

<sup>1</sup> Traits predict forest phenological responses to photoperiod  
<sup>2</sup> more than temperature

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<sup>4</sup> January 10, 2026

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<sup>13</sup> Running title: Traits drive photoperiod cues in budburst

<sup>14</sup> **Summary**

<sup>15</sup> As the timing of plant life cycle events—phenology—has shifted with climate change, there is growing  
<sup>16</sup> interest to incorporate phenology within plant strategies has received growing interest as phenology  
<sup>17</sup> has shifted with climate change. But integrating phenology into to existing spectra (like the leaf  
<sup>18</sup> economic spectrum and wood economic spectrum) that consider traits across species has been slow in  
<sup>19</sup> part because of high trait variation within-species, which is especially high for phenology. Addressing  
<sup>20</sup> this requires data on many traits across space and better estimates of phenology, which is less variable  
<sup>21</sup> when determined through experiments that can be used to decompose its environmental drivers (such  
<sup>22</sup> as chilling and forcing temperatures or photoperiod). Here, working across eight forest communities to  
<sup>23</sup> collect *in situ* trait measurements from 1428 individuals of 47 species, we find phenology connects to  
<sup>24</sup> four major plant functional traits (height, diameter, leaf mass area and nitrogen content) via responses  
<sup>25</sup> to photoperiod, but not temperature. These results provide insight into the complexity of phenology-  
<sup>26</sup> trait relationships in relation to cues, as well as novel support for the inclusion of phenology in studies  
<sup>27</sup> of woody plant growth to accurately forecasts changes in species growth with climate change.

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

<sup>29</sup> Climate change is causing species phenologies—the timing of life history events—to shift, with widespread  
<sup>30</sup> advances being observed across the tree of life (Parmesan and Yohe, 2003; Hoegh-Guldberg et al., 2018).  
<sup>31</sup> This common phenological fingerprint, however, averages over high variability across species (Thack-  
<sup>32</sup> eray et al., 2016; Cohen et al., 2018; Kharouba et al., 2018), posing a challenge to accurate forecasts.

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39 In plants, species variation can be explained, in part, by differences in growth strategies, which are generally inferred from traits (Violle et al., 2007). Decades of research on plant traits have worked to build  
40 predictive models of species responses to their environment (Green et al., 2022), which could explain  
41 species-level variability in phenological responses. Phenology, however, has generally been excluded from  
42 plant trait research due to its high inter- and intra-specific variability, making it difficult to leverage  
43 existing frameworks to explain phenological variation and predictions future changes. Previous studies  
44 have found high variation in phenology in observational studies—even for the same species when ob-  
45 served over different years or sites (Primack et al., 2009; Chuine et al., 2010), but variation is usually  
46 much smaller when calculated from controlled experiments, which suggest that phenological variation  
47 can be consistently decomposed into its environmental cues (e.g., temperature and photoperiod Chuine  
48 and Cour, 1999; Harrington and Gould, 2015; Flynn and Wolkovich, 2018).

50  
51 Correlations between plant traits, growth strategies, and responses to environments have been synthe-  
52 sized into several global frameworks, including the leaf economic spectrum (Wright et al., 2004) and  
53 wood economic spectrum (Chave et al., 2009). These frameworks have identified key traits that ex-  
54 hibit distinct gradients, ranging from acquisitive strategies—fast growing plants that produce cheaper  
55 tissue—to conservative strategies—with plants that invest in long-lived tissue but slower growth rates  
56 (Wright et al., 2004; Díaz et al., 2016). In temperate systems, changes in temperature and frost risk in  
57 spring can produce gradients in abiotic stress, including frost risk, soil nutrients, and light availability  
58 (Sakai and Larcher, 1987; Gotelli and Graves, 1996; Augspurger, 2009), in addition to differences in  
59 biotic interactions from herbivory or competition later in the season (Lopez et al., 2008; Wolkovich  
60 and Ettinger, 2014). Species that vary in their timing of leafout, should therefore exhibit traits and  
61 growth strategies that allow them to tolerate or avoid these abiotic and biotic factors. Leveraging in-  
62 sights from predictive models of phenology with these well established trait frameworks could begin to  
63 disentangle the environmental cues that shape phenology from those shaped by other trait differences  
64 in plant growth strategies.

65  
66 To determine whether phenology fits within major functional trait frameworks requires working across  
67 within- and between-species variation. Phenological variation is generally observed in natural condi-  
68 tions where the environmental cues that trigger many phenological events—primarily temperature and  
69 photoperiod (Chuine, 2000; Körner and Basler, 2010)—vary across space and time. But experiments  
70 that control for this variation generally find smaller effects across space (Basler and Körner, 2014;  
71 Vitasse et al., 2009). Within-species variation also occurs across other plant traits (e.g., leaf and wood  
72 structure traits), including across latitudinal (Wiemann and Bruce, 2002) and other environmental  
73 gradients (Pollock et al., 2012), though generally to a smaller scale compared to phenology. To better  
74 understand how phenology and other traits correlate across species will require methods that incorpo-  
75 rate spatial variation within species.

76  
77 Here, we tested whether phenological variation was aligned with existing trait frameworks using data on  
78 spring budburst paired and a suite of traits that capture acquisitive to conservative growth strategies.  
79 We decompose the high phenological variation in budburst date by using experiments to estimate  
80 three major phenological cues for woody plant budburst: chilling (cool winter temperatures), forcing  
81 (warm spring temperatures), and photoperiod. We predict that early spring species will budburst  
82 before canopy closure, exhibited as smaller responses to temperature and photoperiod. These species  
83 should have traits associated with acquisitive growth, particularly shorter heights, smaller trunk or  
84 stem diameters, with lower investment in wood structure and leaf tissue, resulting in low wood specific  
85 density, diffuse-porous wood anatomy, and low leaf mass area, but high leaf nitrogen content for a  
86 greater photosynthetic potential. In contrast, we predict species with later budburst to predominately  
87 include canopy species that express more conservative growth strategies and require more chilling,  
88 warmer forcing, and longer photoperiods. These species should incur greater investments in long-lived  
89 tissue, with ring-porous wood anatomy, taller heights and greater diameter, denser wood and high  
90 leaf mass area, but low leaf nitrogen content. We then used a joint-modeling approach to estimate

91 the relationships between these plant traits and phenological responses to cues, while partitioning the  
92 variance from species- and population-level differences.

## 93 Materials and Methods

### 94 Field sampling

95 We combined *in situ* trait data with budburst data from two growth chamber cutting experiments  
96 conducted across eastern and western temperate deciduous forests in North America. We collected  
97 both suites of data from populations that span a latitudinal gradient of 4-6° for the eastern and  
98 western communities respectively. We took trait measurements from across eight populations, of  
99 which there were four eastern populations—Harvard Forest, Massachusetts, USA (42.55°N, 72.20°W),  
100 White Mountains, New Hampshire, USA (44.11°N, 52.14°W), Second College Grant, New Hampshire,  
101 USA (44.79°N, 50.66°W), and St. Hippolyte, Quebec, Canada (45.98°N, 74.01°W), and four western  
102 population—E.C. Manning Park (49.06°N, 120.78°W), Sun Peaks (50.88°N, 119.89°W), Alex Fraser  
103 Research Forest (52.14°N, 122.14°W), and Smithers (54.78°N, 127.17°W), British Columbia (BC),  
104 Canada (Fig. 1). For the two growth chamber studies on budburst phenology, we collected cuttings  
105 from the most southern and northern populations in each transect ( $n_{pop}=4$ ).  
106

### 107 Functional traits

108 We measured all traits in the summer prior to each growth chamber study (eastern transect: 8-25 June  
109 2015, western transect: 29 May to 30 July 2019), following full leafout but before budset. At each  
110 population and for each species, we measured a total of five traits from 1-10 healthy adult individuals:  
111 height, diameter of the main trunk or stem (hereafter referred to as diameter), wood specific density,  
112 leaf mass area, and the percent leaf nitrogen content. We also obtained xylem structure data from the  
113 WSL xylem database (Schweingruber and Landolt, 2010) for 72.3% of our species.  
114

115 We measured traits in accordance to the methods discussed by Pérez-Harguindeguy et al. (2013).  
116 We calculated tree height using trigonometric methods and used a base height of 1.37 m to measure  
117 diameter (Magarik et al., 2020). For shrub heights, we measured the distance from the ground to the  
118 height of the top foliage and measured stem diameters at approximately 1 cm above ground-level. All  
119 stem and leaf samples were kept cool during transport and measurements of leaf area and stem volume  
120 taken within 3 and 12 hours of sample collection respectively. To measure wood specific density, we  
121 collected a 10 cm sample of branch wood, taken close to the base of the branch at the stem and  
122 calculated stem volume using the water displacement method. For our leaf traits, we haphazardly  
123 selected and sampled five, fully expanded, and hardened leaves, with no to minimal herbivore damage.  
124 We took a high resolution scan of each leaf using a flatbed scanner and estimated leaf area using the  
125 ImageJ software (version 2.0.0).

### 126 Growth chamber study

127 For our growth chamber studies, we collected branch cuttings from our highest and lowest latitude  
128 populations in each transect, with sampling in our eastern study occurring from 20-28 January 2015  
129 and sampling for our western study from 19-28 October 2019. In using cuttings from dormant branches,  
130 we are able to experimentally manipulate environmental cues while still approximating whole plant  
131 responses in budburst (Vitasse and Basler, 2014). In both studies, we included a total of eight distinct  
132 treatments consisting of two levels of chilling, forcing, and photoperiods (Fig. 1). We recorded bud-  
133 burst stages of each sample every 1-3 days for up to four months, defining the day of budburst as the  
134 day of budbreak or shoot elongation (denoted as code 07 by Finn et al. (2007)). For a more detailed  
135 discussion of study sample collection and methods see Flynn and Wolkovich (2018) for details on our

136 eastern study and Loughnan and Wolkovich (in prep) for details on our western study.

137

## 138 Statistical Analysis

139 Our analysis combined our *in situ* trait data with budburst data from the controlled environment. For  
140 each trait, we developed a joint Bayesian model, in which the relationship between traits and cues  
141 is used to estimate budburst. This statistical approach improves upon previous analyses of multiple  
142 traits, as it allows us to carry through uncertainty between trait and phenology data—and better  
143 partitions the drivers of variation in species phenologies

144

145 Our joint model consists of two parts. The first is a hierarchical linear model, which partitions the vari-  
146 ation of individual observations ( $i$ ) of a given trait value ( $Y_{\text{trait}}$ ) to account for the effects of species  
147 ( $j$ ), population-level differences arising from transects, latitude, as well as the interaction between  
148 transects and latitude ( $\text{transect} \cdot \text{latitude}$ ), and finally, residual variation or ‘measurement error’ ( $\sigma_m^2$ ).  
149

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

$$\mu_{i,j} = \alpha_{\text{grand trait}} + \alpha_{\text{trait}_j} + \beta_{\text{transect}} \times \text{transect} + \quad (2)$$

$$\beta_{\text{latitude}} \times \text{latitude} + \beta_{\text{transect} \cdot \text{latitude}} \times (\text{transect} \cdot \text{latitude}) \quad (3)$$

(4)

150

$$\boldsymbol{\alpha}_{\text{trait}} \begin{bmatrix} \alpha_{\text{trait}_1} \\ \alpha_{\text{trait}_2} \\ \dots \\ \alpha_{\text{trait}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{trait}} \sim \text{Normal}(0, \sigma_{\text{trait}}^2) \quad (5)$$

(6)

151 We include transect as a dummy variable (0/1) and latitude as a continuous variable in our model.  
152 We modeled traits using their original units, with the exception of leaf mass area which was rescaled  
153 by 100 and wood specific density which was rescaled by 10 for numeric stability in the model. Our  
154 model also includes partial pooling for species—which controls for variation in the number of trait  
155 estimates per species and trait variability—using these species-level estimates as predictors for each  
156 cue ( $\beta_{\text{chilling},j}$ ,  $\beta_{\text{forcing},j}$ ,  $\beta_{\text{photoperiod},j}$ ).  
157

$$\beta_{\text{chilling},j} = \alpha_{\text{chilling},j} + \beta_{\text{trait.chilling}} \times \alpha_{\text{trait},j} \quad (7)$$

$$\beta_{\text{forcing},j} = \alpha_{\text{forcing},j} + \beta_{\text{trait.forcing}} \times \alpha_{\text{trait},j}$$

$$\beta_{\text{photoperiod},j} = \alpha_{\text{photoperiod},j} + \beta_{\text{trait.photoperiod}} \times \alpha_{\text{trait},j}$$

158 In addition to the species-level estimates, the second part of our model estimates the overall effect of  
159 each trait on each cue ( $\beta_{\text{trait.chilling}}$ ,  $\beta_{\text{trait.forcing}}$ ,  $\beta_{\text{trait.photoperiod}}$ ). From this we can estimate how well  
160 traits explain species-level differences—by estimating the the species-level cue variation not explained  
161 by traits ( $\alpha_{\text{chilling},j}$ ,  $\alpha_{\text{forcing},j}$ ,  $\alpha_{\text{photoperiod},j}$ ) and individual species responses to cues (*chilling*, *forcing*,  
162 *photoperiod*, respectively). Finally, our model estimates the residual budburst variation across species  
163 ( $Y_{\text{pheno},j}$ ), observations ( $\sigma_d^2$ ), as well as the variation in cues not attributed to the trait (using partial  
164 pooling).

$$Y_{\text{pheno}_{i,j}} \sim \mathcal{N}(\mu_{i,j}, \sigma_d^2) \quad (8)$$

<sup>165</sup> with

$$\mu_{i,j} = \alpha_{\text{pheno}_j} + \beta_{\text{chilling}_j} \cdot \text{chilling} + \beta_{\text{forcing}_j} \cdot \text{forcing} + \beta_{\text{photoperiod}_j} \cdot \text{photoperiod} \quad (9)$$

<sup>166</sup> where  $\alpha_{\text{pheno}_j}$ ,  $\alpha_{\text{chilling}_j}$ ,  $\alpha_{\text{forcing}_j}$ , and  $\alpha_{\text{photoperiod}_j}$  are elements of the normal random vectors:

$$\boldsymbol{\alpha}_{\text{pheno}} = \begin{bmatrix} \alpha_{\text{pheno}_1} \\ \alpha_{\text{pheno}_2} \\ \dots \\ \alpha_{\text{pheno}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \text{Normal}(\mu_{\text{pheno}}, \sigma_{\text{pheno}}^2) \quad (10)$$

$$\boldsymbol{\alpha}_{\text{chilling}} = \begin{bmatrix} \alpha_{\text{chilling}_1} \\ \alpha_{\text{chilling}_2} \\ \dots \\ \alpha_{\text{chilling}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{chilling}} \sim \text{Normal}(\mu_{\text{chilling}}, \sigma_{\text{chilling}}^2) \quad (11)$$

$$\boldsymbol{\alpha}_{\text{forcing}} = \begin{bmatrix} \alpha_{\text{forcing}_1} \\ \alpha_{\text{forcing}_2} \\ \dots \\ \alpha_{\text{forcing}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{forcing}} \sim \text{Normal}(\mu_{\text{forcing}}, \sigma_{\text{forcing}}^2) \quad (12)$$

$$\boldsymbol{\alpha}_{\text{photoperiod}} = \begin{bmatrix} \alpha_{\text{photoperiod}_1} \\ \alpha_{\text{photoperiod}_2} \\ \dots \\ \alpha_{\text{photoperiod}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{photoperiod}} \sim \text{Normal}(\mu_{\text{photoperiod}}, \sigma_{\text{photoperiod}}^2) \quad (13)$$

(14)

<sup>167</sup> We modeled each trait individually, with the exception of ring-porosity, which we compared across  
<sup>168</sup> species using the posterior estimates of our wood stem density model, allowing us to account for inher-  
<sup>169</sup> ent differences in wood anatomy across species and growth form. We included all three cues (chilling,  
<sup>170</sup> forcing, and photoperiod) as continuous variables in our model, as well as all two-way interactions  
<sup>171</sup> between cues and between cues and sites. We converted chilling temperatures to total chill portions,  
<sup>172</sup> including both the chilling experienced in the field prior to sampling and during the experiment. For  
<sup>173</sup> this we used local weather station data and the chillR package (v. 0.73.1, Luedeling, 2020). To account  
<sup>174</sup> for differences in thermoperiodicity between the two studies (Buonaiuto et al., 2023), we also converted  
<sup>175</sup> forcing temperatures to mean daily temperatures for each treatment. Finally, we z-scored each cue  
<sup>176</sup> and site using two standard deviations to allow direct comparisons between results across parameters  
<sup>177</sup> (Gelman, 2008).

<sup>178</sup>

<sup>179</sup> For each model we used trait specific priors that were weakly informative. We validated our choice  
<sup>180</sup> of priors using prior predictive checks and confirmed model stability under wider priors. All models  
<sup>181</sup> were coded in the Stan programming language for Bayesian models using the rstan package (Stan  
<sup>182</sup> Development Team, 2018) in R version 4.3.1 (R Development Core Team, 2017). All models met basic  
<sup>183</sup> diagnostic checks, including no divergences, high effective sample sizes ( $n_{eff}$ ) that exceeded 10% of  
<sup>184</sup> the number of iterations, and  $\hat{R}$  values close to 1. We report our model estimates as the mean values  
<sup>185</sup> with 90% uncertainty intervals (UI), interpreting parameter estimates with intervals that overlap to  
<sup>186</sup> be statistically similar to each other and those that include zero to have small effects.

<sup>187</sup>

188 **Results**

189 Across our eight populations, we measured 47 species of which 28 were in our eastern transect and  
190 22 in our western transect. These include species dominant in both the understory and canopy layer,  
191 with our eastern community consisting of 13 shrubs and 15 trees, our western community consisting of  
192 18 shrubs and 4 trees, and three species that occurred in both transects. In total we measured traits  
193 of 1428 unique individuals between the two transects across our five *in situ* traits: height ( $n = 1317$ ),  
194 diameter ( $n = 1220$ ), wood stem density ( $n = 1359$ ), leaf mass area ( $n = 1345$ ), leaf nitrogen con-  
195 tent ( $n = 1351$ ). Across our two growth chamber studies, we made observations of 4211 samples, with  
196 our observations of budburst spanning 82 and 113 days for our eastern and western studies respectfully.

197  
198 Most of our traits showed some variation by latitude within each transect, with a strong interactive  
199 effect between transect and latitude (Fig. 2). Leaf nitrogen content was the only trait to vary with  
200 latitude alone, with low latitude communities on both our eastern and western transects having greater  
201 values of leaf nitrogen content than communities at higher latitudes (-0.1 percent per degree latitude,  
202 UI: -0.2, 0.0, Table S6). The strongest negative interaction was observed for height, while the strongest  
203 positive interaction was observed for leaf mass area. Height and wood stem density both exhibited  
204 negative transect by latitude interactions (-0.2 m per degree latitude, UI: -0.4, 0.0 for our height model  
205 and  $-0.01 \text{ g/cm}^3$  per degree latitude, UI: -0.02, 0.0 for our wood stem density model), with woody  
206 species in our eastern communities exhibiting greater heights and wood stem densities with increasing  
207 latitude, but decreasing values with latitude in our western communities (Fig. 2 a and c). In contrast,  
208 diameter and leaf mass area both exhibited positive transect by latitude interactions (0.5 cm per degree  
209 latitude, UI: 0.1, 0.9 for our diameter model and  $0.005 \text{ g/cm}^2$  per degree latitude, UI: 0.004, 0.006  
210 for our leaf mass area model), with plants at higher latitudes having increasing diameters in both  
211 our eastern and western communities but decreasing leaf mass areas in our eastern communities and  
212 increasing values in our western communities (Fig. 2 b and d). In addition to the differences we found  
213 across populations, we also observed considerable differences between individual species, which varied  
214 considerably and up to 7 fold for some traits (Fig. 3).

215  
216 We found that three of our four traits had a strong relationship with photoperiod, but not always in  
217 the direction we predicted. Taller species with larger trunk diameters and leaves with high nitrogen  
218 content had larger responses with longer photoperiods (Fig. 3 c, i, o; Tables S2, S3, S6). But, contrary  
219 to our expectation, species with denser, high leaf mass area leaves had smaller photoperiod responses,  
220 allowing them to potentially budburst under shorter photoperiods (Fig. 3f).

221  
222 Temperature cues ( $\beta_{\text{trait.chilling}}$  and  $\beta_{\text{trait.forcing}}$ ) exhibited no relationships with individual traits, but  
223 by accounting for the effects of leaf or wood traits, we found the importance of our three cues on bud-  
224 burst to vary by trait. Of the three cues, chilling ( $\beta_{\text{chilling}}$ ) was the strongest in our models of height  
225 (-13.4 days per standardized chill portions, UI: -17.2, -9.9), diameter (-12.5 days per standardized chill  
226 portions, UI: -16.2, -8.6), wood stem density (-20.9 days per standardized chill portions, UI: -33.2,  
227 -9.8), and leaf nitrogen content (-35.1 days per standardized chill portions, UI: -68.1, -4.1), with more  
228 chilling advancing budburst. Our model of leaf mass area, however, estimated photoperiod as the  
229 strongest cue ( $\beta_{\text{photoperiod}}$ , -14.0 days per standardized photoperiod, UI: -23.1, -3.5). After accounting  
230 for the effects of traits, only our height and diameter model found all three environmental cues to drive  
231 budburst timing (Tables S2, S3). Our models of wood stem density and leaf nitrogen content in turn  
232 found temperature cues alone to shape budburst (Tables S4, S6), while our model of leaf mass area  
233 found a large response to only photoperiod (Table S5).

234  
235 In synthesizing the effects of multiple traits across species, our results can be used to make general-  
236 izations across ecologically important groups of species. But only some of our models estimated clear  
237 gradients in species timing between trees and shrubs. In particular, we found height to have large  
238 correlations between budburst timing and trait values, with earlier estimates of budburst for shrubs

(with a mean day of budburst of 10)—especially under greater cues—and later budburst estimates for trees (with a mean day of budburst of (17.3, Fig. S1). Diameter at breast height showed similar trends as estimates from our height model (results not shown). But this was not the case for our two leaf traits. Leaf nitrogen content, for example, showed no distinct separation between shrub and tree functional groups (Fig. S1).

244

## 245 Discussion

246 Using our joint modeling approach, we estimated how leaf and wood traits interact with temperature  
247 and photoperiod cues to shape species budburst. We found that photoperiod—often the weakest cue  
248 of budburst (Laube et al., 2014; Zohner et al., 2016; Flynn and Wolkovich, 2018)—was the most im-  
249 portant cue in trait-phenology relationships. In general, we also found trait patterns varied between  
250 our eastern and western transects and with latitude. These spatial differences in trait variation may be  
251 due to differences in the community assemblages, as our western community is more shrub dominated,  
252 with shorter plants with less dense branch wood. This more acquisitive growth strategy suggests these  
253 species are more likely to utilize resources early in the season prior to canopy closure. **Collectively our**  
254 **results provide new insights into the complex tradeoffs between cues and traits and how they differ**  
255 **across large spatial scales.**

256

## 257 Cues and functional traits

258 We found only partial support for our prediction that species with acquisitive traits—particularly  
259 small trees with low wood density, low leaf mass area, and high leaf nitrogen content—would have  
260 early budburst via smaller temperature and photoperiod responses. We did find species with smaller  
261 heights and diameters to have smaller photoperiod responses. But contrary to our prediction, species  
262 with less dense leaves showed larger responses to photoperiod, while leaves with high nitrogen content  
263 had stronger photoperiod responses. None of our focal traits, however, showed a relationship with tem-  
264 perature (chilling or forcing), which may be due to selection on other physiological processes. Many of  
265 our traits are associated with one or more ecological function (Wright et al., 2004; Pérez-Harguindeguy  
266 et al., 2013; Reich, 2014). In particular, leaf mass area is known to correlate with traits like leaf lifespan  
267 or decomposition rates in addition to light capture (De La Riva et al., 2016). While our results high-  
268 light the ways in which phenology partially aligns with gradients found in established trait frameworks,  
269 they also offer new insight into potential tradeoffs in how varying physiological processes shape species  
270 growth strategies.

271

272 Decades of previous phenology research have found budburst timing to be primarily driven by tem-  
273 perature (chilling and forcing) and weakly by photoperiod (Chuine et al., 2010; Basler and Körner,  
274 2014; Laube et al., 2014). But we found no other traits that correlate with responses to tempera-  
275 ture, **suggesting other cues or biotic interactions may impact** leaf and structural traits in temperate  
276 forests. Leaf mass area also varies with soil moisture, with variation in leaf area allowing plants to  
277 reduce evaporation under dry conditions, and thus selecting for high trait values (De La Riva et al.,  
278 2016). Soil moisture shapes other phenological events in woody plants, including radial growth phe-  
279 nology and shoot elongation (Cabon et al., 2020; Peters et al., 2021). If selection by soil moisture  
280 is shaping phenological responses, it may be contributing to the unexpected trends we observed in  
281 leaf traits and the absence of relationships with temperature. **To fully understand how species growth**  
282 **strategies correlate with phenology may thus require additional environmental factors to be considered.**

283

284 The absence of trait-cue relationships between budburst and wood structure and wood stem density  
285 contrasts the findings of previous work linking these traits. Previous studies have found some evidence

286 that trees with diffuse-porous wood structure leafout earlier than species with ring-porous structures  
287 (Lechowicz, 1984; Panchen et al., 2014; Yin et al., 2016; Osada, 2017; Savage et al., 2022). But,  
288 using wood density as an alternative measure of wood structure (wood density positively correlates  
289 with xylem resistance to embolism, Hacke et al., 2001), we did not find clear association between our  
290 three phenological cues and xylem structure, despite our data also including similar temperate forest  
291 species. Most of the individuals we measured, however, did have a fairly narrow range of wood specific  
292 densities (varying from 0.2 to 0.6 g/cm<sup>3</sup>) relative to the variation in wood density observed in studies  
293 that include tropical species or span a more global distribution (Galvão et al., 2021; Savage et al.,  
294 2022; Mo et al., 2024). We did find some variation in wood density across our different sites and with  
295 latitude. The larger wood densities we observed at higher latitudes in our eastern transect could be  
296 caused by the differences in winter conditions experienced by canopy versus understory species. The  
297 canopy tree species that dominate our eastern communities may experience greater horizontal stress  
298 from wind and downward pressure from snow, explaining the greater wood densities they exhibit at  
299 higher latitudes (MacFarlane and Kane, 2017; MacFarlane, 2020), while species in the shrub dominated  
300 western communities experience greater protection from being in the understory.

301

302 In addition to our study providing insight into how trait-budburst relationships vary with latitude, our  
303 sites also span North America, encompassing a gradient of 55° in longitude. At this continental scale,  
304 our data spans a large portion of the temperate forest biome of North America, which may partially  
305 explain the lack of stronger correlations between phenology and traits. While both the leaf and wood  
306 economic spectra find large variation in traits across species, the foundational studies from which they  
307 arose all used large global datasets that include both temperate and tropical species (Wright et al.,  
308 2004; Díaz et al., 2016; Chave et al., 2009) and functional groups that span from trees to grasses  
309 (Wright et al., 2004). Previous research also suggests that global patterns in trait variation are often  
310 not found at smaller spatial scales (Wright and Sutton-Grier, 2012; Messier et al., 2017a,b). This  
311 suggests that comparing trait-phenology relationships at larger spatial scales or across more diverse  
312 pools of species would better align with the patterns predicted by existing economic spectra.  
313 While our results explain trait correlations in temperate forests, they could potentially be extended to  
314 similar forest biomes Europe that experience comparable environmental conditions.

315

316 In comparing our results with a global meta-analysis of tree trait relationships with budburst cues  
317 (Loughnan et al., 2025), we found similar trait-cue relationships for height and leaf mass area. At  
318 both the global and continental scales, trees with taller heights leafed out with longer photoperiods.  
319 We also found species with high specific leaf area—which is the inverse of leaf mass area and thus  
320 equivalent to low values—exhibited large responses to photoperiod (Loughnan et al., 2025). The con-  
321 sistency of these results, despite the differences in the two spatial scales of these datasets, provides  
322 further support that alternate underlying mechanisms are shaping how woody species respond to pho-  
323 toperiod cues.

324

### 325 Functional traits predict climate change responses

326 Our results offer novel insights into how broader correlations between growth strategies and phenologi-  
327 cal cues can help predict responses in woody plant communities with climate change. As temperatures  
328 rise, particularly at higher latitudes (Hoegh-Guldberg et al., 2018), warmer winter and spring temper-  
329 atures may select for earlier budburst in some species. But, since photoperiod will remain fixed, our  
330 observed relationships between photoperiod and other traits has the potential to limit species abilities  
331 to track temperatures. This could constrain the extent to which some species growth will advance with  
332 climate change. Our results suggest that these effects will likely be greater for taller species or canopy  
333 trees and species with relatively low leaf mass area. These constraints could have cascading effects  
334 on forest communities, as variable species responses to increasing temperatures further alter species  
335 growth strategies and their interactions with competitors or herbivores within their communities.

336

337 Our findings of correlations between phenology and other commonly measured traits highlight how  
 338 accurate forecasts of future changes in phenology can benefit from accounting for the response of other  
 339 traits to climate change. Across temperature and precipitation gradients, leaf size and shape also  
 340 change, as species shift to conserve water and mitigate effects of transpiration under higher temper-  
 341 atures (De La Riva et al., 2016). These changes could impact species photosynthetic potential and  
 342 ultimately ecosystem services, such as carbon sequestration. While phenological research has focused  
 343 on forecasting responses to temperature, the correlation of other traits with photoperiod suggests it is  
 344 also an important cue. By considering the tradeoffs and differences in cues that simultaneously shape  
 345 plants growth strategies, we can more accurately forecast species phenology and community dynamics  
 346 under future climates.

347

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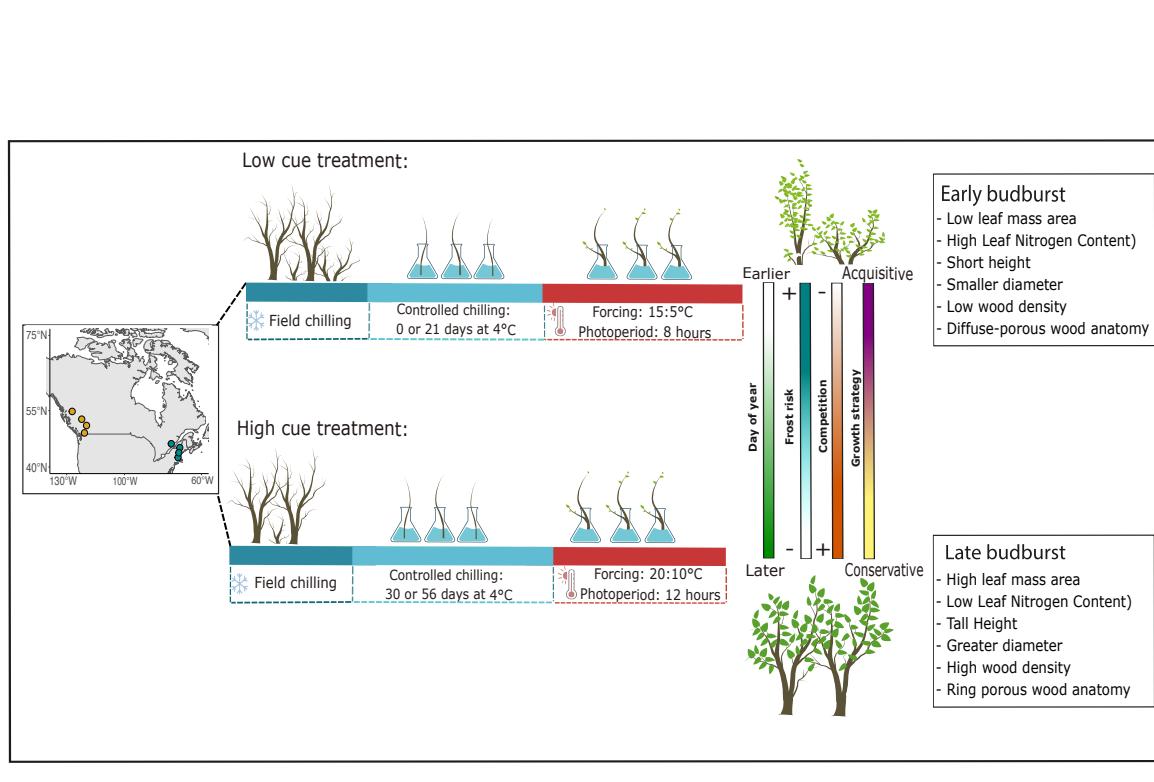


Figure 1: We collected trait data and branch cuttings from woody plants growing within eight sites, across two transects in eastern and western North America. Cuttings were used in two controlled environment studies in which we applied high and low chilling, forcing, and photoperiod treatments and recorded the day of budburst. Using our paired *in situ* trait and experimental budburst data, we tested whether earlier budbursting species exhibited traits associated with more acquisitive growth strategies and smaller responses to cues and later budbursting species a more conservative growth strategy and larger responses to cues.

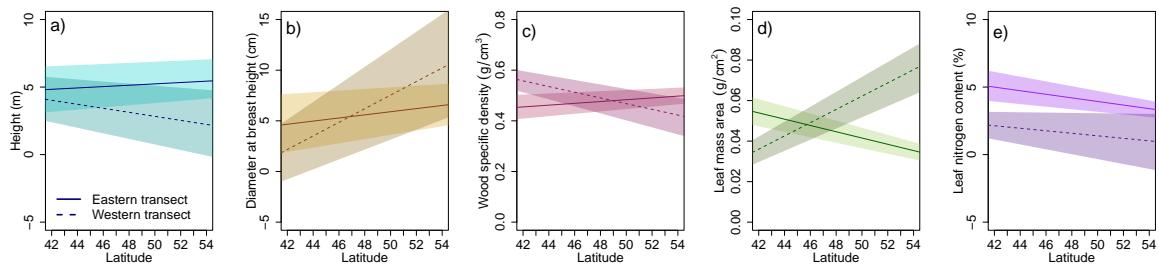


Figure 2: We found a. height, b. diameter, c. branch stem density, and d. leaf mass area to all experience a strong interaction between latitude and transect, e. while leaf nitrogen content showed a strong effect of latitude alone.

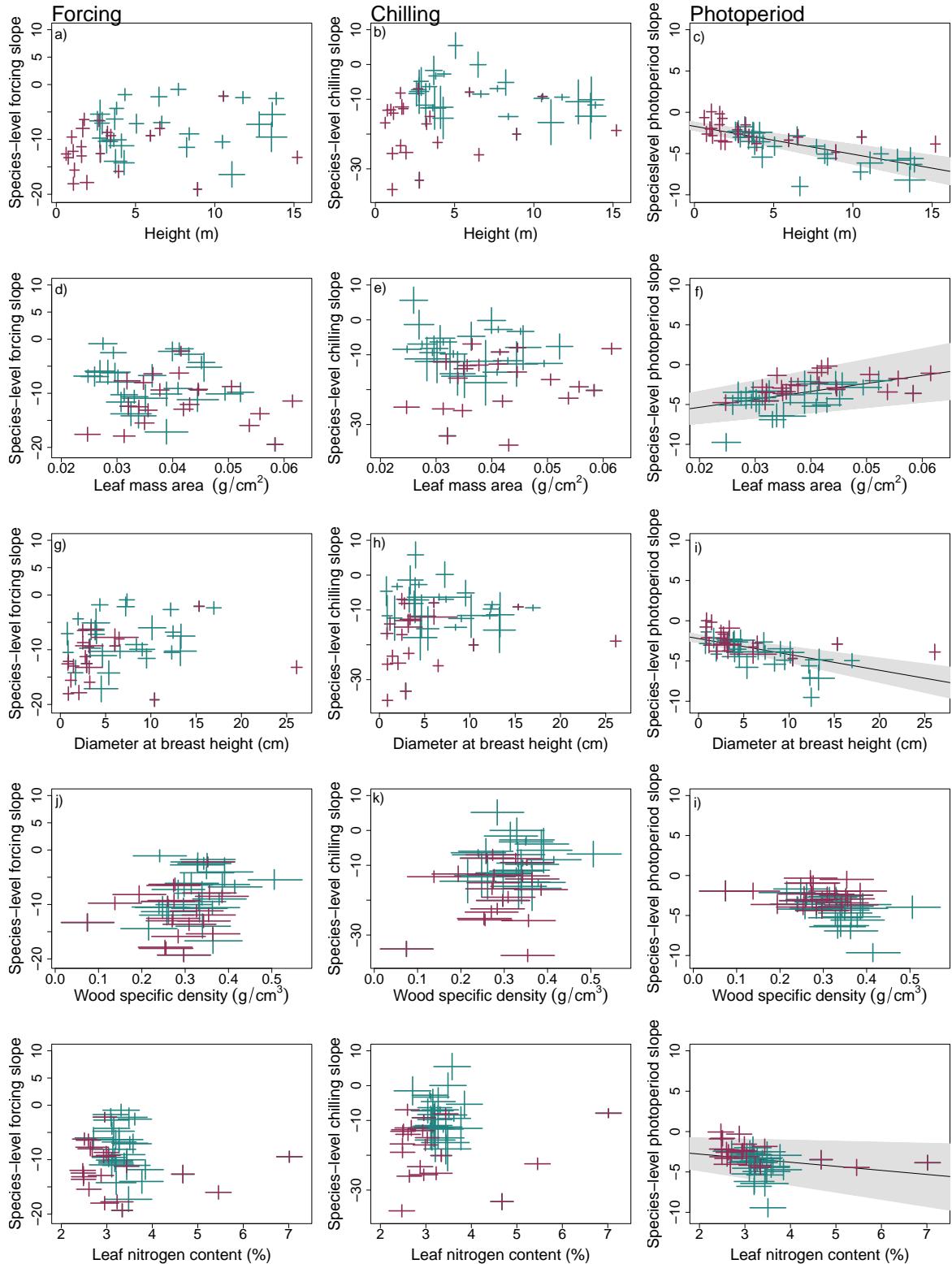


Figure 3: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species shown in red and shrub species in blue. Crosses depict the 50% uncertainty interval of the model estimates of species trait values and estimated responses to cues. Grey bands depict large relationships between a trait and cue, representing the 90% uncertainty interval, and black lines the mean response.

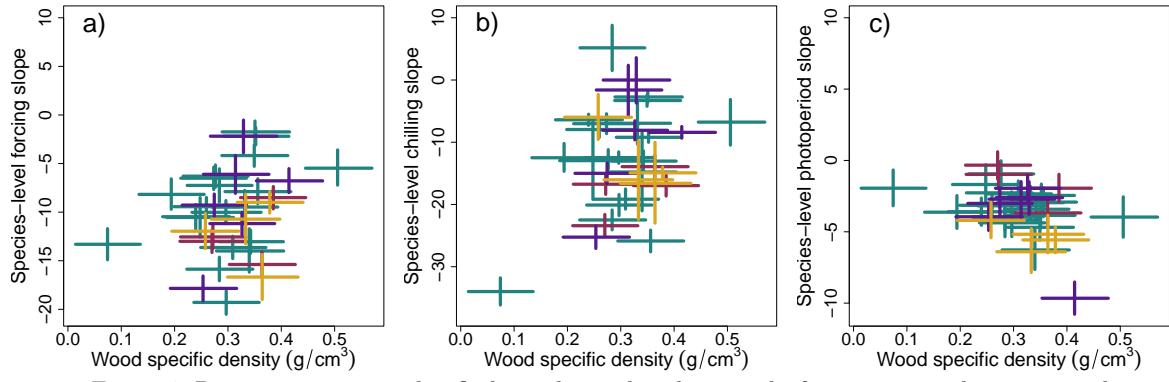


Figure 4: Despite previous studies finding relationships between leaf out timing and species wood xylem structures, we did not find clear differences in species-level estimates of cue responses with wood structure or relative to their wood specific densities. Each cross represents the 50% uncertainty interval of **a.** forcing, **b.** chilling, and **c.** photoperiod responses and wood specific density, with colors depicting different types of wood structure. The lowest wood specific density was estimated for *Sambucus racemosa* and the highest wood specific density for *Viburnum lantanoides*.