

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 generally inferred from traits (Violle et al., 2007). Decades of research on plant traits have worked to build predictive models of species responses to their environment (Green et al., 2022), which could explain species-level variability in phenological responses. Phenology, however, has generally been excluded from plant trait research due to its high inter- and intra-specific variability, making it difficult to leverage existing frameworks to explain phenological variation and predictions future changes.
⁴⁰

⁴¹ Previous studies have found high variation in phenology for the same species when observed over different years or sites (Primack et al., 2009; Chuine et al., 2010). But many studies of phenology are observational and conducted at the landscape scale (Fitter and Fitter, 2002; Menzel et al., 2006). In contrast, findings from controlled environment experiments suggest that phenological variation can be consistently decomposed into its cues (Chuine and Cour, 1999; Harrington and Gould, 2015; Flynn and Wolkovich, 2018). Given the importance of phenology in defining when a species grows and the environmental conditions during growth periods, we predict that these phenology-cue relationships may also correlate with other functional traits and vary along an axis of acquisitive to conservative growth strategies.
⁴²

⁴³ Correlations between plant traits, growth strategies, and responses to environments have been synthesized into several global frameworks, including the leaf economic spectrum (Wright et al., 2004) and wood economic spectrum (Chave et al., 2009). These frameworks have identified key traits that exhibit distinct gradients, ranging from acquisitive strategies—fast growing plants that produce cheaper tissue—to conservative strategies—with plants that invest in long-lived tissue but slower growth rates (Wright et al., 2004; Díaz et al., 2016). In temperate systems, changes in temperature and frost risk in spring can produce gradients in abiotic stress, including frost risk, soil nutrients, and light availability (Sakai and Larcher, 1987; Gotelli and Graves, 1996; Augspurger, 2009), in addition to differences in biotic interactions from herbivory or competition later in the season (Lopez et al., 2008; Wolkovich and Ettinger, 2014). Species that vary in their timing of leafout, should therefore exhibit traits and growth strategies that allow them to tolerate or avoid these abiotic and biotic factors. Leveraging insights from predictive models of phenology with these well established trait frameworks, we can begin to disentangle the environmental cues that shape phenology from those shaped by other traits differences in plant growth strategies.
⁴⁴

⁴⁵ To determine whether phenology fits within major functional trait frameworks will require a better understanding of the causes of variation within species. Phenological variation is generally observed in natural conditions where considerable differences in the environmental cues that trigger many phenological events—primarily temperature and photoperiod (Chuine, 2000; Körner and Basler, 2010)—vary across space and time. Within-species variation may also occur across other plant traits (e.g., leaf and wood structure traits), and across latitudinal (Wiemann and Bruce, 2002) or environmental gradients (Pollock et al., 2012), though generally to a smaller scale compared to phenology. While our previous growth chamber study found no evidence that phenological cues varied spatially (Loughnan and Wolkovich, in prep), previous work in functional traits has found some traits to exhibit greater spatial variation in response to environmental gradients (Gross et al., 2000; Wright et al., 2003). These results suggest that to better understand how phenology and other traits correlate across species will require methods that incorporate spatial variation within species.
⁴⁶

⁴⁷ Here, we tested whether phenological variation was aligned with existing trait frameworks using data on spring budburst paired and a suite of traits that capture acquisitive to conservative growth strategies.
⁴⁸ We decompose the high phenological variation in budburst date, using experiments to estimate three major phenological cues for woody plant budburst: chilling (cool winter temperatures), forcing (warm
⁴⁹

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 an assemblage of 47 species from the understory and canopy layers, with 28 species at our
118 eastern transect and 22 species at our western transect, with three species occurring in both transects.
119 We measured all traits in the summer prior to each growth chamber study (eastern transect: 8-25 June
120 2015, western transect: 29 May to 30 July 2019), following full leafout but before budset. At each
121 population and for each species, we measured a total of five traits from 1-10 healthy adult individuals:
122 height, diameter of the main trunk or stem (hereafter referred to as diameter), wood specific density,
123 leaf mass area, and the percent leaf nitrogen content. We also obtained xylem structure data from the
124 WSL xylem database (Schweingruber and Landolt, 2010) for 72.3% of our species.
125

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

135 We took a high resolution scan of each leaf using a flatbed scanner and estimated leaf area using the
136 ImageJ software (version 2.0.0).

137 Growth chamber study

138 For our growth chamber studies, we collected branch cuttings from our highest and lowest latitude
139 populations in each transect, with sampling in our eastern study occurring from 20-28 January 2015
140 and sampling for our western study from 19-28 October 2019. In both studies, we included a total of
141 eight distinct treatments consisting of two levels of chilling, forcing, and photoperiods (Fig. 1). We
142 recorded budburst stages of each sample every 1-3 days for up to four months, defining the day of
143 budburst as the day of budbreak or shoot elongation (denoted as code 07 by Finn et al. (2007)). For
144 a more detailed discussion of study sample collection and methods see Flynn and Wolkovich (2018)
145 for details on our eastern study and Loughnan and Wolkovich (in prep) for details on our western study.

146

147 Statistical Analysis

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

153

154 Our joint model consists of two parts. The first is a hierarchical linear model, which partitions the
155 variation of individual observations (i) of a given trait value (Y_{trait}) to account for the effects of species
156 (j), population-level differences arising from transects, latitude, as well as the interaction between tran-
157 sects and latitude ($\text{transect} \times \text{latitude}$), and finally, residual variation or ‘measurement error’ (σ_m^2).
158

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

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

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

(4)

159

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

(6)

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

165

$$\begin{aligned}\beta_{\text{chilling}_j} &= \alpha_{\text{chilling},j} + \beta_{\text{trait.chilling}} \cdot \alpha_{\text{trait},j} \\ \beta_{\text{forcing}_j} &= \alpha_{\text{forcing},j} + \beta_{\text{trait.forcing}} \cdot \alpha_{\text{trait},j} \\ \beta_{\text{photoperiod}_j} &= \alpha_{\text{photoperiod},j} + \beta_{\text{trait.photoperiod}} \cdot \alpha_{\text{trait},j}\end{aligned}\tag{7}$$

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

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

173 with

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

174 where α_{pheno_j} , $\alpha_{\text{chilling}_j}$, $\alpha_{\text{forcing}_j}$, and $\alpha_{\text{photoperiod}_j}$ are elements of the normal random vectors:

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

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

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

195

196 **Results**

197 Across our eight populations, we measured 47 species of which 28 were in our eastern transect and 22
198 in our western transect. These include species dominant in both the understory and canopy layer, with
199 our eastern community consisting of 13 shrubs and 15 trees, our western community consisting of 18
200 shrubs and 4 trees, and three species that occurred in both transects. In total we measured traits of
201 1428 unique individuals between the two transects across our five traits: height ($n = 1317$), diameter
202 ($n = 1220$), wood stem density ($n = 1359$), leaf mass area (LMA, $n = 1345$), leaf nitrogen content
203 (LNC, $n = 1351$). Across our two growth chamber studies, we made observations of 4211 samples, with
204 our observations of budburst spanning 82 and 113 days for our eastern and western studies respectfully.
205

206 Most of our traits showed some variation by latitude within each transect (with a strong interactive
207 effect between transect and latitude, Fig. 2). Leaf nitrogen content was the only trait to vary with
208 latitude alone, with low latitude communities on both our eastern and western transects having greater
209 values of LNC than communities at higher latitudes (-0.1, UI: -0.2, -0.06, Table S6). The strongest
210 negative interaction was observed for height (-0.2, UI: -0.4, 0), while the strongest positive interaction
211 was observed for LMA (0.5, UI: 0.4, 0.6). Overall, woody species in our eastern community exhibited
212 greater heights, diameter, and WSD but decreases in LMA with increasing latitude. But in our western
213 communities height and WSD decreased with latitude, while diameter and leaf mass area both increased
214 (Fig. 2). In addition to the differences we found across populations, we also observed considerable dif-
215 fferences between individual species, which varied considerably and up to 7 fold for some traits (Fig. 3).
216

217 We found that three of our four traits had a strong relationship with photoperiod, but not always in
218 the direction we predicted. Taller species with larger trunk diameters and leaves with high nitrogen
219 content had stronger responses to photoperiod (Table S6), Fig. 3 c, i, o; Tables S2, S3, S5). Contrary
220 to our expectation, species with denser, high LMA leaves, however, had weaker photoperiod responses,
221 allowing them to potentially budburst under shorter photoperiods (Fig. 3 f).

222 Temperature cues exhibited no relationships with individual traits ($\beta_{\text{trait.chilling}}$), but by accounting
223 for the effects of leaf or wood traits, we found the importance of our three cues the vary by trait.
224 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,
225 -9.8), and LNC (-35.1, UI: -68.1, -4.1) all estimated chilling as the strongest cue of budburst (β_{chilling}),
226 with more chilling advancing budburst. Our model of LMA, however, estimated photoperiod as the
227 strongest cue ($\beta_{\text{photoperiod}}$, (-2.7, UI: -30.3, 26)). After accounting for the effects of traits, only our
228 height and diameter model found all three environmental cues to drive budburst timing (Tables S2,
229 S3). Our models of WSD and LNC in turn found temperature cues alone to shape budburst (Tables
230 S4, S6), while our model of LMA found a large response to only photoperiod (Table S5).
231

232 In synthesizing the effects of multiple traits across species, our results can be used to make general-
233 izations across ecologically important groups of species. But only some of our models estimated clear
234 gradients in species timing between trees and shrubs. In particular, we found height to have large
235 correlations between budburst timing and trait values, with earlier estimates of budburst for shrubs
236 (with a mean day of budburst of 10)—especially under greater cues—and later budburst estimates
237 for trees (with a mean day of budburst of 17.3). Diameter at breast height showed similar trends as
238 estimates from our height model (results not shown). But this was not the case for our two leaf traits.
239 Leaf nitrogen content, for example, showed no distinct separation between shrub and tree functional
240 groups
241

242 **Discussion**

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

254

255 **Cues and functional traits**

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

268

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

283

284 The absence of trait-cue relationships between budburst and wood structure and WSD also contrasts
285 the findings of previous work linking these traits. Previous studies have found some evidence that
286 trees with diffuse-porous wood structure leafout earlier than species with ring-porous structures (Le-
287 chowicz, 1984; Panchen et al., 2014; Yin et al., 2016; Osada, 2017; Savage et al., 2022). But using
288 wood density as a proxy for wood structure, with wood density positively correlating with xylem re-
289 sistance to embolism (Hacke et al., 2001), we did not find clear association between our three cues and
290 xylem structure. However, the positive relationship between wood density and latitude in our east-

ern community may in part 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.

297

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 several of our traits. At both the global and continental scales, we found taller tree heights to leafout with longer photoperiods, while in both studies, species with high specific leaf area (which is the inverse and thus equivalent to low leaf mass area) exhibited large responses to photoperiod (Loughnan et al., 2025). The consistency of these results, despite the differences in their two spatial scales of study, provides further evidence that alternate underlying mechanisms are shaping how species respond to photoperiod cues.

305

306 **Functional traits predict climate change responses**

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

318

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

329

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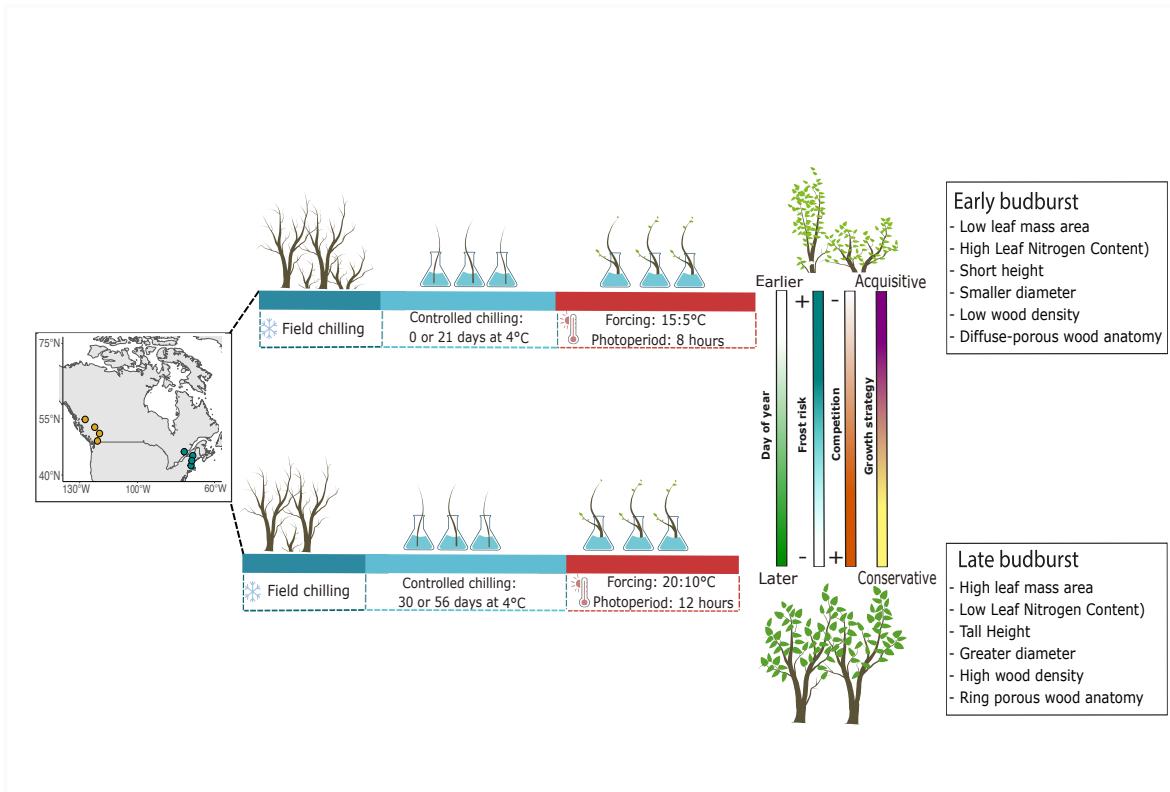


Figure 1: We found a. height, b. diameter, c. branch stem density, and d. leaf mass area to all experience a strong interaction between latitude and transect, e. while leaf nitrogen content showed a strong effect of latitude alone.

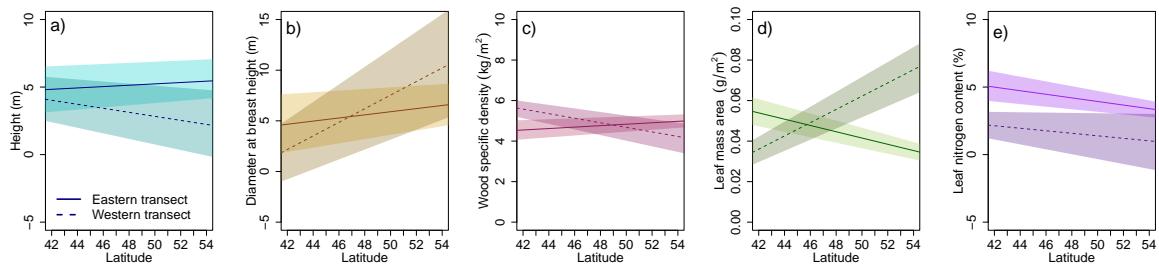


Figure 2: We found a. height, b. diameter, c. branch stem density, and d. leaf mass area to all experience a strong interaction between latitude and transect, e. while leaf nitrogen content showed a strong effect of latitude alone.

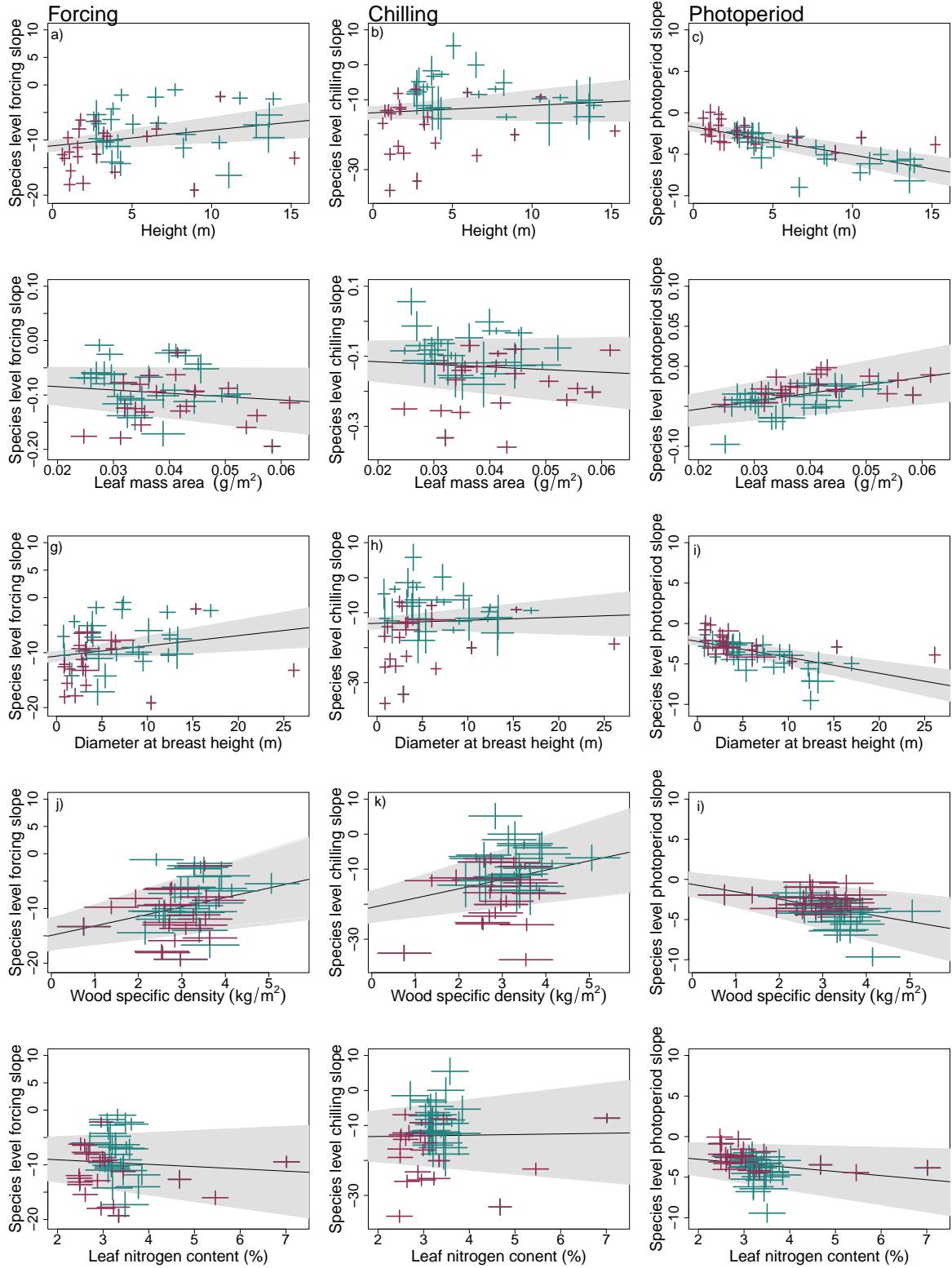


Figure 3: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species shown in red and 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.

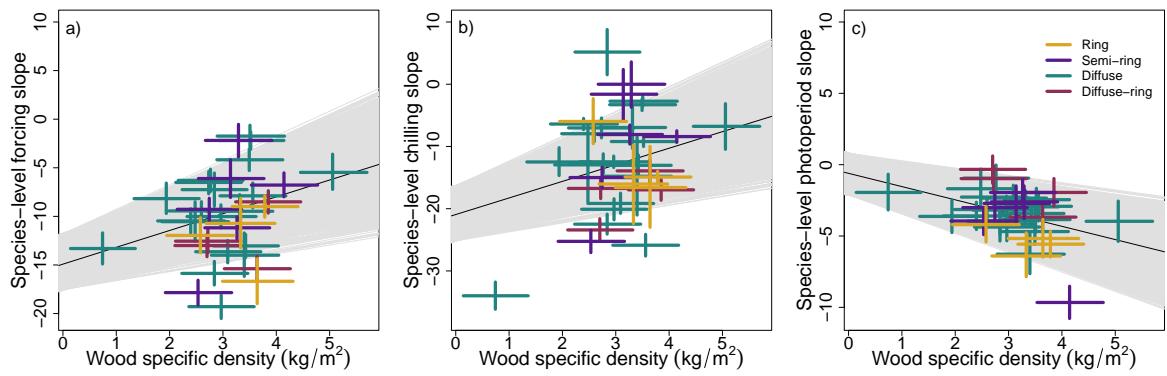


Figure 4: Despite previous studies finding relationships between leaf out timing and species wood xylem structures, we did not find clear differences in species-level estimates of cue responses with wood structure or relative to their wood specific densities. Each cross represents the 50% uncertainty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