the lowest end,  
 233 study-level variation in SLA was approximately half the value of the species-level variation (3.3 mm<sup>2</sup>  
 234 mg<sup>-1</sup> versus 7.8 mm<sup>2</sup> mg<sup>-1</sup> for  $\sigma_{\text{study}}^2$  and  $\sigma_{\text{trait}}^2$ , respectively, Fig 4b).

235

## 236 Discussion

237 We found species traits influenced the timing of budburst in response to the three primary cues of  
 238 spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or

239 later phenology following well-established gradients in growth strategies predicted by functional trait  
 240 frameworks (Westoby, 1998; Westoby and Wright, 2006; Wright et al., 2004; Chave et al., 2009; Díaz  
 241 et al., 2016): early species tended to have traits associated with fast and acquisitive strategies while  
 242 later species had traits associated with conservative, slower strategies. We found the largest budburst  
 243 responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and height  
 244 all showing large responses across our three cues. In contrast, our one reproductive trait—seed mass—  
 245 showed a smaller response. Our results provide a major step forward in integrating phenology into  
 246 broader trait syndromes that shape species growth strategies, and support previous findings from more  
 247 local scales that found strong relationships between height and species phenology (Sun and Frelich,  
 248 2011; Sporbert et al., 2022; Segrestin et al., 2020). Our findings also suggest other traits—such as seed  
 249 mass—show no relationship with phenology in our more global analysis.

250

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

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

264

265 The traits with cue responses that deviated from our expectations also offer novel insights into the  
 266 tradeoffs between traits and environmental cues. All of our traits are associated with numerous aspects  
 267 of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our pre-  
 268 dictions, we found large responses to forcing for short trees, which could prevent frost damage or xylem  
 269 cavitation under a late spring frost (Clements et al., 1972; Marquis et al., 2020) and influence annual  
 270 cambial meristem growth (Lenz et al., 2016). Similarly, the lack of a response to chilling or forcing by  
 271 high SLA individuals could be driven by other trait attributes and environmental cues—selecting for  
 272 species relative growth rates or leaf longevity—and not photosynthetic potential (Westoby, 1998; Re-  
 273 ich, 2014). These findings highlight the complexity of determining the drivers of species trait profiles,  
 274 and further our understanding of how traits affect community dynamics under variable environments.

275

## 276 Phenology-trait relationships under future climates

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

282 Our results suggest this phenology-performance relationship could be driven in part by a suite of traits  
 283 that covary with phenological cues to determine how responsive species are to warming. Species with  
 284 smaller responses to all cues, especially chilling and photoperiod, would tend to advance more with  
 285 warming, our results suggest these species may also grow more quickly. These results could further aid  
 286 in predicting the potential for invasion, as communities with similar phenologies and suites of traits,

287 appear more susceptible to fast growing, phenologically more responsive invasive species (Wolkovich  
288 and Cleland, 2011; Alexander and Levine, 2019; Schuster et al., 2021).

289 Our analytical approach and results may be especially useful to help forecast changes in forest dynamics.  
290 Identifying the trait syndromes of forest communities over spring season can aid predictions about how  
291 climate change will alter species growth and productivity. For example, our results suggest that, by  
292 favoring more phenologically responsive species (i.e., with small chilling and photoperiod responses),  
293 warming may also favor species with acquisitive growth strategies. In contrast, conservative species,  
294 which appear less phenologically responsive to changes in temperature (due to larger chilling and  
295 photoperiod responses) could therefore face greater abiotic and biotic stress (Guy, 2014).

296 Our results could further help identify which species are most likely to be negatively impacted under  
297 future climates, and develop better strategies for climate change mitigation and conservation. Species  
298 that fail to advance phenologically with warming might experience more competition (Carter et al.,  
299 2018; Alexander and Levine, 2019), as species that begin growth increasingly earlier with warming have  
300 more time to deplete resources. In addition to altering the timing and interactions between species  
301 within a season, species trait syndromes have the potential to redefine the environmental conditions  
302 under which growth occurs, and as a result, shape community assembly, and productivity of diverse  
303 ecological communities. By identifying the species most vulnerable to climate change impacts, we can  
304 develop more effective management practices that prevent the loss of ecosystem services and commu-  
305 nity diversity.

306

307

**308 References**

- 309 Alexander, J. M., and J. M. Levine. 2019. Earlier phenology of a nonnative plant increases impacts  
310 on native competitors. *PNAS* 116:6199–6204.
- 311 Augspurger, C. K. 2009. Spring 2007 warmth and frost : phenology , damage and refoliation in a  
312 temperate deciduous forest. *Functional Ecology* 23:1031–1039.
- 313 Beard, K. H., K. C. Kelsey, A. J. Leffler, and J. M. Welker. 2019. The Missing Angle : Ecosystem  
314 Consequences of Phenological Mismatch. *Trends in Ecology and Evolution* 34:885–888.
- 315 Carter, S. K., D. Saenz, and V. H. Rudolf. 2018. Shifts in phenological distributions reshape interaction  
316 potential in natural communities. *Ecology Letters* 21:1143–1151.
- 317 Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a  
318 worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- 319 Chuine, I., M. Bonhomme, J. M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and  
320 T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The  
321 unrevealed hurdle of endodormancy break. *Global change biology* 22:3444–3460.
- 322 Chuine, I., and P. Cour. 1999. Climatic determinants of budburst seasonality in four temperate-zone  
323 tree species. *New Phytologist* 143:339–349.
- 324 Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta,  
325 and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate  
326 change.pdf. *Ecology* 93:1765–1771.
- 327 Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology  
328 in response to global change. *Trends in Ecology and Evolution* 22:357–365.
- 329 Clements, J. R., W. Fraser, J, and C. W. Yeatman. 1972. Frost Damage to White Spruce Buds.  
330 Canadian Journal of Forest Research 2:62–63.
- 331 Crick, H., C. Dudley, D. E. Glue, and D. L. Thomson. 1997. UK birds are laying eggs earlier. *Nature*  
332 388:526–527.
- 333 D'Alba, L., P. Monaghan, and R. G. Nager. 2010. Advances in laying date and increasing population  
334 size suggest positive responses to climate change in Common Eiders Somateria mollissima in Iceland.  
335 International Journal of Avian Science 152:19–28.
- 336 Diaz, S., J. Kattge, J. H. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth,  
337 I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie,  
338 A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet Ev, H. Jactel, C. Baraloto,  
339 B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falcuk,  
340 N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function.  
341 *Nature* 529:167–171.
- 342 Ettinger, A. K., C. J. Chamberlain, I. Morales-Castilla, D. M. Buonaiuto, D. F. Flynn, T. Savas,  
343 J. A. Samaha, and E. M. Wolkovich. 2020. Winter temperatures predominate in spring phenological  
344 responses to warming. *Nature Climate Change* 10:1137–1142.
- 345 Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology  
346 across all species in a temperate forest community. *New Phytologist* 219:1353–1362.
- 347 Gorné, L. D., S. Diaz, V. Minden, Y. Onoda, K. Kramer, C. Muir, S. T. Michaletz, S. Lavorel,  
348 J. Sharpe, S. Jansen, M. Slot, E. Chacon, and G. Boenisch. 2020. The acquisitive–conservative axis  
349 of leaf trait variation emerges even in homogeneous environments. *Annals of Botany* .

- 350 Grime, J. P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance  
351 to Ecological and Evolutionary Theory Author ( s ): J . P . Grime Source : The American Naturalist  
352 , Vol . 111 , No . 982 ( Nov . - Dec ., 1977 ), pp . 1169-1194 Published. The American Naturalist  
353 111:1169–1194.
- 354 Gu, H., Y. Qiao, Z. Xi, S. Rossi, N. G. Smith, J. Liu, and L. Chen. 2022. Warming-induced increase  
355 in carbon uptake is linked to earlier spring phenology in temperate and boreal forests. *Nature*  
356 Communications 13:1–8.
- 357 Guy, R. D. 2014. The early bud gets to warm. *New Phytologist* 202:7–9.
- 358 Harrington, C. A., and P. J. Gould. 2015. Tradeoffs between chilling and forcing in satisfying dormancy  
359 requirements for Pacific Northwest tree species. *Frontiers in Plant Science* 6:1–12.
- 360 Hufkens, K., M. A. Friedl, T. F. Keenan, O. Sonnentag, A. Bailey, J. O'keefe, and A. D. Richardson.  
361 2012. Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change*  
362 *Biology* 18:2365–2377.
- 363 Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I. C. Prentice, and et al. 2020. TRY plant trait database  
364 – enhanced coverage and open access. *Global Change Biology* 26:119–188.
- 365 Kusano, T., and M. Inoue. 2008. Long-Term Trends toward Earlier Breeding of Japanese Amphibians.  
366 *Journal of Herpetology* 42:608–614.
- 367 Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs  
368 photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- 369 Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf-  
370 height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*  
371 24:493–501.
- 372 Lenz, A., G. Hoch, C. Körner, and Y. Vitasse. 2016. Convergence of leaf-out towards minimum risk  
373 of freezing damage in temperate trees. *Functional Ecology* 30:1480–1490.
- 374 Lopez, O. R., K. Farris-Lopez, R. A. Montgomery, and T. J. Givnish. 2008. Leaf phenology in relation  
375 to canopy closure in southern Appalachian trees. *American Journal of Botany* 95:1395–1407.
- 376 Macgregor, C. J., C. D. Thomas, D. B. Roy, M. A. Beaumont, J. R. Bell, T. Brereton, J. R. Bridle,  
377 C. Dytham, R. Fox, K. Gotthard, A. A. Hoffmann, G. Martin, I. Middlebrook, S. Nylin, P. J.  
378 Platts, R. Rasteiro, I. J. Saccheri, R. Villoutreix, C. W. Wheat, and J. K. Hill. 2019. Climate-  
379 induced phenology shifts linked to range expansions in species with multiple reproductive cycles per  
380 year. *Nature Communications* 10:1–10.
- 381 Maitner, B. S., B. Boyle, N. Casler, R. Condit, J. Donoghue, S. M. Durán, D. Guaderrama, C. E.  
382 Hinchliff, P. M. Jørgensen, N. J. Kraft, B. McGill, C. Merow, N. Morueta-Holme, R. K. Peet,  
383 B. Sandel, M. Schildhauer, S. A. Smith, J. C. Svenning, B. Thiers, C. Violette, S. Wiser, and B. J.  
384 Enquist. 2018. The bien r package: A tool to access the Botanical Information and Ecology Network  
385 (BIEN) database. *Methods in Ecology and Evolution* 9:373–379.
- 386 Marquis, B., Y. Bergeron, M. Simard, and F. Tremblay. 2020. Growing-season frost is a better predictor  
387 of tree growth than mean annual temperature in boreal mixedwood forest plantations. *Global Change*  
388 *Biology* 26:6537–6554.
- 389 Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aaasa, R. Ahas, K. Alm-Kübler, P. Bissolli,  
390 O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Don-  
391 nelly, Y. Filella, K. Jatczak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová,  
392 H. Scheifinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Zust. 2006.

- 393 European phenological response to climate change matches the warming pattern. *Global Change  
394 Biology* 12:1969–1976.
- 395 Morales-Castilla, I., T. J. Davies, G. Legault, D. M. Buonaiuto, C. J. Chamberlain, A. K. Ettinger,  
396 M. Garner, F. A. M. Jones, D. Loughnan, W. D. Pearse, D. Sodhi, and E. M. Wolkovich. 2024.  
397 Phylogenetic estimates of species-level phenology improve ecological forecasting. *Nature Climate  
398 Change* .
- 399 Ovaskainen, O., S. Skorokhodova, M. Yakovleva, A. Sukhov, A. Kutenkov, N. Kutenkova,  
400 A. Shcherbakov, E. Meyke, and M. del Mar Delgado. 2013. Community-level phenological response  
401 to climate change. *PNAS* 110:13434–13439.
- 402 Rathcke, B., and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of  
403 Ecology and Systematics* 16:179–214.
- 404 Reich, P. B. 2014. The world-wide ‘fast – slow’ plant economics spectrum : a traits manifesto. *Journal  
405 of Ecology* 102:275–301.
- 406 Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman.  
407 1999. Generality of leaf trait relationships: A test across six biomes. *Ecology* 80:1955–1969.
- 408 Sakai, A., and W. Larcher. 1987. Frost Survival of Plants: Responses and adaptation to freezing stress.  
409 Springer-Verlag, Berlin, Heidelberg.
- 410 Schuster, M. J., P. D. Wragg, and P. B. Reich. 2021. Phenological niche overlap between invasive buck-  
411 thorn (*Rhamnus cathartica*) and native woody species. *Forest Ecology and Management* 498:119568.
- 412 Segrestin, J., M.-l. Navas, and E. Garnier. 2020. Reproductive phenology as a dimension of the  
413 phenotypic space in 139 plant species from the Mediterranean. *New Phytologist* 225:740–753.
- 414 Sporbert, M., D. Jakubka, S. F. Bucher, I. Hensen, M. Freiberg, K. Heubach, A. Konig, B. Nordt,  
415 C. Plos, I. Blinova, A. Bonn, B. Knickmann, T. Koubek, A. Linstadter, T. Maskova, R. Primack,  
416 C. Rosche, M. A. Shah, A.-D. Stevens, K. Teilborger, S. Trager, C. Wirth, and C. Romermann.  
417 2022. Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-  
418 botanical garden study. *New Phytologist* 235:2199–2210.
- 419 Stan Development Team. 2018. RStan: the R interface to Stan. R package version 2.17.3.
- 420 Sun, S., and L. E. Frelich. 2011. Flowering phenology and height growth pattern are associated with  
421 maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland  
422 species. *Journal of Ecology* 99:991–1000.
- 423 Tryjanowski, P., M. Rybacki, and T. Sparks. 2003. Changes in the first spawning dates of common  
424 frogs and common toads in western Poland in 1978–2002. *Annales Zoologici Fennici* 40:459–464.
- 425 Violette, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier.  
426 2012. The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology  
427 and Evolution* 27:244–252.
- 428 Vitasse, Y., S. Ursenbacher, G. Klein, T. Bohnenstengel, Y. Chittaro, A. Delestrade, C. Monnerat,  
429 M. Rebetez, C. Rixen, N. Strelbel, B. R. Schmidt, S. Wipf, T. Wohlgemuth, N. G. Yoccoz, and  
430 J. Lenoir. 2021. Phenological and elevational shifts of plants , animals and fungi under climate  
431 change in the European Alps. *Biological Reviews* 96:1816–1835.
- 432 Wainwright, C. E., E. M. Wolkovich, and E. E. Cleland. 2012. Seasonal priority effects : implications  
433 for invasion and restoration in a semi-arid system. *Journal of Applied Ecology* 49:234–241.
- 434 Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.

- 435 Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in  
436 Ecology and Evolution* 21:261–268.
- 437 Wolkovich, E. M., and E. E. Cleland. 2011. The phenology of plant invasions: A community ecology  
438 perspective. *Frontiers in Ecology and the Environment* 9:287–294.
- 439 ———. 2014. Phenological niches and the future of invaded ecosystems with climate change. *AoB  
440 PLANTS* 6:1–16.
- 441 Wolkovich, E. M., and M. J. Donahue. 2021. How phenological tracking shapes species and communities  
442 in non-stationary environments. *Biological Reviews* 96:2810–2827.
- 443 Wolkovich, E. M., and A. K. Ettinger. 2014. Back to the future for plant phenology research. *New  
444 Phytologist* 203:1021–1024.
- 445 Wright, I. J., M. Westoby, P. B. Reich, J. Oleksyn, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-  
446 Bares, T. Chapin, J. H. C. Cornellissen, M. Diemer, J. Flexas, J. Gulias, E. Garnier, M. L. Navas,  
447 C. Roumet, P. K. Groom, B. B. Lamont, K. Hikosaka, T. Lee, W. Lee, C. Lusk, J. J. Midgley,  
448 Ü. Niinemets, H. Osada, H. Poorter, P. Pool, E. J. Veneklaas, L. Prior, V. I. Pyankov, S. C. Thomas,  
449 M. G. Tjoelker, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.

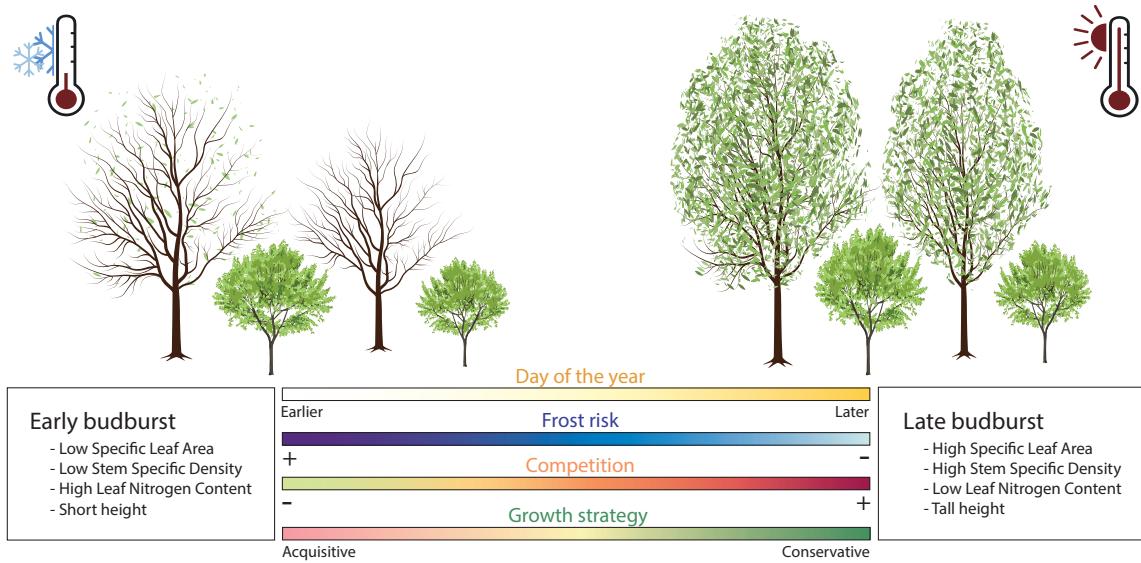


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost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

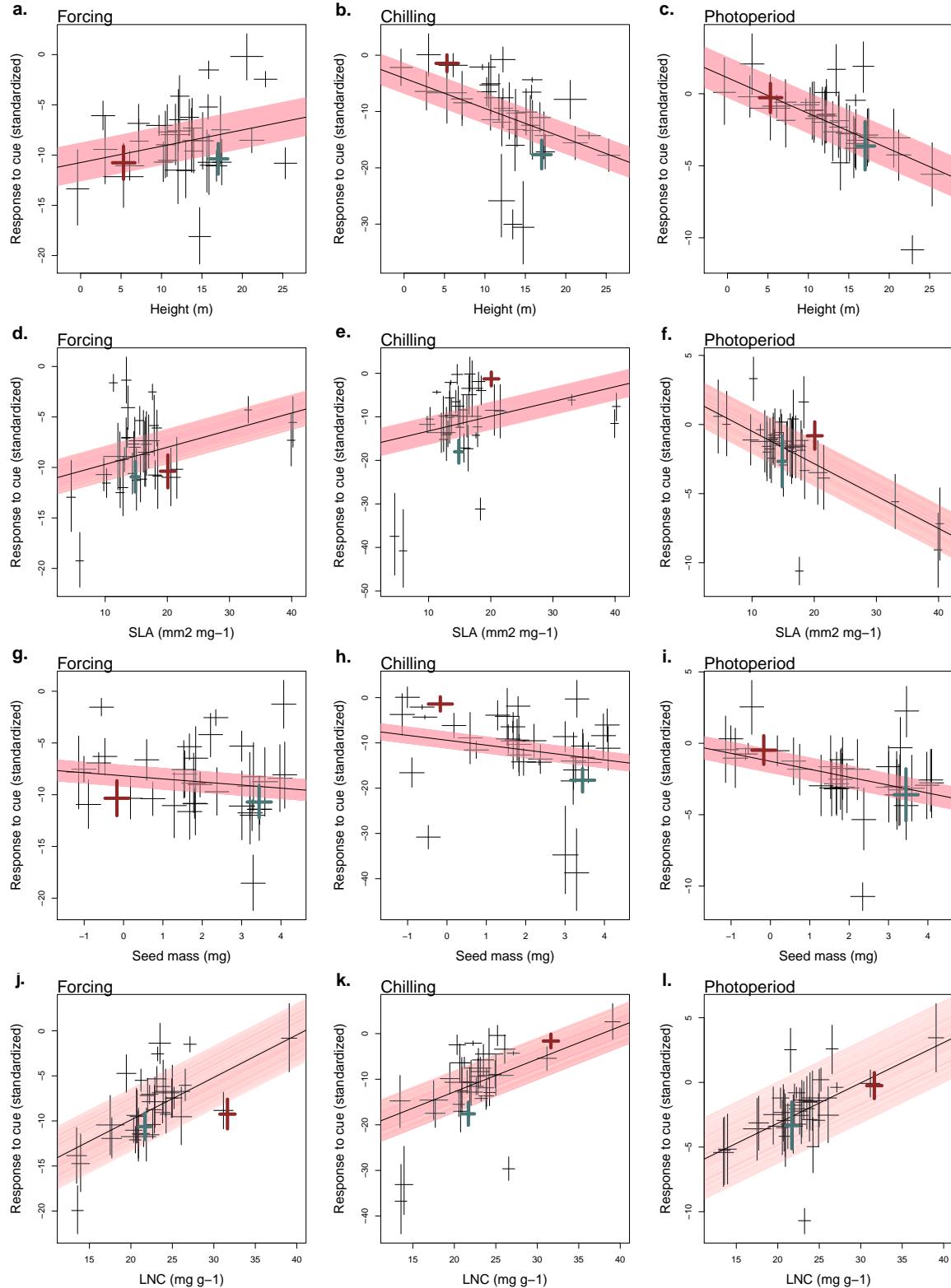


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third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

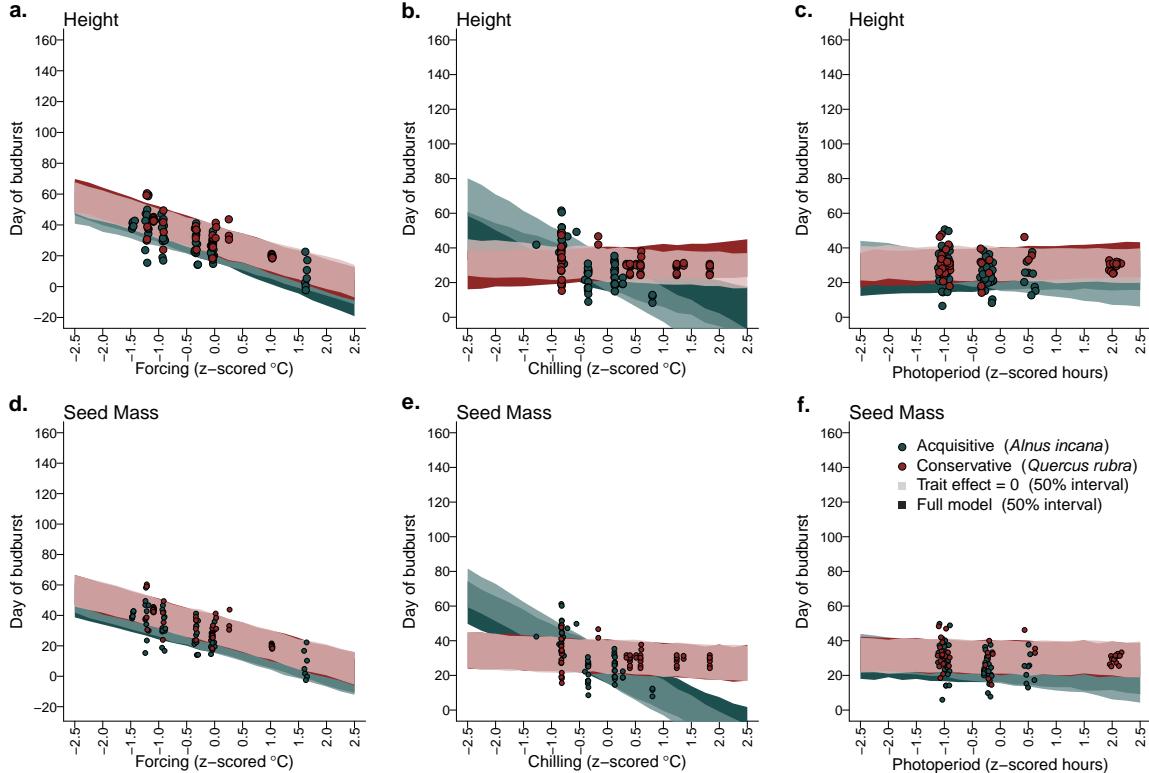


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with 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. Band represent the 50% uncertainty intervals of the model estimates. The coloured bands represent the 50% uncertainty intervals of the model estimates and points individual trait measurements.

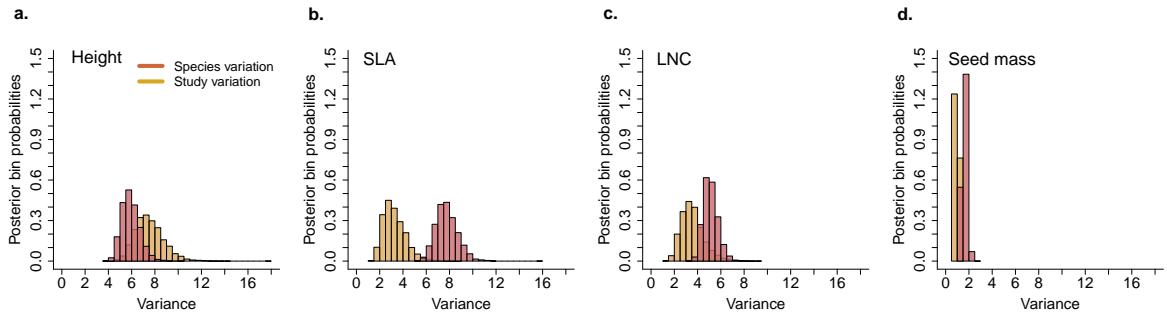


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation, with only a. the height model estimating greater study-level variation than species-level, while our b. specific leaf area, c. leaf nitrogen content, and d. seed mass models all estimated higher species-level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