

¹ Traits predict forest phenological responses to photoperiod
² more than temperature

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¹³ Running title: Traits drive photoperiod cues in budburst

¹⁴ **Summary**

¹⁵ Climate change has advanced the timing of major life cycle events globally, with considerable variation
¹⁶ across species and communities. In plants, differences in species growth strategies correlate with
¹⁷ variation in leaf and structural traits, creating the basis of frameworks like the leaf economic spectrum.
¹⁸ But whether traits related to the timing of growth fit within these frameworks is unclear. We combined
¹⁹ trait data from six commonly measured traits with experimental data of woody plant budburst to
²⁰ identify shared relationships between traits, environmental cues—like temperature and photoperiod—
²¹ and the timing of spring growth. Working across eight forest communities, we collected *in situ* trait
²² measurements from 1428 individuals of 48 species. We paired trait data with budburst data from 4211
²³ cuttings taken from the same individuals in a controlled environment study in which temperature and
²⁴ photoperiod cues varied. We found differences in traits between communities and across latitude, but
²⁵ only four of our six traits related to budburst and only in relation to photoperiod. Despite photoperiod
²⁶ being the weakest cue of woody species budburst, our results suggest that its association with other
²⁷ traits influences the timing of species growth, potentially impacting community composition and species
²⁸ interactions under future climates.

²⁹ **Introduction**

³⁰ Climate change is causing species phenologies—the timing of life history events—to shift, with widespread
³¹ advances being observed across the tree of life (Parmesan and Yohe, 2003; Hoegh-Guldberg et al., 2018).

³⁷ This common phenological fingerprint, however, averages over high variability across species (Thackray et al., 2016; Cohen et al., 2018; Kharouba et al., 2018), posing a challenge to accurate forecasts.
³⁸

³⁹ In plants, species variation can be explained, in part, by differences in growth strategies, which are
⁴⁰ generally inferred from traits (Violle et al., 2007). Decades of research on plant traits have worked
⁴¹ to build predictive models of species responses to their environment (Green et al., 2022), which could
⁴² explain species-level variability in phenological responses. Phenology, however, has generally been ex-
⁴³ cluded from plant trait research due to its high inter- and intra-specific variability, making it difficult to
⁴⁴ leverage existing frameworks to explain phenological variation and predictions future changes.
⁴⁵

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⁴⁷ Previous studies have found high variation in phenology for the same species when observed over dif-
⁴⁸ ferent years or sites (Primack et al., 2009; Chuine et al., 2010). But many studies of phenology are
⁴⁹ observational and conducted at the landscape scale (Fitter and Fitter, 2002; Menzel et al., 2006). In
⁵⁰ contrast, findings from controlled environment experiments suggest that phenological variation can be
⁵¹ consistently decomposed into its cues (Chuine and Cour, 1999; Harrington and Gould, 2015; Flynn
⁵² and Wolkovich, 2018). Given the importance of phenology in defining when a species grows and the
⁵³ environmental conditions during growth periods, we predict that these phenology-cue relationships
⁵⁴ may also correlate with other functional traits and vary along an axis of acquisitive to conservative
⁵⁵ growth strategies.

⁵⁶

⁵⁷ Correlations between plant traits, growth strategies, and responses to environments have been synthe-
⁵⁸ sized into several global frameworks, including the leaf economic spectrum (Wright et al., 2004) and
⁵⁹ wood economic spectrum (Chave et al., 2009). These frameworks have identified key traits that ex-
⁶⁰ hibit distinct gradients, ranging from acquisitive strategies—fast growing plants that produce cheaper
⁶¹ tissue—to conservative strategies—with plants that invest in long-lived tissue but slower growth rates
⁶² (Wright et al., 2004; Díaz et al., 2016). In temperate systems, changes in temperature and frost risk in
⁶³ spring can produce gradients in abiotic stress, including frost risk, soil nutrients, and light availability
⁶⁴ (Sakai and Larcher, 1987; Gotelli and Graves, 1996; Augspurger, 2009), in addition to differences in
⁶⁵ biotic interactions from herbivory or competition later in the season (Lopez et al., 2008; Wolkovich and
⁶⁶ Ettinger, 2014). Species that vary in their timing of leafout, should therefore exhibit traits and growth
⁶⁷ strategies that allow them to tolerate or avoid these abiotic and biotic factors. Leveraging insights
⁶⁸ from predictive models of phenology with these well established trait frameworks, we can begin to
⁶⁹ disentangle the environmental cues that shape phenology from those shaped by other traits differences
⁷⁰ in plant growth strategies.

⁷¹

⁷² To determine whether phenology fits within major functional trait frameworks will require a better
⁷³ understanding of the causes of variation within species. Phenological variation is generally observed in
⁷⁴ natural conditions where considerable differences in the environmental cues that trigger many pheno-
⁷⁵ logical events—primarily temperature and photoperiod (Chuine, 2000; Körner and Basler, 2010)—vary
⁷⁶ across space and time. Within-species variation may also occur across other plant traits (e.g., leaf and
⁷⁷ wood structure traits), and across latitudinal (Wiemann and Bruce, 2002) or environmental gradients
⁷⁸ (Pollock et al., 2012), though generally to a smaller scale compared to phenology. While our previ-
⁷⁹ ous growth chamber study found no evidence that phenological cues varied spatially (Loughnan and
⁸⁰ Wolkovich, in prep), previous work in functional traits has found some traits to exhibit greater spatial
⁸¹ variation in response to environmental gradients (Gross et al., 2000; Wright et al., 2003). These results
⁸² suggest that to better understand how phenology and other traits correlate across species will require
⁸³ methods that incorporate spatial variation within species.

⁸⁴

⁸⁵ Here, we tested whether phenological variation was aligned with existing trait frameworks using data on
⁸⁶ spring budburst paired and a suite of traits that capture acquisitive to conservative growth strategies.
⁸⁷ We decompose the high phenological variation in budburst date, using experiments to estimate three
⁸⁸ major phenological cues for woody plant budburst: chilling (cool winter temperatures), forcing (warm

89 spring temperatures), and photoperiod. We predict that early spring species will budburst before
90 canopy closure—when chilling is lower, forcing temperatures are cooler, and photoperiods shorter—
91 exhibited as smaller responses to temperature and photoperiod. These species should have traits
92 associated with acquisitive growth, particularly shorter heights, smaller trunk or stem diameters, with
93 lower investment in wood structure and leaf tissue, resulting in low wood specific density, diffuse-porous
94 wood anatomy, and low leaf mass area, but high leaf nitrogen content for a greater photosynthetic
95 potential. In contrast, we predict species with later budburst to predominately include canopy species
96 that express more conservative growth strategies and require more chilling, warmer forcing, and longer
97 photoperiods. These species should incur greater investments in long-lived tissue, with ring-porous
98 wood anatomy, taller heights and greater diameter, denser wood and high leaf mass area, but low leaf
99 nitrogen content. We used a powerful joint-modeling approach to estimate the relationships between
100 these plant traits and phenological responses to cues, while partitioning the variance from species- and
101 population-level differences.

102 Materials and Methods

103 Field sampling

104 We combined *in situ* trait data with budburst data from two growth chamber cutting experiments
105 conducted across eastern and western temperate deciduous forests in North America. We collected
106 both suites of data from populations that span a latitudinal gradient of 4-6° for the eastern and
107 western communities respectively. We took trait measurements from across eight populations, of
108 which there were four eastern populations—Harvard Forest, Massachusetts, USA (42.55°N, 72.20°W),
109 White Mountains, New Hampshire, USA (44.11°N, 52.14°W), Second College Grant, New Hampshire,
110 USA (44.79°N, 50.66°W), and St. Hippolyte, Quebec, Canada (45.98°N, 74.01°W), and four western
111 population—E.C. Manning Park (49.06°N, 120.78°W), Sun Peaks (50.88°N, 119.89°W), Alex Fraser
112 Research Forest (52.14°N, 122.14°W), and Smithers (54.78°N, 127.17°W), British Columbia (BC),
113 Canada (Fig. 1). For the two growth chamber studies on budburst phenology, we collected cuttings
114 from the most southern and northern populations in each transect ($n_{pop}=4$).
115

116 Functional traits

117 We measured all traits in the summer prior to each growth chamber study (eastern transect: 8-25 June
118 2015, western transect: 29 May to 30 July 2019), following full leafout but before budset. At each
119 population and for each species, we measured a total of five traits from 1-10 healthy adult individuals:
120 height, diameter of the main trunk or stem (hereafter referred to as diameter), wood specific density,
121 leaf mass area, and the percent leaf nitrogen content. We also obtained xylem structure data from the
122 WSL xylem database (Schweingruber and Landolt, 2010) for 72.3% of our species.
123

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

135 **Growth chamber study**

136 For our growth chamber studies, we collected branch cuttings from our highest and lowest latitude
 137 populations in each transect, with sampling in our eastern study occurring from 20-28 January 2015
 138 and sampling for our western study from 19-28 October 2019. In both studies, we included a total of
 139 eight distinct treatments consisting of two levels of chilling, forcing, and photoperiods (Fig. 1). We
 140 recorded budburst stages of each sample every 1-3 days for up to four months, defining the day of
 141 budburst as the day of budbreak or shoot elongation (denoted as code 07 by Finn et al. (2007)). For
 142 a more detailed discussion of study sample collection and methods see Flynn and Wolkovich (2018)
 143 for details on our eastern study and 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 Our joint model consists of two parts. The first is a hierarchical linear model, which partitions the vari-
 152 ation of individual observations (i) of a given trait value (Y_{trait}) to account for the effects of species
 153 (j), population-level differences arising from transects, latitude, as well as the interaction between
 154 transects and latitude ($\text{transect} \cdot \text{latitude}$), and finally, residual variation or ‘measurement error’ (σ_m^2).
 155

156

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

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

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

$$(4)$$

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. We
 159 modeled traits using natural units, with the exception of leaf mass area, 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

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

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

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

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 (σ_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 α_{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)

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

184 For each model we used trait specific priors that were weakly informative. We validated our choice
 185 of priors using prior predictive checks and confirmed model stability under wider priors. All models
 186 were coded in the Stan programming language for Bayesian models using the rstan package (Stan
 187 Development Team, 2018) in R version 4.3.1 (R Development Core Team, 2017). All models met basic

189 diagnostic checks, including no divergences, high effective sample sizes (n_{eff}) that exceeded 10% of
190 the number of iterations, and \hat{R} values close to 1. We report our model estimates as the mean values
191 with 90% uncertainty intervals (UI), interpreting parameter estimates with intervals that overlap to
192 be statistically similar to each other and those 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
196 22 in our western transect. These include species dominant in both the understory and canopy layer,
197 with our eastern community consisting of 13 shrubs and 15 trees, our western community consisting of
198 18 shrubs and 4 trees, and three species that occurred in both transects. In total we measured traits
199 of 1428 unique individuals between the two transects across our five *in situ* traits: height ($n = 1317$),
200 diameter ($n = 1220$), wood stem density ($n = 1359$), leaf mass area ($n = 1345$), leaf nitrogen con-
201 tent ($n = 1351$). 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. 2). 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 leaf nitrogen content than communities at higher latitudes (-0.1, UI: -0.2, 0.0, Table S6). The
208 strongest negative interaction was observed for height (-0.2, UI: -0.4, 0.0), while the strongest positive
209 interaction was observed for leaf mass area (0.5, UI: 0.4, 0.6). Overall, woody species in our eastern
210 community exhibited greater heights, diameter, and wood stem density but decreases in leaf mass area
211 with increasing latitude. But in our western communities height and wood stem density decreased with
212 latitude, while diameter and leaf mass area both increased (Fig. 2). In addition to the differences we
213 found across populations, we also observed considerable differences between individual species, which
214 varied 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 stronger responses with longer photoperiods (Fig. 3 c, i, o; Tables S2, S3, S6). But,
219 contrary to our expectation, species with denser, high leaf mass area leaves had weaker photoperiod
220 responses, 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 the
224 vary by trait. Our models of height (-13.4, UI: -17.2, -9.9), diameter (-12.5, UI: -16.2, -8.6), wood
225 stem density (-20.9, UI: -33.2, -9.8), and leaf nitrogen content (-35.1, UI: -68.1, -4.1) all estimated
226 chilling as the strongest cue of budburst (β_{chilling}), with more chilling advancing budburst. Our model
227 of leaf mass area, however, estimated photoperiod as the strongest cue ($\beta_{\text{photoperiod}}$, -14.0, UI: -23.1,
228 -3.5). After accounting for the effects of traits, only our height and diameter model found all three
229 environmental cues to drive budburst timing (Tables S2, S3). Our models of wood stem density and
230 leaf nitrogen content in turn found temperature cues alone to shape budburst (Tables S4, S6), while
231 our model of leaf mass area found a large response to only photoperiod (Table S5).

232

233 In synthesizing the effects of multiple traits across species, our results can be used to make general-
234 izations across ecologically important groups of species. But only some of our models estimated clear
235 gradients in species timing between trees and shrubs. In particular, we found height to have large
236 correlations between budburst timing and trait values, with earlier estimates of budburst for shrubs
237 (with a mean day of budburst of 10)—especially under greater cues—and later budburst estimates

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

242

243 Discussion

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

255

256 Cues and functional traits

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

270

271 Decades of previous phenology research has found budburst timing to be primarily driven by temper-
272 ature and weakly by photoperiod (Chuine et al., 2010; Basler and Körner, 2014; Laube et al., 2014).
273 But we found no other traits that correlate with responses to temperature, suggesting other cues are
274 impacting leaf and structural traits in temperate forests. Leaf mass area also varies with soil moisture,
275 with variation in leaf area allowing plants to reduce evaporation under dry conditions, and thus select-
276 ing for high trait values (De La Riva et al., 2016). Soil moisture also shapes other phenological events
277 in woody plants, including radial growth phenology and shoot elongation (Cabon et al., 2020; Peters
278 et al., 2021). If selection by soil moisture is shaping phenological responses, it may be contributing to
279 the unexpected trends we observed in leaf traits and the absence of relationships with temperature.
280 To fully understand how species growth strategies correlate with phenology may thereby require the
281 consideration of cues known to shape plant traits more broadly.

282

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

evidence that trees with diffuse-porous wood structure leafout earlier than species with ring-porous structures (Lechowicz, 1984; Panchen et al., 2014; Yin et al., 2016; Osada, 2017; Savage et al., 2022). But using wood density as a proxy for wood structure, with wood density positively correlating with xylem resistance to embolism (Hacke et al., 2001), we did not find clear association between our three cues and xylem structure. The positive relationship between wood density and latitude in our eastern community could be caused by the differences in winter conditions experienced by canopy versus understory species. The canopy tree species that dominate our eastern communities may experience greater horizontal stress from wind and downward pressure from snow, explaining the greater wood densities they exhibit at higher latitudes (MacFarlane and Kane, 2017; MacFarlane, 2020), while species in the shrub dominated western communities experience greater protection from being in the understory.

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

Functional traits predict climate change responses

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

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

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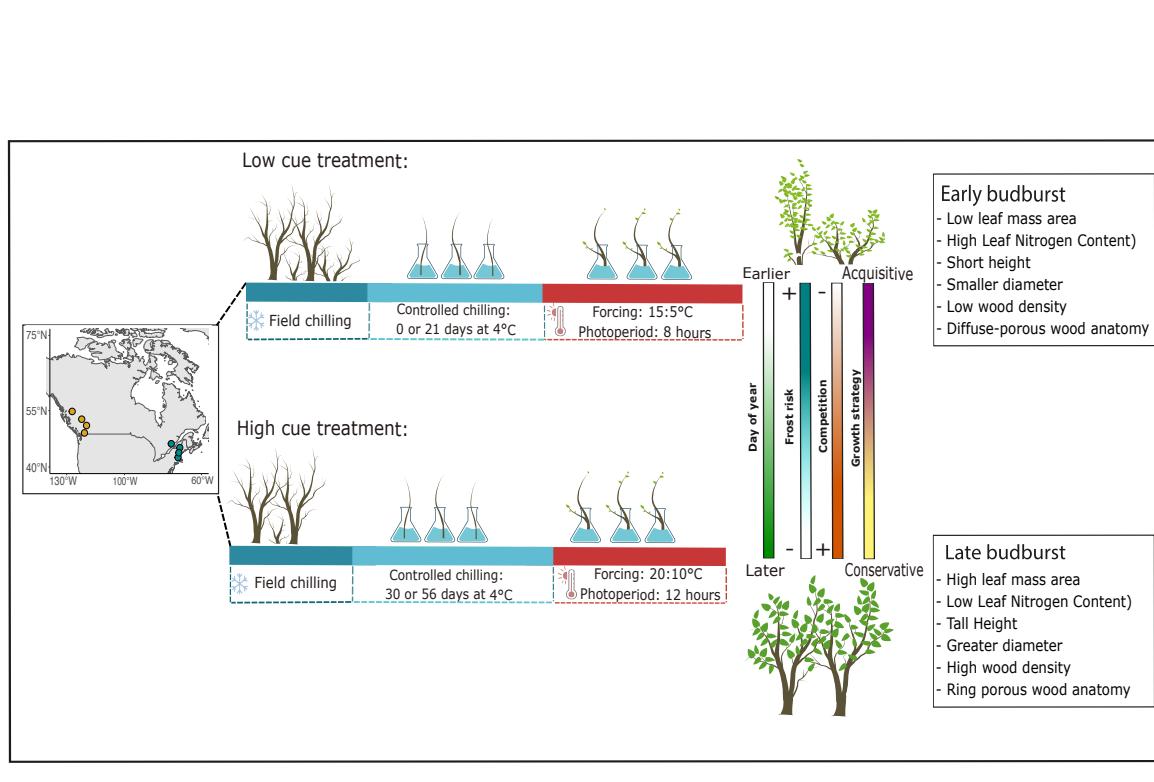


Figure 1: We collected traits data and branch cuttings from plants growing within eight sites, across two transects in eastern and western North America. Cuttings were used in two controlled environment studies in which we applied an high and low chilling, forcing, and photoperiod treatments respectively and recorded the day of budburst of each individual. 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.

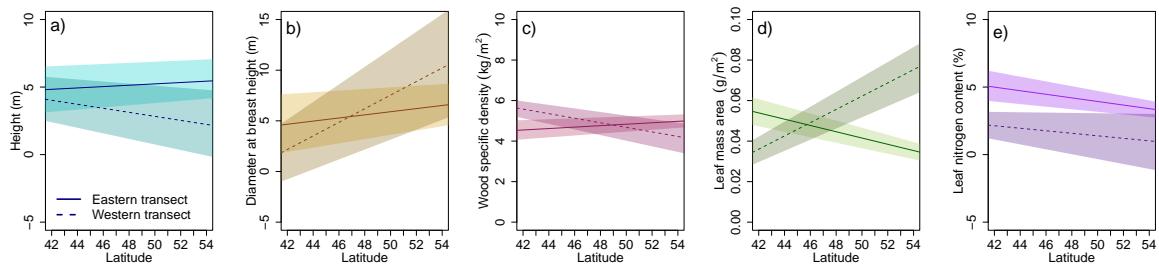


Figure 2: We found a. height, b. diameter, c. branch stem density, and d. leaf mass area to all experience a strong interaction between latitude and transect, e. while leaf nitrogen content showed a strong effect of latitude alone.

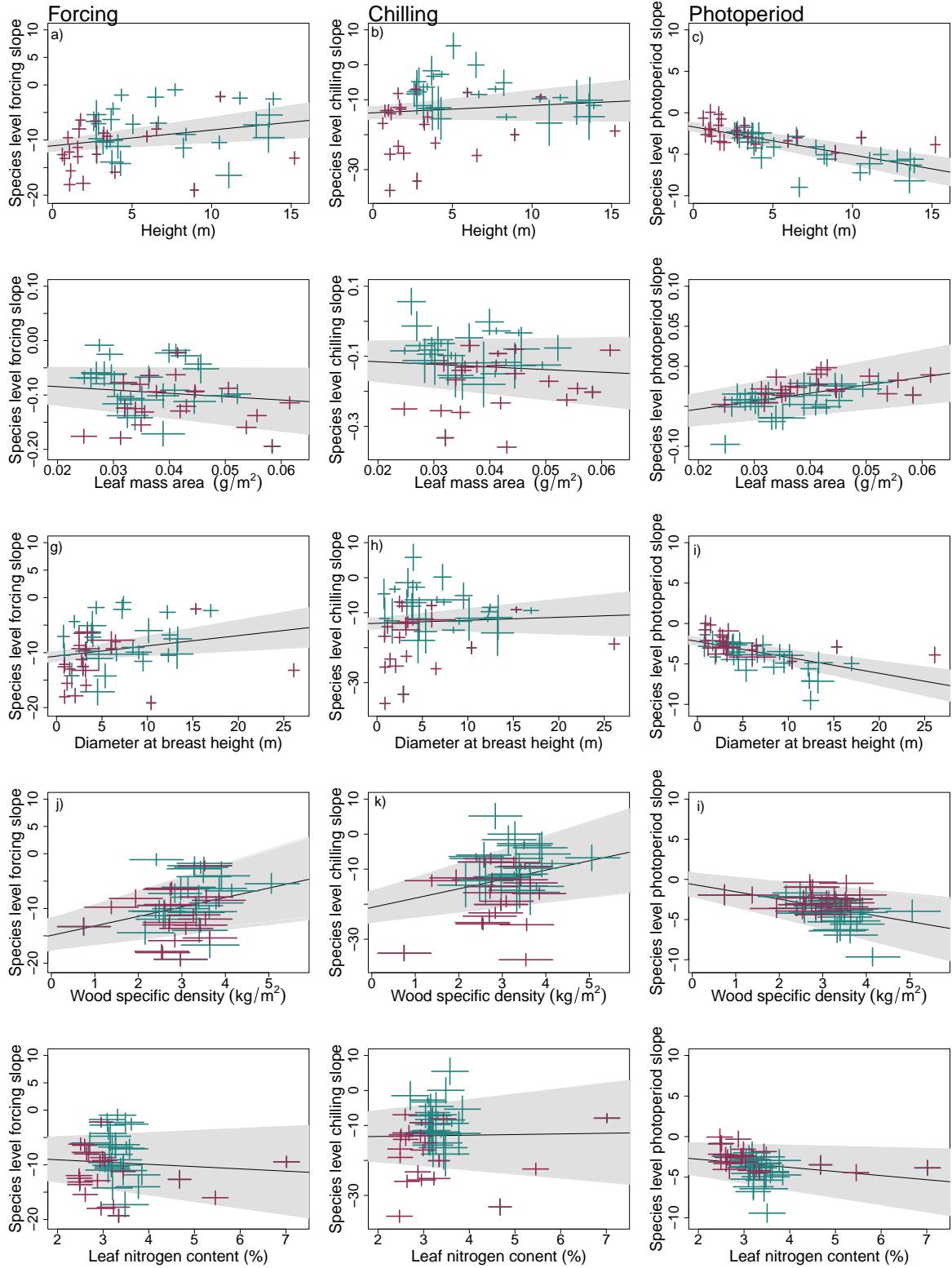


Figure 3: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species shown in red and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

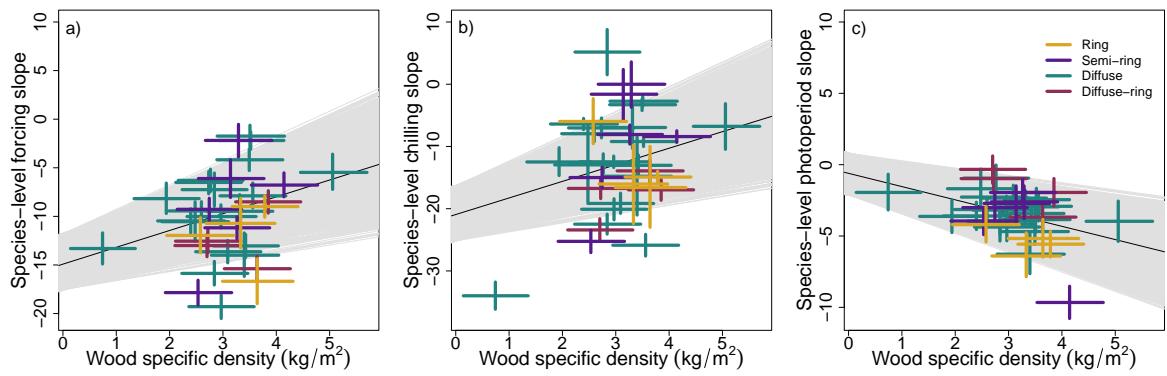


Figure 4: Despite previous studies finding relationships between leaf out timing and species wood xylem structures, we did not find clear differences in species-level estimates of cue responses with wood structure or relative to their wood specific densities. Each cross represents the 50% uncertainty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