

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 Shifts in the timing of spring phenology, such as budburst and leafout, can have major ecosystem
¹⁶ consequences. Our ability to identify what these consequences are—and predict future impacts—may
¹⁷ be further improved if species phenological responses fit within broader frameworks of plant strategies.
¹⁸ Research has often suggested that species with early spring phenology may fit within an acquisitive
¹⁹ strategy while later species may be more conservative in their growth. Yet testing these predictions has
²⁰ been slow given the high variability of spring phenology when measured in different natural settings
²¹ across space and time. Here, using controlled environment studies to reduce phenological variation into
²² its component responses to chilling (cool winter temperatures), forcing (spring warming temperatures)
²³ and photoperiod, we test for trait relationships across 47 species sampled from eight forest communities
²⁴ (1428 individuals) across North America. We find phenology connects to four major plant functional
²⁵ traits—height, diameter, leaf mass area and nitrogen content—via responses to photoperiod, but not
²⁶ temperature. In contrast with previous findings, we found no relationship across two different metrics
²⁷ of wood density. Our results suggest photoperiod responses may be a critical component of how spring
²⁸ phenology fits within plant strategies, which could help predict how forest growth will shift in the
²⁹ future with continued climate change.

³⁰ **Introduction**

³¹ Climate change is causing species phenologies—the timing of life history events—to shift, with widespread
³² advances being observed across the tree of life (Parmesan and Yohe, 2003; Hoegh-Guldberg et al., 2018).

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

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

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

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

78
79 Here, we tested whether phenological variation was aligned with existing trait frameworks using data on
80 spring budburst paired with a suite of traits that capture acquisitive to conservative growth strategies.
81 We decomposed the high phenological variation in budburst date by using experiments to estimate
82 three major phenological cues for woody plant budburst: chilling (cool winter temperatures), forcing
83 (warm spring temperatures), and photoperiod. We predicted that early spring species, which generally
84 budburst before canopy closure due to smaller responses to temperature and photoperiod, would have
85 traits associated with acquisitive growth. They would thus be shorter, with smaller trunks or stem
86 diameters, and a lower investment in wood structure and leaf tissue, resulting in low wood specific
87 density, diffuse-porous wood anatomy, and low leaf mass area, but high leaf nitrogen content for a
88 greater photosynthetic potential. In contrast, we predict species with later budburst to predominately
89 include canopy species that express more conservative growth strategies and require more chilling,

90 warmer forcing, and longer photoperiods. These species should incur greater investments in long-lived
91 tissue, with ring-porous wood anatomy, taller heights and greater diameter, denser wood and high
92 leaf mass area, but low leaf nitrogen content. We then used a joint-modeling approach to estimate
93 the relationships between these plant traits and phenological responses to cues, while partitioning the
94 variance from species- and population-level differences.

95 Materials and Methods

96 Field sampling

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

109 Functional traits

110 We measured all traits in the summer prior to each growth chamber study (eastern transect: 8-25 June
111 2015, western transect: 29 May to 30 July 2019), following full leafout but before budset. At each
112 population and for each species, we measured a total of five traits from 1-10 healthy adult individuals:
113 height, diameter of the main trunk or stem (hereafter referred to as diameter), wood specific density,
114 leaf mass area, and the percent leaf nitrogen content. We also obtained xylem structure data from the
115 WSL xylem database (Schweingruber and Landolt, 2010) for 72.3% of our species.
116

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

128 Growth chamber study

129 For our growth chamber studies, we collected dormant branch cuttings from our highest and lowest
130 latitude populations in each transect, with sampling in our eastern study occurring from 20-28 Jan-
131 uary 2015 and sampling for our western study from 19-28 October 2019. Dormant branch cuttings
132 have been repeatedly shown to approximate whole plant responses in budburst (Vitasse and Basler,
133 2014), allowing us to estimate responses to environmental cues. In both studies, we included a total
134 of eight distinct treatments consisting of two levels of chilling, forcing, and photoperiods (Fig. 1). We

135 recorded budburst stages of each sample every 1-3 days for up to four months, defining the day of
 136 budburst as the day of budbreak or shoot elongation (denoted as code 07 by Finn et al. (2007)). For
 137 a more detailed discussion of study sample collection and methods see (Flynn and Wolkovich, 2018)
 138 for details on our eastern study and Loughnan and Wolkovich (in prep) for details on our western study.
 139

140 Statistical Analysis

141 We combined our *in situ* trait data with budburst data from the controlled environment experiments
 142 through a joint Bayesian model for each trait. This approach improves upon previous analyses of mul-
 143 tiple traits, as it allows us to carry through uncertainty between trait and phenology estimates—and
 144 better partitions the drivers of variation in species phenologies.

145 Our joint model consists of two parts. The first is a hierarchical linear model, which partitions the vari-
 146 ation of individual observations (i) of a given trait value (Y_{trait}) to account for the effects of species
 147 (j), population-level differences arising from transects, latitude, as well as the interaction between
 148 transects and latitude ($\text{transect} \cdot \text{latitude}$), and finally, residual variation or ‘measurement error’ (σ_m^2).
 150

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

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

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

$$(4)$$

151

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

$$(6)$$

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

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

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

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

158 In addition to the species-level estimates, this part of our model estimates the overall effect of each
 159 trait on each cue ($\beta_{\text{trait.chilling}}$, $\beta_{\text{trait.forcing}}$, $\beta_{\text{trait.photoperiod}}$). From this we could estimate how well
 160 traits explain species-level differences—by estimating the the species-level cue variation not explained
 161 by traits ($\alpha_{\text{chilling},j}$, $\alpha_{\text{forcing},j}$, $\alpha_{\text{photoperiod},j}$) and individual species responses to cues (*chilling*, *forcing*,
 162 *photoperiod*, respectively). Finally, our model estimates the residual budburst variation across species

163 $(\alpha_{\text{pheno},j})$, observations (σ_d^2), as well as the variation in cues not attributed to the trait (using partial
164 pooling).

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

165 with

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

166 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)

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

178

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

186

187 **Results**

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

196
197 Most of our traits showed some variation by latitude within each transect, with a strong interactive
198 effect between transect and latitude (Fig. 2). Leaf nitrogen content was the only trait to vary with
199 latitude alone, with low latitude communities on both our eastern and western transects having greater
200 values of leaf nitrogen content than communities at higher latitudes (-0.1 percent per degree latitude,
201 UI: -0.2, 0.0, Table S6). Plant diameter increased with increasing (higher) latitudes in both eastern
202 and western communities (0.5 cm per degree latitude, UI: 0.1, 0.9), with a larger effect in eastern com-
203 munities (Fig. 2d). Relationships with height, woody stem density and leaf mass per area were more
204 complex. Heights and wood stem density increased with increasing latitude in western communities,
205 but decreased with latitude in eastern communities (-0.2 m per degree latitude, UI: -0.4, 0.0 for our
206 height model and -0.01 g/cm³ per degree latitude, UI: -0.02, 0.0 for our wood stem density model; Fig.
207 2 a and c), while for leaf mass we found the reverse (decreasing leaf mass area with increasing latitudes
208 in western communities, while increasing with latitude in eastern communities (0.005 g/cm² per degree
209 latitude, UI: 0.004, 0.006; Fig. 2d). In addition to the differences we found across populations, we also
210 observed large differences between individual species, which varied up to 7 fold for some traits (Fig.
211 3).

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

217
218 Temperature cues ($\beta_{\text{trait.chilling}}$ and $\beta_{\text{trait.forcing}}$) exhibited no relationships with individual traits, but
219 by accounting for the effects of leaf or wood traits, we found the importance of our three cues on
220 budburst to vary by trait. Of the three cues, chilling (β_{chilling}) was the strongest in our models of
221 height (-13.4 days per standardized chill portions, UI: -17.2, -9.9), diameter (-12.5 days per standard-
222 ized chill portions, UI: -16.2, -8.6), wood stem density (-2.1 days per standardized chill portions, UI:
223 -3.3, -9.8), and leaf nitrogen content (-35.1 days per standardized chill portions, UI: -68.1, -4.1), with
224 more chilling advancing budburst. Our model of leaf mass area, however, estimated photoperiod as the
225 strongest cue ($\beta_{\text{photoperiod}}$, -14.0 days per standardized photoperiod, UI: -23.1, -3.5). After accounting
226 for the effects of traits, only our height and diameter model found all three environmental cues to drive
227 budburst timing (Tables S2, S3). Our models of wood stem density and leaf nitrogen content in turn
228 found temperature cues alone to shape budburst (Tables S4, S6), while our model of leaf mass area
229 found a large response to only photoperiod (Table S5).

230
231 We found that only some of our trait models estimated clear gradients in species timing between trees
232 and shrubs, as is commonly expected. In particular, we found height had large correlations between
233 budburst timing and trait values, with earlier estimates of budburst for shrubs (with a mean day of
234 budburst of 10)—especially under greater cues—and later budburst estimates for trees (with a mean
235 day of budburst of 17.3, Fig. S1). Diameter at breast height showed similar trends as estimates from
236 our height model (results not shown). But this was not the case for our two leaf traits. Leaf nitrogen
237 content, in particular, showed no distinct separation between shrub and tree functional groups (Fig.

238 S1).

239

240 Discussion

241 Using a joint modeling approach to understand how phenology may fit within acquisitive to conservative
242 plant strategies we found that photoperiod related to a suite of leaf and wood traits. While budburst
243 responses to photoperiod are often much smaller than temperature responses (chilling and forcing
244 Laube et al., 2014; Zohner et al., 2016; Flynn and Wolkovich, 2018), our results suggest photoperiod
245 may be the most important cue in linking spring phenology to functional traits. Our results suggest
246 that fully predicting these responses also requires considering variation across space given differences
247 between our eastern and western transects and with latitude. These spatial differences in trait variation
248 may be due to differences in the community assemblages, as our western community was more shrub
249 dominated, with shorter plants with less dense branch wood, suggesting a more acquisitive growth
250 strategy to allow species to utilize resources early in the season before canopy closure.

251 Cues and functional traits

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

265

266 Decades of previous phenology research have found budburst timing to be primarily driven by tem-
267 perature (chilling and forcing) and weakly by photoperiod (Chuine et al., 2010; Basler and Körner,
268 2014; Laube et al., 2014). Yet we found no traits that correlated with responses to temperature, sug-
269 gesting other drivers may impact leaf and structural traits in temperate forests. One potential abiotic
270 driver we did not consider is soil moisture, which covaries with a number of traits, including leaf mass
271 area, as higher leaf area allows plants to reduce evaporation under dry conditions (De La Riva et al.,
272 2016). Soil moisture also shapes other phenological events in woody plants, including radial growth
273 phenology and shoot elongation (Cabon et al., 2020; Peters et al., 2021). Though temperate forests
274 are generally moist compared to other systems, previous studies also suggests soil moisture can shape
275 spring phenology across xeric systems as well (Crimmins et al., 2011, Park 2014) thus including it in
276 future studies could help understand how species growth strategies correlate with phenology.

277

278 Our finding that budburst was not related to wood structure or wood stem density contrasts the
279 findings of previous work linking these traits. Previous studies have found some evidence that trees
280 with diffuse-porous wood structure leafout earlier than species with ring-porous structures (Lechowicz,
281 1984; Panchen et al., 2014; Yin et al., 2016; Osada, 2017; Savage et al., 2022). Using wood density as
282 an alternative measure of wood structure (wood density positively correlates with xylem resistance to
283 embolism, Hacke et al., 2001), we did not find an association between our three phenological cues and
284 xylem structure, despite our data including similar temperate forest species. This could be because

285 we captured additional variation by sampling many individuals for each species across a large spatial
286 gradient. In particular, we found larger wood densities at higher latitudes in our western transect,
287 which could be caused by the differences in winter conditions experienced across this transect. The
288 understory shrub species that dominate our western communities may experience greater horizontal
289 stress from wind and downward pressure from snow, explaining the greater wood densities they exhibit
290 at higher latitudes (MacFarlane and Kane, 2017; MacFarlane, 2020), while shrub species in the tree
291 dominated eastern communities likely experience greater protection in the understory. Relationships
292 with wood density may also be more apparent over a larger span of wood specific densities (our values
293 varied from 0.2 to 0.6 g/cm³, which is smaller than seen studies that span a more global distribution
294 Galvão et al., 2021; Savage et al., 2022; Mo et al., 2024).

295

296 In addition to our study providing insight into how trait-budburst relationships vary with latitude, our
297 sites also spanned North America, encompassing a gradient of 55° in longitude. At this continental
298 scale we found correlations between phenology and traits for woody species in temperate forests, but
299 these may shift with data that expands across biomes and more plant functional groups. Indeed, both
300 the leaf and wood economic spectra find large variation in traits across species arose from large global
301 datasets that include both temperate and tropical species (Wright et al., 2004; Díaz et al., 2016; Chave
302 et al., 2009) and functional groups that span from trees to grasses (Wright et al., 2004). Previous
303 research also suggests that global patterns in trait variation are often not found at smaller spatial
304 scales (Wright and Sutton-Grier, 2012; Messier et al., 2017a,b). This suggests that comparing trait-
305 phenology relationships at larger spatial scales or across more diverse pools of species may better align
306 with the patterns predicted by existing economic spectra.

307 In comparing our results with a global meta-analysis of tree trait relationships with budburst cues
308 (Loughnan et al., 2025), we found similar trait-cue relationships for two traits: height and leaf mass
309 area. At both the global and continental scales, trees with taller heights leafed out with longer photo-
310 periods. We also found species with high specific leaf area—which is the inverse of leaf mass area and
311 thus equivalent to low values—exhibited large responses to photoperiod (Loughnan et al., 2025). The
312 consistency of these results, despite the differences in the two spatial scales of these datasets, provides
313 further support that how woody species respond to photoperiod may be part of a larger plant strategy.

314

315 Functional traits predict climate change responses

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

326

327 Our findings of correlations between phenology and other commonly measured traits highlight how
328 accurate forecasts of future changes in phenology could benefit from accounting for the response of
329 other traits to climate change. Across temperature and precipitation gradients, leaf size and shape
330 also change, as species shift to conserve water and mitigate effects of transpiration under higher tem-
331 peratures (De La Riva et al., 2016). These changes could impact species photosynthetic potential and
332 ultimately ecosystem services, such as carbon sequestration. While phenological research has focused
333 on forecasting responses to temperature, the correlation of other traits with photoperiod suggests it is
334 also an important cue. By considering the tradeoffs and differences in cues that simultaneously shape

335 plants growth strategies, we can more accurately forecast species phenology and community dynamics
336 under future climates.

337

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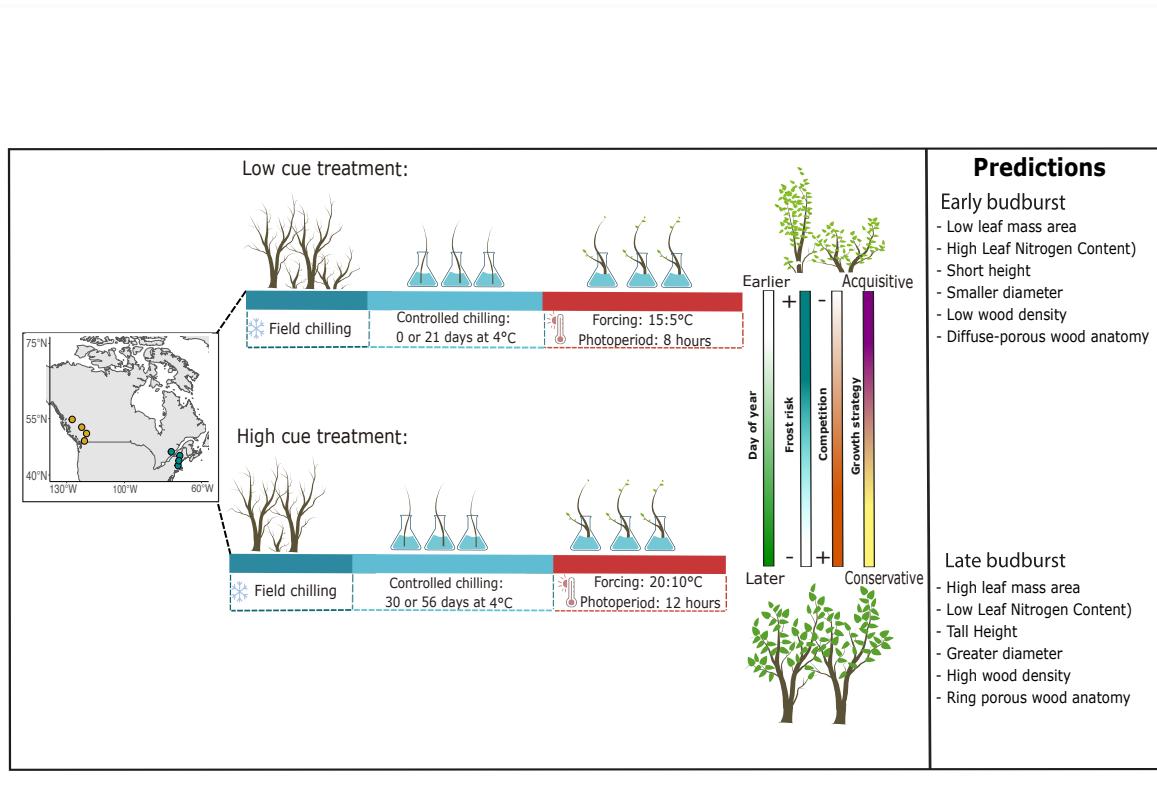


Figure 1: We collected trait data and branch cuttings from woody plants growing within eight sites, across two transects in eastern and western North America. Cuttings were used in two controlled environment studies in which we applied high and low chilling, forcing, and photoperiod treatments and recorded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

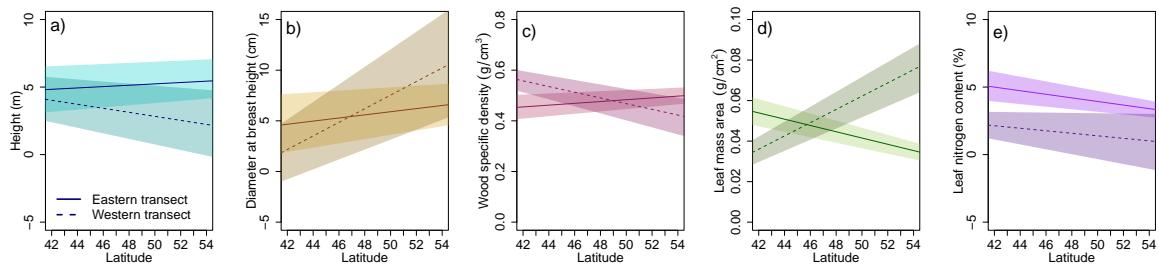


Figure 2: We found a. height, b. diameter, c. branch stem density, and d. leaf mass area to all experience a strong interaction between latitude and transect, e. while leaf nitrogen content showed a strong effect of latitude alone.

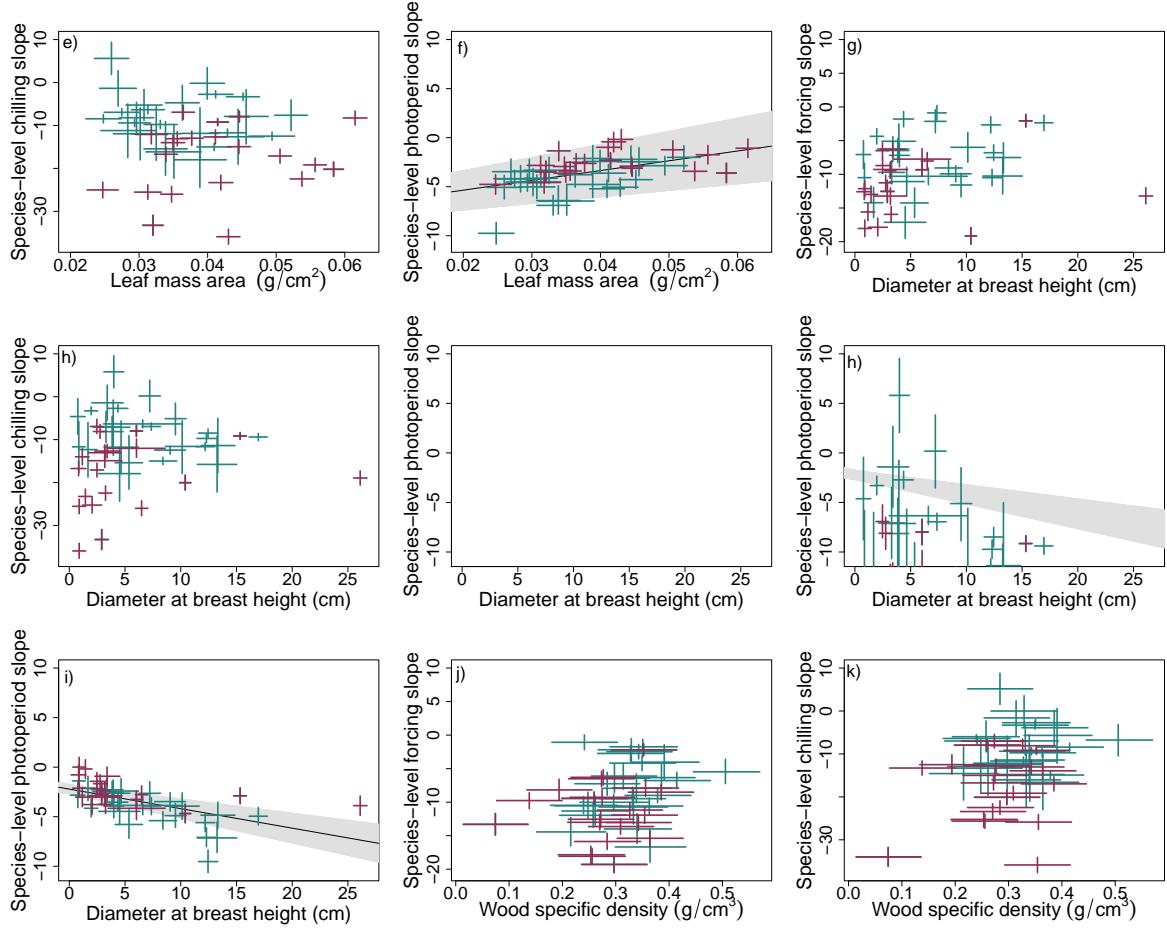


Figure 3: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species shown in red and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

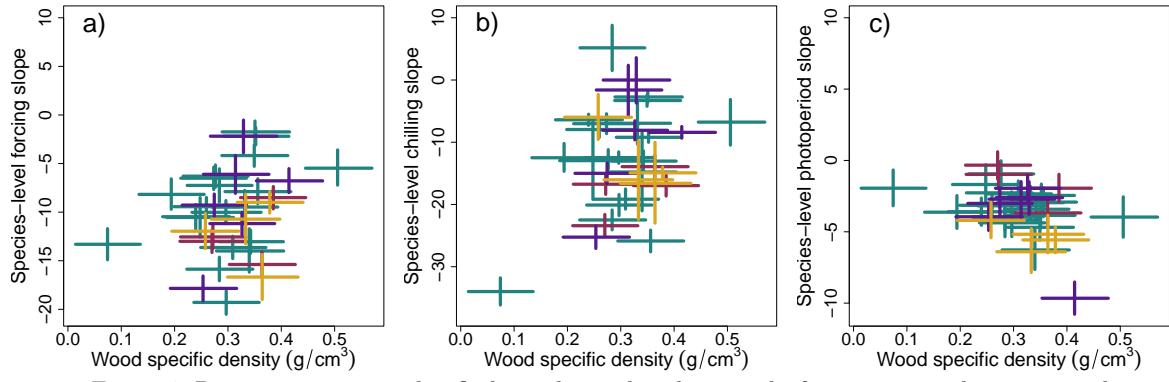


Figure 4: Despite previous studies finding relationships between leaf out timing and species wood xylem structures, we did not find clear differences in species-level estimates of cue responses with wood structure or relative to their wood specific densities. Each cross represents the 50% uncertainty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