

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

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<sup>30</sup> Running title: Budburst responses associated with traits

<sup>31</sup> **Summary**

- <sup>32</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 in phenology 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>42</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>45</sup> 3. We found that earlier species (which have smaller responses to all cues) are shorter with denser, lower nitrogen leaves, while later-active species (which have larger responses to chilling and photoperiod) 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>49</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.

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<sup>53</sup> Key Words: Budburst, spring phenology, traits, trees, climate change, forest communities

<sup>54</sup> **Introduction**

<sup>55</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

59 et al., 2021) have thus led to growing concerns over their possible impacts.

60

61 Predicting these changes requires understanding the drivers of phenology both at a proximate scale—  
62 the environmental triggers of phenology each year, such as temperature and daylength—and at an  
63 ultimate scale, where long-term environmental pressures may select for different phenologies across  
64 species, (e.g., certain species are early or late relative to other species each year Ovaskainen et al.,  
65 2013; Wolkovich and Donahue, 2021). At the proximate level, environmental conditions throughout  
66 the winter and spring cause species to start growth at different times. Similar environmental conditions  
67 appear to trigger spring phenological events across taxa, including the start of growth in woody plants  
68 each year (Flynn and Wolkovich, 2018; Laube et al., 2014), the timing of egg laying in birds (Crick  
69 et al., 1997; D’Alba et al., 2010), and the advance of spawning in amphibians (Kusano and Inoue,  
70 2008; Tryjanowski et al., 2003), but current work provides limited insights into the drivers of species  
71 differences (Chuine et al., 2016; Flynn and Wolkovich, 2018; Laube et al., 2014).

72

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

81

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

89

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

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

101

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

109

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

122

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

<sup>129</sup> a step towards predicting variation via species traits instead of species identity (when traits explain  
<sup>130</sup> a significant portion of the variation, species identity will explain only a small amount), which could  
<sup>131</sup> help forecast species phenological responses based on trait values alone.

<sup>132</sup>

## <sup>133</sup> Methods

<sup>134</sup> We merged three major databases for our analysis. We gathered phenological data from the OSPREE  
<sup>135</sup> database (Ettinger et al., 2020), which contains budburst data for woody, species from experiments of  
<sup>136</sup> forcing, chilling and photoperiod. This database was constructed by performing a systematic review  
<sup>137</sup> of the literature, using the following two search terms to search both ISI Web of Science and Google  
<sup>138</sup> Scholar:

<sup>139</sup>

- <sup>140</sup> 1. TOPIC = (budburst OR leafout) AND (photoperiod or daylength) AND temperature\*
- <sup>141</sup> 2. TOPIC = (budburst OR leafout) AND dorman\*

<sup>142</sup>

<sup>143</sup> Data was scraped all articles of woody species that experimentally manipulated both photoperiod  
<sup>144</sup> and/or temperature cues of budburst, leafout, or flowering phenology, with a quantifiable response to  
<sup>145</sup> each cue. We updated this database in July 2019 reviewing all new articles found using the previous  
<sup>146</sup> search terms. Additional details on the methods used to assemble, clean, and update this database are  
<sup>147</sup> discussed by Ettinger et al. (2020) and Morales-Castilla et al. (2024). For the purpose of this study,  
<sup>148</sup> we used a subset of the OSPREE database, using data only for budburst phenology and for the subset  
<sup>149</sup> of 234 species used in Morales-Castilla et al. (2024).

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<sup>151</sup> We gathered trait data from TRY and BIEN (v. 4.0) (Kattge et al., 2020; Maitner et al., 2018), both  
<sup>152</sup> of which are large trait databases that include plant trait data across many individuals, species, and  
<sup>153</sup> studies (Table S1). We obtained data from both databases on 5 December, 2018, and requested an  
<sup>154</sup> updated version of the TRY data obtained 10 April, 2019. We again focused our search for trait data  
<sup>155</sup> on the subset of 234 OSPREE species used in Morales-Castilla et al. (2024). Using the BIEN R package  
<sup>156</sup> (v. 1.2.5) (Maitner et al., 2018), we downloaded all available trait data for the 94 species available,  
<sup>157</sup> for which there were 13 unique traits. The TRY database included data for 10 unique traits for 96 of  
<sup>158</sup> our focal species (Kattge et al., 2020). Given our focus on the phenology of adult trees, we susbet the  
<sup>159</sup> available data to only includ traits measured from adult individuals with a minimum height of 1.38  
<sup>160</sup> m. We further removed all data from manipulative experiments or from plants growing in non-natural  
<sup>161</sup> habitats. We also grouped trait values where appropriate, for example pooling trait values for specific

162 leaf area (SLA) with those denoted as “SLA with petioles”, and “SLA without petioles” in our analysis  
163 (see Table S1). Duplicated data in both the TRY and BIEN datasets were also removed ( $n = 434905$ ).

164

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

179

## 180 Joint model of trait and phenology

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

## 190 Trait sub-model

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

<sup>194</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>195</sup> where  $\alpha_{\text{species}_i}$  and  $\alpha_{\text{study}_j}$  are elements of the normal random vectors:

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

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

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

<sup>196</sup> The latent parameter or overall mean trait value,  $\alpha_{\text{grand trait}}$  represents a trait value that is independent  
<sup>197</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>198</sup> is the measurement error, and  $\sigma_{\text{species}}^2$  and  $\sigma_{\text{study}}^2$  represent species and study-level variances in trait  
<sup>199</sup> values. Of these parameters, the  $\boldsymbol{\alpha}_{\text{trait}}$  are shared by the phenology sub-model.

## <sup>200</sup> Phenology sub-model

<sup>201</sup> The phenology sub-model describes the processes that determine the relationships between traits and  
<sup>202</sup> environment cues and their effects on phenological observations for 1 to  $n$  species, specifically the  
<sup>203</sup> timing (day of year) of budburst from the updated OSPREE dataset. We assume that an observation  
<sup>204</sup> of budburst for species  $k$  under  $g$  treatments levels of chilling, forcing, and photoperiod ( $c_g, f_g, p_g$ ),  
<sup>205</sup> parameter  $Y_{\text{pheno}_{k,g}}$  representing the observed day of budburst (which we  $z$ -scored to allow direct  
<sup>206</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

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

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

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

207 where  $\alpha_{\text{pheno}_k}$ ,  $\alpha_{\text{chilling}_k}$ ,  $\alpha_{\text{forcing}_k}$ , and  $\alpha_{\text{photoperiod}_k}$  are elements of the normal random vectors:

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

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

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

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

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

217

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

## 224 Results

225 Across traits, height, SLA, and LNC strongly related to chilling ( $\beta_{\text{chilling}_k}$ ), forcing ( $\beta_{\text{forcing}_k}$ ), and  
226 photoperiod ( $\beta_{\text{photoperiod}_k}$ ) treatments, Fig 2 a-f & j-l), but the direction of these relationships only

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

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

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We found species-level variation across traits ( $\sigma_{\text{trait}}^2$ ) were comparable to or greater than variation across studies ( $\sigma_{\text{study}}^2$ , Fig 4). The magnitude of study-level variation ( $\sigma_{\text{study}}^2$ ) that we found, however, suggests that models using large trait databases that fail to separate out study from species-level variation ( $\sigma_{\text{trait}}^2$ ) may poorly estimate species traits. Variation across studies was greatest 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-level variation was less than that of the species-level variation, with estimates of 1 mg for study-level variation versus 1.6 mg for species-level variation in seed mass and estimates of 3.6 mg g<sup>-1</sup> for study-level variation 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 variation in SLA was approximately half the value of the species-level variation (3.3 mm<sup>2</sup> 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).

258

<sup>259</sup> **Discussion**

<sup>260</sup> We found species traits influenced the timing of budburst in response to the three primary cues of  
<sup>261</sup> spring phenology: chilling, forcing and photoperiod. These trait effects were associated with earlier or  
<sup>262</sup> later phenology following well-established gradients in growth strategies predicted by functional trait  
<sup>263</sup> frameworks (Chave et al., 2009; Díaz et al., 2016; Westoby, 1998; Westoby and Wright, 2006; Wright  
<sup>264</sup> et al., 2004): early species tended to have traits associated with fast and acquisitive strategies while  
<sup>265</sup> later species had traits associated with conservative, slower strategies. We found the largest bud-  
<sup>266</sup> burst responses occurred for traits related to resource acquisition and structure, with SLA, LNC, and  
<sup>267</sup> height all showing large responses across our three cues. In contrast, our one reproductive trait—seed  
<sup>268</sup> mass—showed a smaller response. Our results provide a major step forward in integrating phenology  
<sup>269</sup> into broader trait syndromes that shape species growth strategies, and support previous findings from  
<sup>270</sup> more local scales that found strong relationships between height and species phenology (Segrestin et al.,  
<sup>271</sup> 2020; Sporbert et al., 2022; Sun and Frelich, 2011). Our more global analysis is also in agreement with  
<sup>272</sup> previous studies of plant phenological events, in which no relation is found between phenology and  
<sup>273</sup> seed mass in woody plants (Bolmgren and Cowan, 2008; Ettinger et al., 2018).

<sup>274</sup>

<sup>275</sup> **Effects of phenology-trait relationships on community assembly**

<sup>276</sup> Our findings suggest the changing pressures across the early growing season may affect the temporal  
<sup>277</sup> assembly of communities. Strong abiotic pressures alongside weak competition early in the season were  
<sup>278</sup> associated with early-budbursting species with acquisitive traits (shorter heights and low LNC) that  
<sup>279</sup> allow faster return on resource investments (Chave et al., 2009; Grime, 1977; Westoby, 1998). These  
<sup>280</sup> traits should allow early species to more easily replace tissue if lost to frost or other abiotic distur-  
<sup>281</sup> bances, and benefit from greater light availability in the open canopy of many temperate forests in  
<sup>282</sup> the early spring. In contrast, later-budbursting species had traits associated with greater competitive  
<sup>283</sup> abilities and slower growth (Chave et al., 2009; Grime, 1977; Westoby, 1998) (Fig 2), which may help  
<sup>284</sup> them compete for soil and light resources when most other species are already growing. These traits  
<sup>285</sup> can be linked to other ecological processes and species characteristics, such as species successional po-  
<sup>286</sup> sition, as illustrated by the differences between early and late successional species (e.g., *Alnus incana*  
<sup>287</sup> and *Quercus rubra*; Fig 2).

<sup>288</sup>

<sup>289</sup> The traits with cue responses that deviated from our expectations also offer novel insights into the  
<sup>290</sup> tradeoffs between traits and environmental cues. All of our traits are associated with multiple aspects  
<sup>291</sup> of species growth, and may be adaptive for reasons other than those we predicted. Contrary to our

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

300

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

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

307

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

315

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

323

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

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

334

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## 338 **Author Contributions Statement**

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

## 343 **Competing Interests Statement**

344 The authors declare no competing interests.

## 345 **Data availability statement**

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

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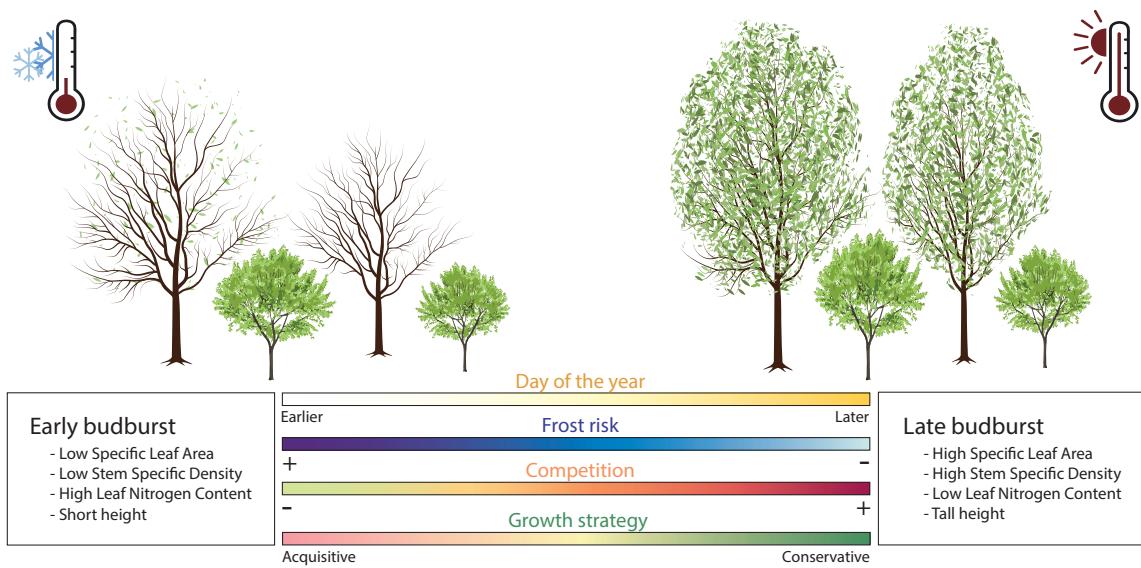


Figure 1: Leaf and wood traits follow a gradient that varies from acquisitive versus conservative growth strategies, which may also include phenology. We predicted early-budbursting species would have traits associated with acquisitive growth, as they are more likely to experience greater risk of frost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

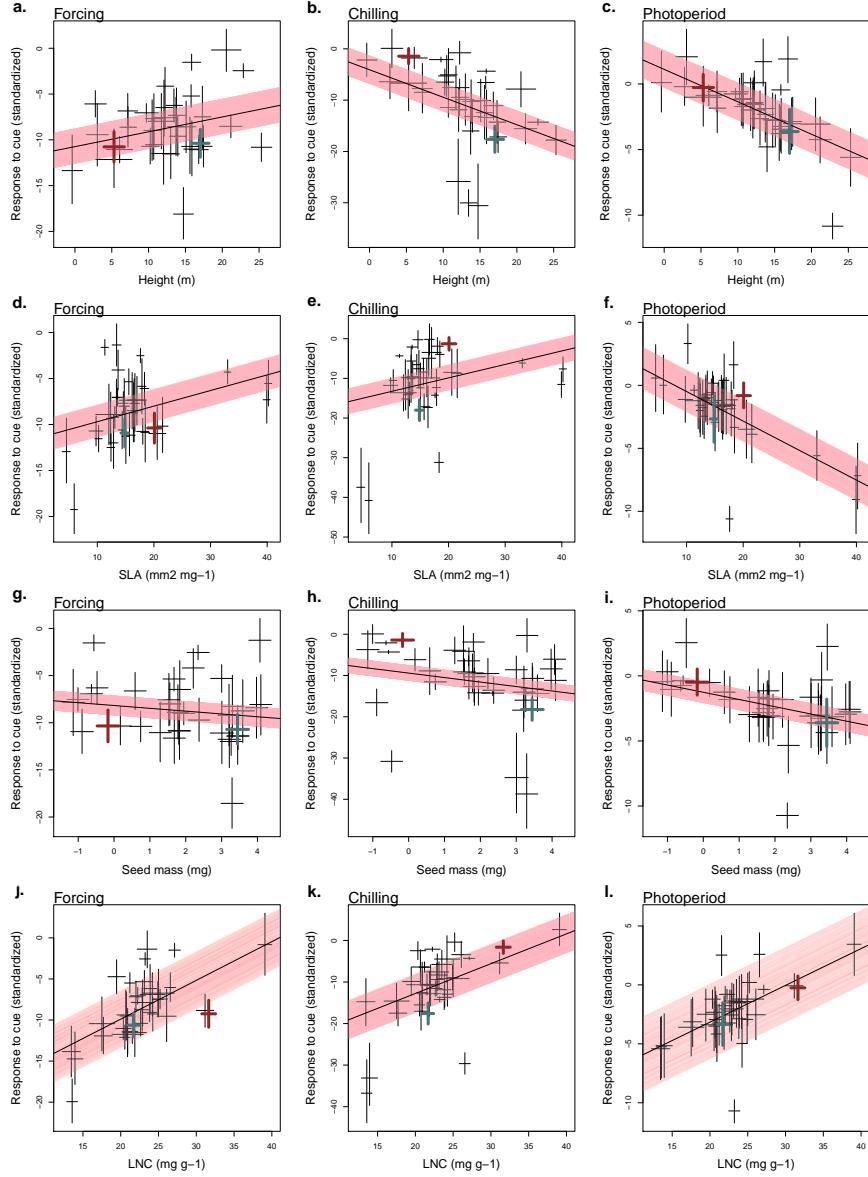


Figure 2: Estimated species-level responses to standardized forcing (left column: a, d, g & j), chilling (middle column: b, e, h & k), and photoperiod treatments (right column: c, f, i & l) predicted by estimated trait values for height (first row: a-c), SLA (second row: d-f), log10 Seed mass (third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

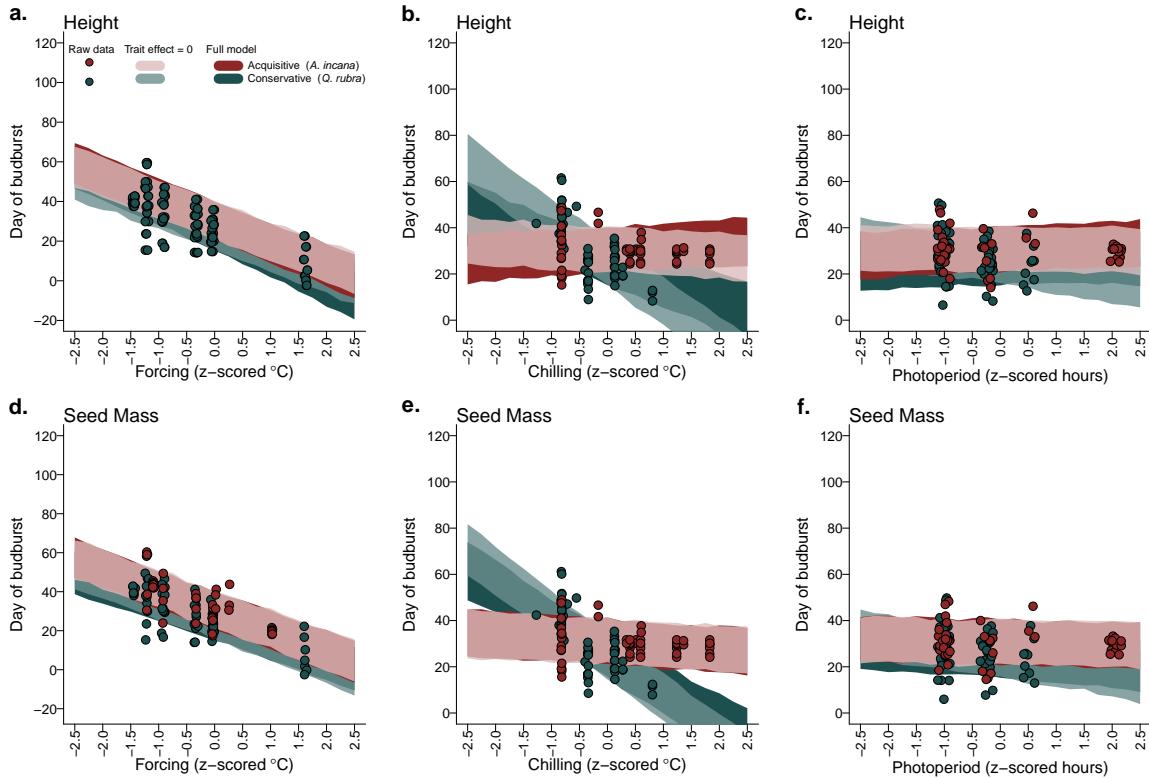


Figure 3: We expected species with traits associated with acquisitive (e.g., smaller heights and small seed mass) versus conservative (e.g., taller with larger seeds) growth strategies would have different budburst responses to phenological cues. Shown here is an example of the cue relationships with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

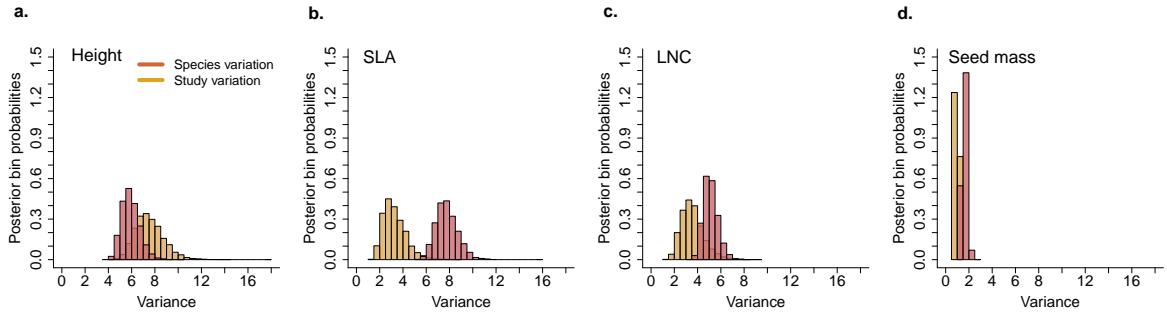


Figure 4: Traits differed in the relative magnitude of their species-level and study-level variation

( $\sigma_{\text{species}}^2$  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.