

<sup>1</sup> Differences in traits predict forest phenological responses to  
<sup>2</sup> photoperiod more than temperature

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<sup>10</sup> Running title: Traits drive photoperiod cues in budburst

<sup>11</sup> **Summary**

<sup>12</sup> Climate change has advanced the timing of major life cycle events in most systems, with considerable  
<sup>13</sup> variation across species and communities. In plants, differences in species growth strategies correlate  
<sup>14</sup> with variation in leaf and structural traits, creating the basis of frameworks like the leaf economic  
<sup>15</sup> spectrum. But whether traits related to the timing of growth fit within these frameworks is unclear.  
<sup>16</sup> We combined trait data from six commonly measured traits with experimental data of woody plant  
<sup>17</sup> budburst to identify shared relationships between traits, environmental cues—like temperature and  
<sup>18</sup> photoperiod—and the timing of spring growth. Working across eight forest communities, we collected  
<sup>19</sup> *in situ* trait measurements from 1428 individuals of 48 species. We paired trait data with budburst  
<sup>20</sup> data from 4211 cuttings taken from the same individuals in a controlled environment study in which  
<sup>21</sup> temperature and photoperiod cues varied. We found differences in traits between communities and  
<sup>22</sup> across latitude, but only four of our six traits related to budburst and only in relation to photoperiod.  
<sup>23</sup> Despite photoperiod being the weakest cue of woody species budburst, our results suggest that its asso-  
<sup>24</sup> ciation with other traits will influence the timing of species growth, impacting community composition  
<sup>25</sup> and species interactions under future climates.

<sup>26</sup> **Introduction**

<sup>27</sup> Climate change is causing species phenologies—the timing of life history events—to shift, with widespread  
<sup>28</sup> advances being observed across the tree of life (Parmesan and Yohe, 2003; ?). This common phenolog-  
<sup>29</sup> ical fingerprint, however, averages over high variability across species (Thackeray et al., 2016; Cohen  
<sup>30</sup> et al., 2018; Kharouba et al., 2018), posing a challenge to accurate forecasts.

<sup>31</sup> In plants, species variation can be explained, in part, by differences in growth strategies, which are  
<sup>32</sup> generally inferred from traits (Violette et al., 2007). Decades of research on plant traits have worked  
<sup>33</sup> to build predictive models of species responses to their environment (Green et al., 2022), which could  
<sup>34</sup> be promising to explain species-level variability in phenological responses. Phenology, however, has  
<sup>35</sup> generally been excluded from plant trait research due to its high inter- and intra-specific variability,

39 making it difficult to leverage existing frameworks to explain phenological variation and predictions  
40 future changes.

41 Previous studies have found high variation in phenology for the same species when observed over different  
42 years or sites (Primack et al., 2009; Chuine et al., 2010). But many of these studies are observational  
43 and conducted at the landscape scale (?Menzel et al., 2006; ?). In contrast, findings from controlled  
44 environment experiments suggest that phenological variation can be consistently decomposed into its  
45 cues (Laube et al., 2014; ?). Given the importance of phenology in defining species growth strate-  
46 gies and the environmental conditions during growth periods, we predict that these phenology-cue  
47 relationships may also correlate with other functional traits and vary along an axis of acquisitive to  
48 conservative growth strategies.

49  
50 Correlations between plant traits, growth strategies, and responses to environments have been synthe-  
51 sized into several global frameworks, including the leaf economic spectrum (Wright et al., 2004) and  
52 wood economic spectrum (Chave et al., 2009). These frameworks have identified key traits that ex-  
53 hibit distinct gradients, ranging from acquisitive strategies—fast growing plants that produce cheaper  
54 tissue—to conservative strategies—with plants that invest in long-lived tissue but slower growth rates  
55 (Wright et al., 2004; Díaz et al., 2016). In temperate systems, changes in temperature and frost risk  
56 in spring can produce gradients in abiotic stress (Sakai and Larcher, 1987; Gotelli and Graves, 1996;  
57 Augspurger, 2009) and greater competition later in the season (CITES). Species that varying the tim-  
58 ing of leafout, should therefore exhibit traits and growth strategies that allow them to tolerate or avoid  
59 these abiotic risks. Leveraging insights from predictive models of phenology with these well established  
60 trait frameworks, we can begin to disentangle the environmental cues that shape phenology from those  
61 that are shaped by other traits differences in plant growth strategies.

62  
63 To determine whether phenology fits within major functional trait frameworks will require a better  
64 understanding of the causes of variation within species. Phenological variation is generally observed in  
65 natural conditions where considerable differences in the environmental cues that trigger many pheno-  
66 logical events—primarily temperature and photoperiod (Chuine, 2000; Körner and Basler, 2010)—vary  
67 across space and time. Within-species variation may also occur across other plant traits (e.g., leaf and  
68 wood structure traits), and across latitudinal (Wiemann and Bruce, 2002) or environmental gradients  
69 (Pollock et al., 2012), though generally to a smaller scale compared to phenology. While our previ-  
70 ous growth chamber study found no evidence that phenological cues varied spatially (Loughnan and  
71 Wolkovich, in prep), previous work in functional traits has found other traits to exhibit greater spatial  
72 variation in response to environmental gradients (Gross et al., 2000; Wright et al., 2003). These results  
73 suggest that to better understand how phenology and other traits correlate across species will require  
74 methods that incorporate spatial variation within species.

75  
76 We tested whether phenological variation was aligned with existing trait frameworks using data on  
77 spring budburst paired with a suite of traits that capture acquisitive to conservative growth strategies  
78 (Wright et al., 2004; Reich, 2014). Seasonal differences in environmental conditions between early and  
79 late spring create gradients in frost risk, soil nutrients, and light availability, in addition to differences  
80 in biotic interactions, from herbivory or competition. These seasonal differences in the environment  
81 may select for variation in species growth strategies and as a result, correlate with woody plant traits.  
82 Here, we decompose high phenological variation in budburst date, using experiments to estimate three  
83 major phenological cues for woody plant budburst: chilling (associated with cool winter temperatures),  
84 forcing (associated with warm spring temperatures), and photoperiod. We predict that early spring  
85 species will budburst before canopy closure—when chilling is lower, forcing temperatures are cooler, and  
86 photoperiods shorter (exhibited as smaller responses to temperature and photoperiod). These species  
87 should have traits associated with acquisitive growth—particularly shorter heights, small trunk or stem  
88 diameters, with lower investment in wood structure and leaf tissue, as reflected by low wood specific  
89 density (WSD), diffuse-porous wood anatomy, and low leaf mass area, but high leaf nitrogen content

91 (LNC) for a greater photosynthetic potential. In contrast, we predict species with later budburst will  
92 predominately include canopy species that express more conservative growth strategies and require  
93 more chilling, warmer forcing conditions, and longer photoperiods. These species should incur greater  
94 investments in long-lived tissue, with ring-porous wood anatomy, taller heights and greater diameter,  
95 WSD and LMA, but low LNC. We Use a powerful joint-modeling approach to estimate the relationships  
96 between these plant traits and phenological responses to cues, while partitioning the variance from  
97 species- and population-level differences.

## 98 Materials and Methods

### 99 Field sampling

100 We combined *in situ* trait data with budburst data from two growth chamber cutting experiments  
101 conducted across eastern and western temperate deciduous forests in North America, and include both  
102 shrubs and tree species. We collected both suites of data from populations that span a latitudinal  
103 gradient of 4-6° for the eastern and western communities respectively. We took trait measurements  
104 from across eight populations, of which there were four eastern populations—Harvard Forest, Mas-  
105 sachusetts, USA (42.55°N, 72.20°W), White Mountains, New Hampshire, USA (44.11°N, 52.14°W),  
106 Second College Grant, New Hampshire, USA (44.79°N, 50.66°W), and St. Hippolyte, Quebec, Canada  
107 (45.98°N, 74.01°W), and four western population—E.C. Manning Park (49.06°N, 120.78°W), Sun  
108 Peaks (50.88°N, 119.89°W), Alex Fraser Research Forest (52.14°N, 122.14°W), and Smithers (54.78°N,  
109 127.17°W), British Columbia (BC), Canada (Fig. ??). For the two growth chamber studies on bud-  
110 burst phenology, we collected cuttings from the most southern and northern populations in each  
111 transect ( $n_{pop}=4$ ).  
112

### 113 Functional traits

114 We measured all traits in the summer prior to each growth chamber study (eastern transect: 8-25 June  
115 2015, western transect: 29 May to 30 July 2019), following full leafout but before budset. At each  
116 population and for each species, we measured a total of five traits from 1-10 healthy adult individuals:  
117 height, diameter of the main trunk or stem (hereafter referred to as diameter), wood specific density  
118 (WSD), leaf mass area (LMA), and the percent leaf nitrogen content (LNC). We also obtained xylem  
119 structure data from the WSL xylem database (Schweingruber and Landolt, 2010) for 72.3% of our  
120 species.  
121

122 We measured traits in accordance to the methods discussed by Pérez-Harguindeguy et al. (2013).  
123 We calculated tree height using trigonometric methods and used a base height of 1.37 m to measure  
124 diameter (?). For shrub heights, we measured the distance from the ground to the height of the top  
125 foliage and measured stem diameters at approximately 1 cm above ground-level. All stem and leaf  
126 samples were kept cool during transport and measurements of leaf area and stem volume taken within  
127 3 and 12 hours of sample collection respectively. To measure WSD, we collected a 10 cm sample of  
128 branch wood, taken close to the base of the branch at the stem and calculated stem volume using  
129 the water displacement method. For our leaf traits, we haphazardly selected and sampled five, fully  
130 expanded, and hardened leaves, with no to minimal herbivore damage. We took a high resolution scan  
131 of each leaf using a flatbed scanner and estimated leaf area using the ImageJ software (version 2.0.0).

### 132 Growth chamber study

133 For our growth chamber studies, we collected branch cuttings from our highest and lowest latitude  
134 populations in each transect, with sampling in our eastern study occurring from 20-28 January 2015  
135 and sampling for our western study from 19-28 October 2019. In both studies, we included a total of

136 eight distinct treatments consisting of two levels of chilling—with our eastern study having no additional  
 137 chilling or 30 days at 4°C, and our western study 21 days or 56 days of chilling at 4°C, both  
 138 occurring under dark conditions. Our forcing treatments included either a cool regime of 15:5°C or a  
 139 warm regime of 20:10°C, and photoperiods of either 8 or 12 hours. We recorded budburst stages of  
 140 each sample every 1-3 days for up to four months, defining the day of budburst as the day of budbreak  
 141 or shoot elongation, defined as code 07 by Finn et al. (2007). For a more detailed discussion of study  
 142 sample collection and methods see Flynn and Wolkovich (2018) for details on our eastern study and  
 143 Loughnan and Wolkovich (in prep) for details on our western study.  
 144

## 145 Statistical Analysis

146 Our analysis combined our *in situ* trait data with budburst data from the controlled environment. For  
 147 each trait, we developed a joint Bayesian model, in which the relationship between traits and cues  
 148 is used to estimate budburst. This statistical approach improves upon previous analyses of multiple  
 149 traits, as it allows us to carry through uncertainty between trait and phenology data—and better  
 150 partitions the drivers of variation in species phenologies  
 151

152 Our joint model consists of two parts. The first is a hierarchical linear model, which partitions the  
 153 variation of individual observations ( $i$ ) of a given trait value ( $Y_{\text{trait}}$ ) to account for the effects of species  
 154 ( $j$ ), population-level differences arising from transects, latitude, as well as the interaction between tran-  
 155 sects and latitude ( $\text{transect} \times \text{latitude}$ ), and finally, residual variation or ‘measurement error’ ( $\sigma_m^2$ ).  
 156

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

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

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

(4)

157

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

(6)

158 We include transect as a dummy variable (0/1) and latitude as a continuous variable in our model.  
 159 We modeled traits using natural units, with the exception of LMA, which was rescaled by 100 for  
 160 numeric stability in the model. Our model also includes partial pooling for species—which controls for  
 161 variation in the number of trait estimates per species and trait variability—using these species-level  
 162 estimates as predictors for each cue ( $\beta_{\text{chilling},j}$ ,  $\beta_{\text{forcing},j}$ ,  $\beta_{\text{photoperiod},j}$ ).  
 163

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

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

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

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

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

171 with

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

172 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:

$$\begin{aligned} \boldsymbol{\alpha}_{\text{pheno}} &= \{\alpha_{\text{pheno}_1}, \dots, \alpha_{\text{pheno}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \mathcal{N}(\mu_{\text{pheno}}, \sigma_{\text{pheno}}^2) \\ \boldsymbol{\alpha}_{\text{chilling}} &= \{\alpha_{\text{chilling}_1}, \dots, \alpha_{\text{chilling}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chilling}} \sim \mathcal{N}(\mu_{\text{chilling}}, \sigma_{\text{chilling}}^2) \\ \boldsymbol{\alpha}_{\text{forcing}} &= \{\alpha_{\text{forcing}_1}, \dots, \alpha_{\text{forcing}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{forcing}} \sim \mathcal{N}(\mu_{\text{forcing}}, \sigma_{\text{forcing}}^2) \\ \boldsymbol{\alpha}_{\text{photo}} &= \{\alpha_{\text{photo}_1}, \dots, \alpha_{\text{photo}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photo}} \sim \mathcal{N}(\mu_{\text{photo}}, \sigma_{\text{photo}}^2) \end{aligned} \quad (10)$$

173 We modeled each trait individually, with the exception of ring-porosity, which we compared across  
 174 species using the posterior estimates of our WSD model, in order to account for inherent differences  
 175 in wood anatomy across species and growth form. We included all three cues (chilling, forcing, and  
 176 photoperiod) as continuous variables in our model, as well as all two-way interactions between cues  
 177 and between cues and sites. We converting chilling temperatures to total chill portions, including both  
 178 the chilling experienced in the field prior to sampling and during the experiment in our 4°C chilling  
 179 chambers, using local weather station data and used the chillR package to calculate total chill portions  
 180 (v. 0.73.1, Luedeling, 2020). To account for differences in thermoperiodicity between the two studies  
 181 (Buonaiuto et al., 2023), we also converted forcing temperatures to mean daily temperatures for each  
 182 treatment. Finally, we *z*-scored each cue and site using two standard deviations to allow direct com-  
 183 parisons between results across parameters (Gelman, 2008).

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

193

## 194 Results

195 Across our eight populations, we measured 47 species of which 28 were in our eastern transect and 22  
 196 in our western transect. These include species dominant in both the understory and canopy layer, with  
 197 our eastern community consisting of 13 shrubs and 15 trees, our western community consisting of 18  
 198 shrubs and 4 trees, and three species that occurred in both transects. In total we measured traits of

199 1428 unique individuals between the two transects across our five traits: height ( $n = 1317$ ), diameter  
200 ( $n = 1220$ ), wood stem density ( $n = 1359$ ), leaf mass area (LMA,  $n = 1345$ ), leaf nitrogen content  
201 (LNC,  $n = 1351$ ). Across our two growth chamber studies, we made observations of 4211 samples, with  
202 our observations of budburst spanning 82 and 113 days for our eastern and western studies respectfully.  
203

204 Most of our traits showed some variation by latitude within each transect (with a strong interactive  
205 effect between transect and latitude, Fig. 1). Leaf nitrogen content was the only trait to vary with  
206 latitude alone, with low latitude communities on both our eastern and western transects having greater  
207 values of LNC than communities at higher latitudes (-0.1, UI: -0.2, -0.06, Table ??). The strongest  
208 negative interaction was observed for height (-0.2, UI: -0.4, 0), while the strongest positive interaction  
209 was observed for LMA (0.5, UI: 0.4, 0.6). Overall, woody species in our eastern community exhibited  
210 greater heights, diameter, and WSD but decreases in LMA with increasing latitude. But in our western  
211 communities height and WSD decreased with latitude, while diameter and leaf mass area both increased  
212 (Fig. 1). In addition to the differences we found across populations, we also observed considerable dif-  
213 ferences between individual species, which varied considerably and up to 7 fold for some traits (Fig. 2).  
214

215 We found that three of our four traits had a strong relationship with photoperiod, but not always in  
216 the direction we predicted. Taller species with larger trunk diameters and leaves with high nitrogen  
217 content had stronger responses to photoperiod (Table ??), Fig. 2 c, i, o; Tables ??, ??, ??). Contrary  
218 to our expectation, species with denser, high LMA leaves, however, had weaker photoperiod responses,  
219 allowing them to potentially budburst under shorter photoperiods (Fig. 2 f).

220 Temperature cues exhibited no relationships with individual traits ( $\beta_{\text{trait.chilling}}$ ), but by accounting  
221 for the effects of leaf or wood traits, we found the importance of our three cues the vary by trait.  
222 Our models of height (-13.4, UI: -17.2, -9.9), diameter (-12.5, UI: -16.2, -8.6), WSD (-20.9, UI: -33.2,  
223 -9.8), and LNC (-35.1, UI: -68.1, -4.1) all estimated chilling as the strongest cue of budburst ( $\beta_{\text{chilling}}$ ),  
224 with more chilling advancing budburst. Our model of LMA, however, estimated photoperiod as the  
225 strongest cue ( $\beta_{\text{photoperiod}}$ , (-2.7, UI: -30.3, 26)). After accounting for the effects of traits, only our  
226 height and diameter model found all three environmental cues to drive budburst timing (Tables ??,  
227 ??). Our models of WSD and LNC in turn found temperature cues alone to shape budburst (Tables  
228 ??, ??), while our model of LMA found a large response to only photoperiod (Table ??).

229 In synthesizing the effects of multiple traits across species, our results can be used to make general-  
230 izations across ecologically important groups of species. But only some of our models estimated clear  
231 gradients in species timing between trees and shrubs. In particular, we found height to have large  
232 correlations between budburst timing and trait values, with earlier estimates of budburst for shrubs  
233 (with a mean day of budburst of 10)—especially under greater cues—and later budburst estimates  
234 for trees (with a mean day of budburst of 17.3; Fig. ??). Diameter at breast height showed similar  
235 trends as estimates from our height model (results not shown). But this was not the case for our two  
236 leaf traits. Leaf nitrogen content, for example, showed no distinct separation between shrub and tree  
237 functional groups (Fig. ??).  
238

## 239 Discussion

240 Using our joint modeling approach, we estimated how leaf and wood traits interact with temperature  
241 and photoperiod cues to shape species budburst. We found that photoperiod—often the weakest cue of  
242 budburst (Laube et al., 2014; Zohner et al., 2016; Flynn and Wolkovich, 2018)—was the most impor-  
243 tant cue in trait-phenology relationships. In general, we also found trait patterns varied between our  
244 eastern and western transects and with latitude. These spatial differences in trait variation may be due  
245 to differences in the community assemblages found in our eastern versus western forests. Plants at our  
246 western sites were shorter with less dense branch wood, suggesting a more acquisitive growth strategies  
247 on average. Given that our western community is shrub dominated, this suggests these species are

248 more likely to utilize resources early in the season prior to canopy closure. Collectively our results  
249 provide new insights into the complexity of the mechanisms that underlie the relationships between  
250 traits and environmental cues, while also challenging our existing understanding of these processes.  
251

## 252 0.1 Cues and functional traits

253 We predicted species with acquisitive traits—particularly small trees with low wood densities, and  
254 less dense leaves with low leaf mass area, and high leaf nitrogen content—to have early budburst via  
255 small temperature and photoperiod responses. But we found only partial support for this prediction.  
256 In line with our predictions, acquisitive species with smaller heights and diameter did have smaller  
257 photoperiod responses (associated with later budburst). But contrary to our prediction, species with  
258 less dense leaves showed larger responses to photoperiod, while leaves with high nitrogen content had  
259 stronger photoperiod responses. We also did not find any relationships between any of our focal traits  
260 and temperature. These unexpected trends in our results may be due to selection on other physio-  
261 logical processes, as many of our traits are associated with one or more ecological function (Wright  
262 et al., 2004; Pérez-Harguindeguy et al., 2013; Reich, 2014). Our results highlight the ways in which  
263 phenology partially aligns with gradients found in established trait frameworks, while offering new  
264 insight into potential tradeoffs in how varying physiological processes shape species growth strategies.  
265

266 Decades of previous research that only considered phenology found budburst timing to be primarily  
267 driven by temperature and weakly by photoperiod (Chuine et al., 2010; Basler and Körner, 2014; Laube  
268 et al., 2014). We, however, found no traits that correlate with responses to temperature, suggesting  
269 other cues are impacting leaf and structural traits in temperate forests. In particular, leaf mass area is  
270 known to correlate with other traits like leaf lifespan or decomposition rates in addition to light capture  
271 (De La Riva et al., 2016), traits which may respond more strongly to other cues. Leaf mass area also  
272 varies with soil moisture, with variation in the area of a leaf allowing plants to reduce evaporation  
273 under dry conditions, thus selecting for high values of leaf mass area (De La Riva et al., 2016). Soil  
274 moisture is known to shape other phenological events in woody plants, including radial growth phe-  
275 nology and shoot elongation (Cabon et al., 2020; Peters et al., 2021). If selection by soil moisture is  
276 shaping phenological responses, it may be contributing to the unexpected trends we observed in leaf  
277 mass area and the absence of relationships with temperature. Thus, fully understanding how species  
278 growth strategies correlate with phenology may require the consideration of cues known to shape other  
279 plant traits.

280 The absence of trait-cue relationships between budburst and wood structure and WSD also contrasts  
281 the findings of previous work linking these traits. Previous studies have found some evidence that trees  
282 with diffuse-porous wood structure leafout earlier than species with ring-porous structures (Lechowicz,  
283 1984; Panchen et al., 2014; Yin et al., 2016; Osada, 2017; Savage et al., 2022). But using wood density as  
284 a proxy for wood structure, with wood density positively correlating with xylem resistance to embolism  
285 (Hacke et al., 2001), we did not find clear association between our three cues and xylem structure.  
286 However, the positive relationship between wood density and latitude in our eastern community may  
287 in part be caused by the differences in winter conditions experienced by canopy versus understory  
288 species. The canopy tree species that dominate our eastern communities may experience greater  
289 horizontal stress from wind and downward pressure from snow, explaining the greater wood densities  
290 they exhibit at higher latitudes (MacFarlane and Kane, 2017; MacFarlane, 2020), while species in the  
291 shrub dominated western communities experience greater protection from being in the understory.  
292 In comparing our results with a global meta-analysis of tree trait relationships with budburst cues (?),  
293 we found similar trait-cue relationships for several of our traits. At both the global and continental  
294 scales, we found taller tree heights to leafout with longer photoperiods, while in both studies, species  
295 with high specific leaf area (which is the inverse and thus equivalent to low leaf mass area) exhibited  
296 large responses to photoperiod (?). The consistency of these results, despite the differences in their

298 two spatial scales of study, provides further evidence that alternate underlying mechanisms are shaping  
299 how species respond to photoperiod cues.

300

### 301 **Functional traits predict climate change responses**

302 Our results offer novel insights into how broader correlations between growth strategies and phenolog-  
303 ical cues can help predict responses in plant communities with climate change. As temperatures rise,  
304 particularly at higher latitudes (Hoegh-Guldberg et al., 2018), warmer winter and spring temperatures,  
305 may select for earlier budburst in some species, but constrain others as photoperiod will remain fixed.  
306 The relationships between photoperiod and other traits we observed have the potential to limit species  
307 abilities to track temperatures and constrain the extent to which woody plant phenologies will advance  
308 with climate change. Our results suggest that these effects will likely be greater for taller species or  
309 canopy trees and species with relatively low leaf mass area. These constraints could have cascading  
310 effects on forest communities, as variable species responses to increasing temperatures further alter  
311 species growth strategies and their interactions with competitors or herbivores within their communi-  
312 ties.

313

314 Our findings of correlations between phenology and other commonly measured traits highlight how  
315 accurate forecasts of future changes in phenology can benefit from accounting for the response of other  
316 traits to climate change. Across temperature and precipitation gradients, leaf size and shape also  
317 change, as species shift to conserve water and mitigate effects of transpiration under higher temper-  
318 atures (De La Riva et al., 2016). These changes could impact species photosynthetic potential and  
319 ultimately ecosystem services, such as carbon sequestration. While phenological research has focused  
320 on forecasting responses to temperature, the correlation of other traits with photoperiod suggests its  
321 importance as a cue. It is therefore advantageous for additional traits that are likely to respond to  
322 photoperiod to further studied in relation to phenology when forecasting the future impacts of climate  
323 change on communities.

324

## 325 **References**

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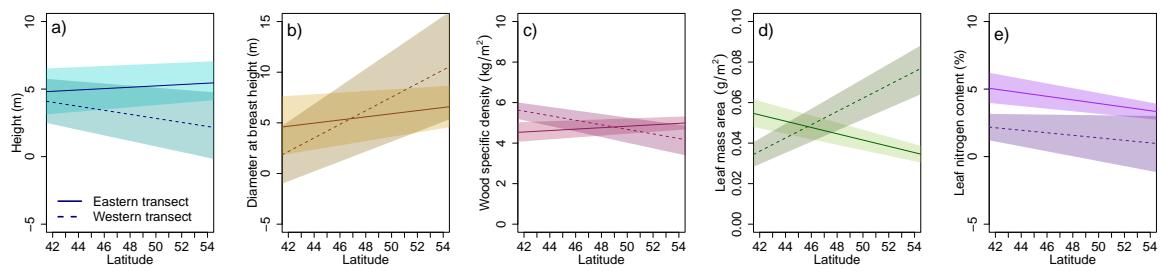


Figure 1: We found a. height, b. diameter, c. branch stem density, and d. leaf mass area to all experience a strong interaction between latitude and transect, e. while leaf nitrogen content showed a strong effect of latitude alone.

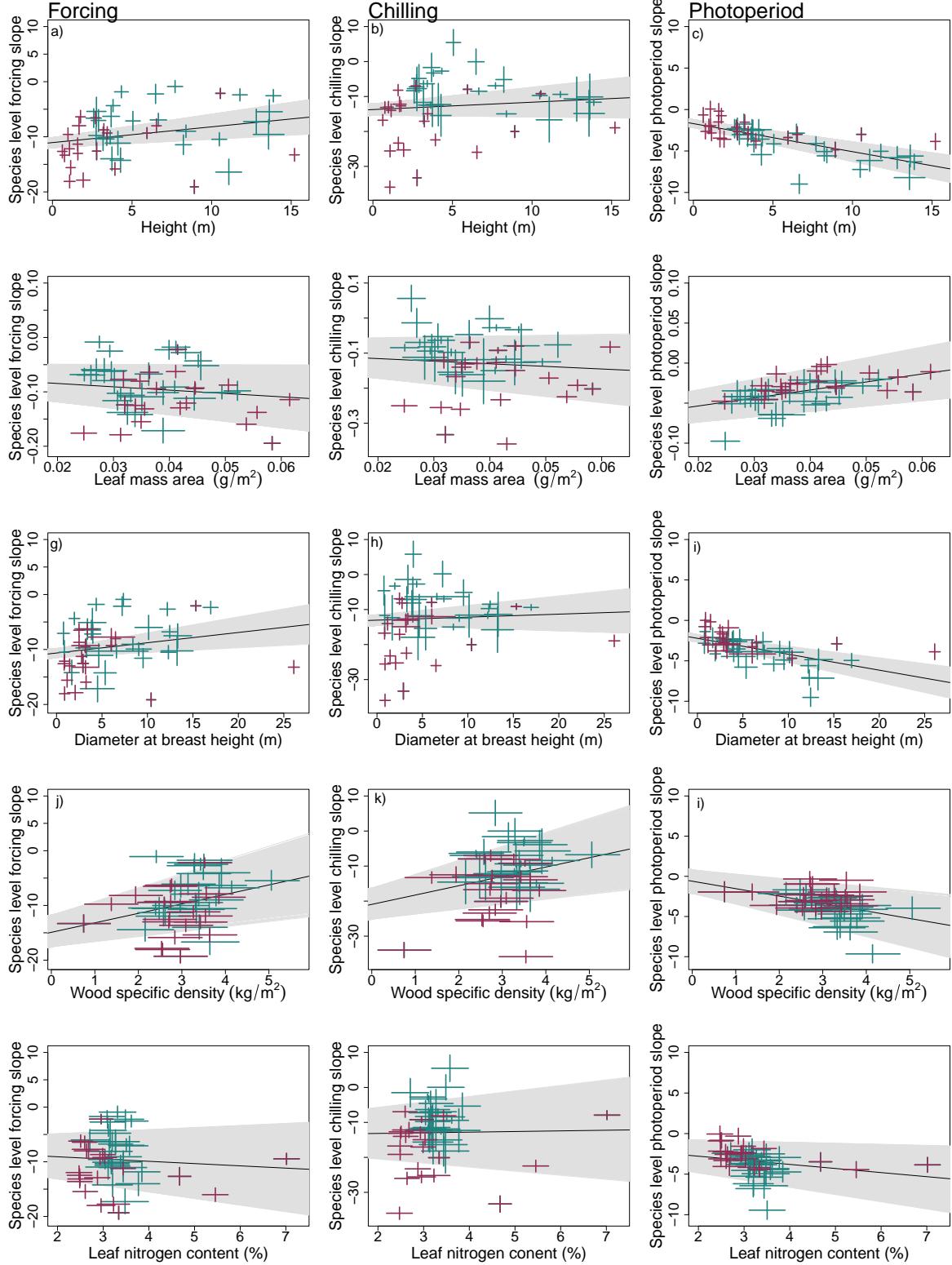


Figure 2: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species shown in red and shrub species in blue. Crosses depict the 50% uncertainty interval of the model estimates of species trait values and estimated responses to cues. The grey band depicts the 90% uncertainty interval and the black line the mean response.

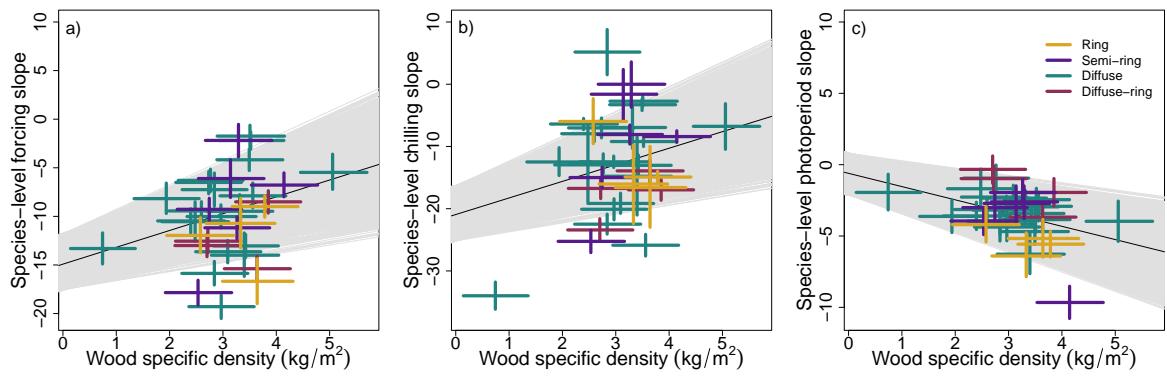


Figure 3: Despite previous studies finding relationships between leaf out timing and species wood xylem structures, we did not find clear differences in species-level estimates of cue responses with wood structure or relative to their wood specific densities. Each cross represents the 50% uncertainty interval of a. forcing, b. chilling, and c. photoperiod responses and WSD, with colors depicting different types of wood structure.