Traits predict forest phenological responses to photoperiod more than temperature

Deirdre Loughnan[1], Faith A M Jones[1,2], and E M Wolkovich[1,3,4]

January 8, 2026

[1] Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, 2424 Main Mall Vancouver, BC Canada V6T 1Z4.

[2] Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.

[3] Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

[4] Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;

Corresponding Author: Deirdre Loughnan deirdre.loughnan@ubc.ca

Running title: Traits drive photoperiod cues in budburst

Summary

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

Introduction

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

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 be 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. Previous studies have found high variation in phenology in observational studies—even for the same species when observed over different years or sites (Primack et al., 2009; Chuine et al., 2010), but variation is usually much smaller when calculated from controlled experiments, which suggest that phenological variation can be consistently decomposed into its environmental cues (e.g., temperature and photoperiod Chuine and Cour, 1999; Harrington and Gould, 2015; Flynn and Wolkovich, 2018).
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 could begin to disentangle the environmental cues that shape phenology from those shaped by other trait differences in plant growth strategies.

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

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. We decompose the high phenological variation in budburst date by using experiments to estimate three major phenological cues for woody plant budburst: chilling (cool winter temperatures), forcing (warm spring temperatures), and photoperiod. We predict that early spring species will budburst before canopy closure, exhibited as smaller responses to temperature and photoperiod. These species should have traits associated with acquisitive growth, particularly shorter heights, smaller trunk or stem diameters, with lower investment in wood structure and leaf tissue, resulting in low wood specific density, diffuse-porous wood anatomy, and low leaf mass area, but high leaf nitrogen content for a greater photosynthetic potential. In contrast, we predict species with later budburst to predominately include canopy species that express more conservative growth strategies and require more chilling, warmer forcing, and longer photoperiods. These species should incur greater investments in long-lived tissue, with ring-porous wood anatomy, taller heights and greater diameter, denser wood and high leaf mass area, but low leaf nitrogen content. We then used a joint-modeling approach to estimate the relationships between these plant traits and phenological responses to cues, while partitioning the variance from species- and population-level differences.

Materials and Methods

Field sampling

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

Functional traits

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

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

Growth chamber study

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

Statistical Analysis

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

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

$$Y_{\text{trait}_{i,j}} \sim Normal(\mu_{i,j}, \sigma^2_{\text{m}}) \tag{1}$$

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

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

$$\tag{4}$$

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

$$\tag{6}$$

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

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

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

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

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

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

with

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

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

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

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

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

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

$$\tag{14}$$

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

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

Results

Across our eight populations, we measured 47 species of which 28 were in our eastern transect and 22 in our western transect. These include species dominant in both the understory and canopy layer,

with our eastern community consisting of 13 shrubs and 15 trees, our western community consisting of 18 shrubs and 4 trees, and three species that occurred in both transects. In total we measured traits of 1428 unique individuals between the two transects across our five *in situ* traits: height (n = 1317), diameter (n = 1220), wood stem density (n = 1359), leaf mass area (n = 1345), leaf nitrogen content (n = 1351). Across our two growth chamber studies, we made observations of 4211 samples, with our observations of budburst spanning 82 and 113 days for our eastern and western studies respectfully.

Most of our traits showed some variation by latitude within each transect, with a strong interactive effect between transect and latitude (Fig. 2). Leaf nitrogen content was the only trait to vary with latitude alone, with low latitude communities on both our eastern and western transects having greater values of leaf nitrogen content than communities at higher latitudes (-0.1, UI: -0.2, 0.0, Table S6). The strongest negative interaction was observed for height (-0.2, UI: -0.4, 0.0), while the strongest positive interaction was observed for leaf mass area (0.5, UI: 0.4, 0.6).Height and wood stem density both exhibited negative transect by latitude interactions (-0.2, UI: -0.4, 0.0 for our height model and -0.1, UI: -0.2, -0.1 for our wood stem density model), with woody species in our eastern communities exhibited greater heights and wood stem densities with increasing latitude, but decreasing values with latitude in our western communities (Fig. 2 a and c). In contrast, diameter and leaf mass area both exhibited positive transect by latitude interactions (0.5, UI: 0.1, 0.9 for our diameter model and 0.5, UI: 0.4, 0.6 for our leaf mass area model), with plants at higher latitudes having increasing diameters in both our eastern and western communities but decreasing leaf mass areas in our eastern communities and increasing values in our western communities (Fig. 2 b and d). In addition to the differences we found across populations, we also observed considerable differences between individual species, which varied considerably and up to 7 fold for some traits (Fig. 3).

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

Temperature cues ($\beta_{\text{trait.chilling}}$ and $\beta_{\text{trait.forcing}}$) exhibited no relationships with individual traits, but by accounting for the effects of leaf or wood traits, we found the importance of our three cues to vary by trait. Chilling (β_{chilling}) was the strongest cue of budburst in our models of height (-13.4 m per standardized chill portions, UI: -17.2, -9.9), diameter (-12.5 cm per standardized chill portions, UI: -16.2, -8.6), wood stem density (-20.9 g/cm^3 per standardized chill portions, UI: -33.2, -9.8), and leaf nitrogen content (-35.1 percent per standardized chill portions, UI: -68.1, -4.1), with more chilling advancing budburst. Our model of leaf mass area, however, estimated photoperiod as the strongest cue ($\beta_{\text{photoperiod}}$, -14.0, UI: -23.1, -3.5). After accounting for the effects of traits, only our height and diameter model found all three environmental cues to drive budburst timing (Tables S2, S3). Our models of wood stem density and leaf nitrogen content in turn found temperature cues alone to shape budburst (Tables S4, S6), while our model of leaf mass area found a large response to only photoperiod (Table S5).

In synthesizing the effects of multiple traits across species, our results can be used to make generalizations across ecologically important groups of species. But only some of our models estimated clear gradients in species timing between trees and shrubs. In particular, we found height to have large correlations between budburst timing and trait values, with earlier estimates of budburst for shrubs (with a mean day of budburst of 10)—especially under greater cues—and later budburst estimates for trees (with a mean day of budburst of (17.3, Fig. S1). Diameter at breast height showed similar trends as estimates from our height model (results not shown). But this was not the case for our two leaf traits. Leaf nitrogen content, for example, showed no distinct separation between shrub and tree functional groups (Fig. S1).

Discussion

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

Cues and functional traits

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

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

The absence of trait-cue relationships between budburst and wood structure and wood stem density 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). Using wood density as alternative measure of wood structure (wood density positively correlates with xylem resistance to embolism, Hacke et al., 2001), we did not find clear association between our three phenological cues and xylem structure, despite our data also focusing on species in temperate forests. Most

of the individuals we measured, however, did have a fairly narrow range of wood specific densities (varying from 0.2 to 0.6 g/cm^3) relative to the variation in wood density observed in studies that focus on tropical species or span a more global distribution (?Savage et al., 2022; ?). We did find some variation in wood density across our different sites and with latitude. The larger wood densities we observed at higher latitudes in our eastern transect 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. By considering the tradeoffs and differences in cues that simultaneously shape plants growth strategies, we can more accurately forecast species phenology and community dynamics under future climates.

References

Augspurger, C. K. 2009. Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. Functional Ecology 23:1031–1039.

Basler, D., and C. Körner. 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. Tree Physiology 34:377–388.

Buonaiuto, D. M., E. M. Wolkovich, and M. J. Donahue. 2023. Experimental designs for testing the interactive effects of temperature and light in ecology : The problem of periodicity. Functional Ecology 37:1747–1756.

Cabon, A., L. Fernández-de-Uña, G. Gea-Izquierdo, F. C. Meinzer, D. R. Woodruff, J. Martínez-Vilalta, and M. De Cáceres. 2020. Water potential control of turgor-driven tracheid enlargement in Scots pine at its xeric distribution edge. New Phytologist 225:209–221.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366.

Chuine, I. 2000. A unified model for budburst of trees. Journal of Theoretical Biology 207:337–347.

Chuine, I., and P. Cour. 1999. Climatic determinants of budburst seasonality in four temperate-zone tree species. New Phytologist 143:339–349.

Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. Science 329:277–278.

Cohen, J. M., M. J. Lajeunesse, and J. R. Rohr. 2018. A global synthesis of animal phenological responses to climate change. Nature Climate Change 8:224–228.

De La Riva, E. G., M. Olmo, H. Poorter, J. L. Ubera, and R. Villar. 2016. Leaf Mass per Area (LMA) and Its Relationship with Leaf Structure and Anatomy in 34 Mediterranean Woody Species along a Water Availability Gradient. PLOS ONE 11:e0148788.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet'ev, H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function. Nature 529:167–171.

Finn, G. A., A. E. Straszewski, and V. Peterson. 2007. A general growth stage key for describing trees and woody plants. Annals of Applied Biology 151:127–131.

Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. New Phytologist 219:1353–1362.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Gotelli, N. J., and G. R. Graves. 1996. The temporal niche. Pages 95–112 *in* Null Models In Ecology. Smithsonian Institution Press, Washington, D. C.

Green, S. J., C. B. Brookson, N. A. Hardy, and L. B. Crowder. 2022. Trait-based approaches to global change ecology: moving from description to prediction. Proceedings of the Royal Society B: Biological Sciences 289:1–10.

Hacke, U. G., J. S. Sperry, W. T. Pockman, S. D. Davis, and K. A. McCulloh. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126:457–461.

Harrington, C. A., and P. J. Gould. 2015. Tradeoffs between chilling and forcing in satisfying dormancy requirements for Pacific Northwest tree species. Frontiers in Plant Science 6:1–12.

Hoegh-Guldberg, O., D. Jacob, M. Taylor, M. Bindi, S. Brown, I. Camilloni, A. Diedhiou, R. Djalante, K. Ebi, F. Engelbrecht, J. Guiot, Y. Hijioka, S. Mehrotra, A. Payne, S. Seneviratne, A. Thomas, R. Warren, and G. Zhou. 2018. Impacts of 1.5 °C Global Warming on Natural and Human Systems. In: Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of . Tech. rep., Cambridge University Press, Cambridge, UK and New York, NY, USA.

Kharouba, H. M., J. Ehrlén, A. Gelman, K. Bolmgren, J. M. Allen, S. E. Travers, and E. M. Wolkovich. 2018. Global shifts in the phenological synchrony of species interactions over recent decades. Proceedings of the National Academy of Sciences 115:5211–5216.

Körner, C., and D. Basler. 2010. Phenology Under Global Warming. Science 327:1461–1463.

Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. Global Change Biology 20:170–182.

Lechowicz, M. J. 1984. Why Do Temperate Deciduous Trees Leaf Out at Different Times? Adaptation and Ecology of Forest Communities. The American Naturalist 124:821–842.

Lopez, O. R., K. Farris-Lopez, R. A. Montgomery, and T. J. Givnish. 2008. Leaf phenology in relation to canopy closure in southern Appalachian trees. American Journal of Botany 95:1395–1407.

Loughnan, D., F. A. Jones, G. Legault, C. J. Chamberlain, D. M. Buonaiuto, A. K. Ettinger, M. Garner, D. S. Sodhi, and E. M. Wolkovich. 2025. Budburst timing within a functional trait framework. Journal of Ecology 00:1–12.

Loughnan, D., and E. M. Wolkovich. in prep. Temporal assembly of woody plant communities shaped equally by evolutionary history as by current environments .

Luedeling, E. 2020. chillR: Statistical Methods for Phenology Analysis in Temperate Fruit Trees. https://CRAN.R-project.org/package=chillR.

MacFarlane, D. W. 2020. Functional Relationships Between Branch and Stem Wood Density for Temperate Tree Species in North America. Frontiers in Forests and Global Change 3.

MacFarlane, D. W., and B. Kane. 2017. Neighbour effects on tree architecture: functional trade-offs balancing crown competitiveness with wind resistance. Functional Ecology 31:1624–1636.

Magarik, Y. A., L. A. Roman, and J. G. Henning. 2020. How should we measure the dbh of multi-stemmed urban trees? Urban Forestry & Urban Greening 47:1–11.

Osada, N. 2017. Relationships between the timing of budburst, plant traits, and distribution of 24 coexisting woody species in a warm-temperate forest in Japan. American Journal of Botany 104:550–558.

Panchen, Z. A., R. B. Primack, B. Nordt, E. R. Ellwood, A. Stevens, S. S. Renner, C. G. Willis, R. Fahey, A. Whittemore, Y. Du, and C. C. Davis. 2014. Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. New Phytologist 203:1208–1219.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, W. K. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas, P. B. Reich, L. Poorter, I. J. Wright, P. Ray, L. Enrico, J. G. Pausas, A. C. de Vos, N. Buchmann, G. Funes, F. Quétier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter Steege, M. G. A. van der Heijden,

L. Sack, B. Blonder, P. Poschlod, M. V. Vaieretti, G. Conti, A. C. Staver, S. Aquino, and J. H. C. Cornelissen. 2013. New handbook for standardized measurement of plant functional traits worldwide. Australian Journal of Botany 61:167–234.

Peters, R. L., K. Steppe, H. E. Cuny, D. J. De Pauw, D. C. Frank, M. Schaub, C. B. Rathgeber, A. Cabon, and P. Fonti. 2021. Turgor – a limiting factor for radial growth in mature conifers along an elevational gradient. New Phytologist 229:213–229.

Pollock, L. J., W. K. Morris, and P. A. Vesk. 2012. The role of functional traits in species distributions revealed through a hierarchical model. Ecography 35:716–725.

Primack, R. B., I. Ibáñez, H. Higuchi, S. D. Lee, A. J. Miller-Rushing, A. M. Wilson, and J. A. Silander. 2009. Spatial and interspecific variability in phenological responses to warming temperatures. Biological Conservation 142:2569–2577.

R Development Core Team. 2017. R: A language and environment for statistical computing.

Reich, P. B. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. Journal of Ecology 102:275–301.

Sakai, A., and W. Larcher. 1987. Frost Survival of Plants: Responses and adaptation to freezing stress. Springer-Verlag, Berlin, Heidelberg.

Savage, J. A., T. Kiecker, N. McMann, D. Park, M. Rothendler, and K. Mosher. 2022. Leaf out time correlates with wood anatomy across large geographic scales and within local communities. New Phytologist 235:953–964.

Schweingruber, F., and W. Landolt. 2010. The xylem database.

Stan Development Team. 2018. RStan: the R interface to Stan. R package version 2.17.3.

Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, D. G. Johns, I. D. Jones, D. I. Leech, E. B. MacKay, D. Massimino, S. Atkinson, P. J. Bacon, T. M. Brereton, L. Carvalho, T. H. Clutton-Brock, C. Duck, M. Edwards, J. M. Elliott, S. J. Hall, R. Harrington, J. W. Pearce-Higgins, T. T. Høye, L. E. Kruuk, J. M. Pemberton, T. H. Sparks, P. M. Thompson, I. White, I. J. Winfield, and S. Wanless. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535:241–245.

Violle, C., M. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Wiemann, M. C., and W. G. Bruce. 2002. Geographic variation in wood specific gravity: effects of latitude, temperature, and preciptitation. Wood and Fiber Science 34:96–107.

Wolkovich, E. M., and A. K. Ettinger. 2014. Back to the future for plant phenology research. New Phytologist 203:1021–1024.

Wright, I. J., M. Westoby, P. B. Reich, J. Oleksyn, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornellissen, M. Diemer, J. Flexas, J. Gulias, E. Garnier, M. L. Navas, C. Roumet, P. K. Groom, B. B. Lamont, K. Hikosaka, T. Lee, W. Lee, C. Lusk, J. J. Midgley, Ü. Niinemets, H. Osada, H. Poorter, P. Pool, E. J. Veneklaas, L. Prior, V. I. Pyankov, S. C. Thomas, M. G. Tjoelker, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Yin, J., J. D. Fridley, M. S. Smith, and T. L. Bauerle. 2016. Xylem vessel traits predict the leaf phenology of native and non-native understorey species of temperate deciduous forests. Functional Ecology 30:206–214.

460 Zohner, C. M., B. M. Benito, J.-C. Svenning, and S. S. Renner. 2016. Day length unlikely to constrain
461 climate-driven shifts in leaf-out times of northern woody plants. Nature Climate Change 6:1120–
462 1123.

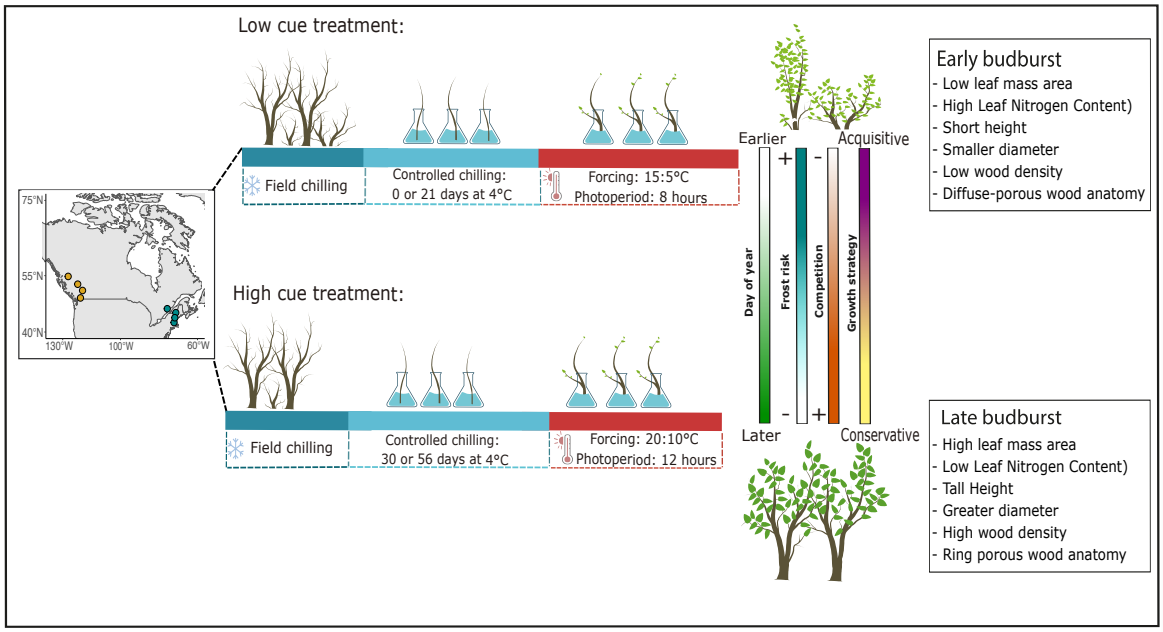

Figure 1: We collected traits data and branch cuttings from plants growing within eight sites, across two transects in eastern and western North America. Cuttings were used in two controlled environment studies in which we applied an high and low chilling, forcing, and photoperiod treatments respectively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

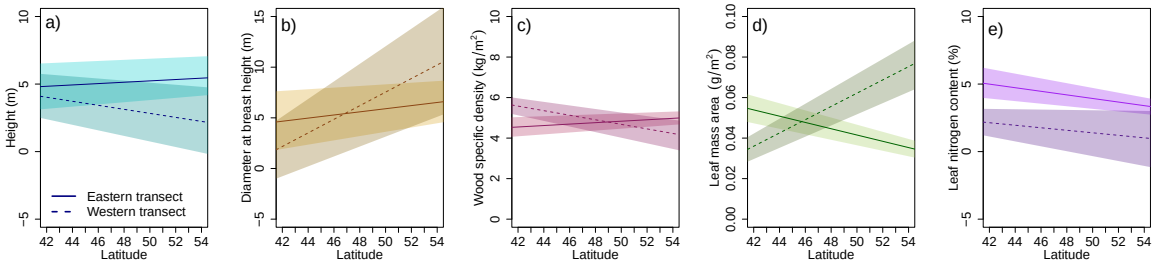

Figure 2: We found a. height, b. diameter, c. branch stem density, and d. leaf mass area to all experience a strong interaction between latitude and transect, e. while leaf nitrogen content showed a strong effect of latitude alone.

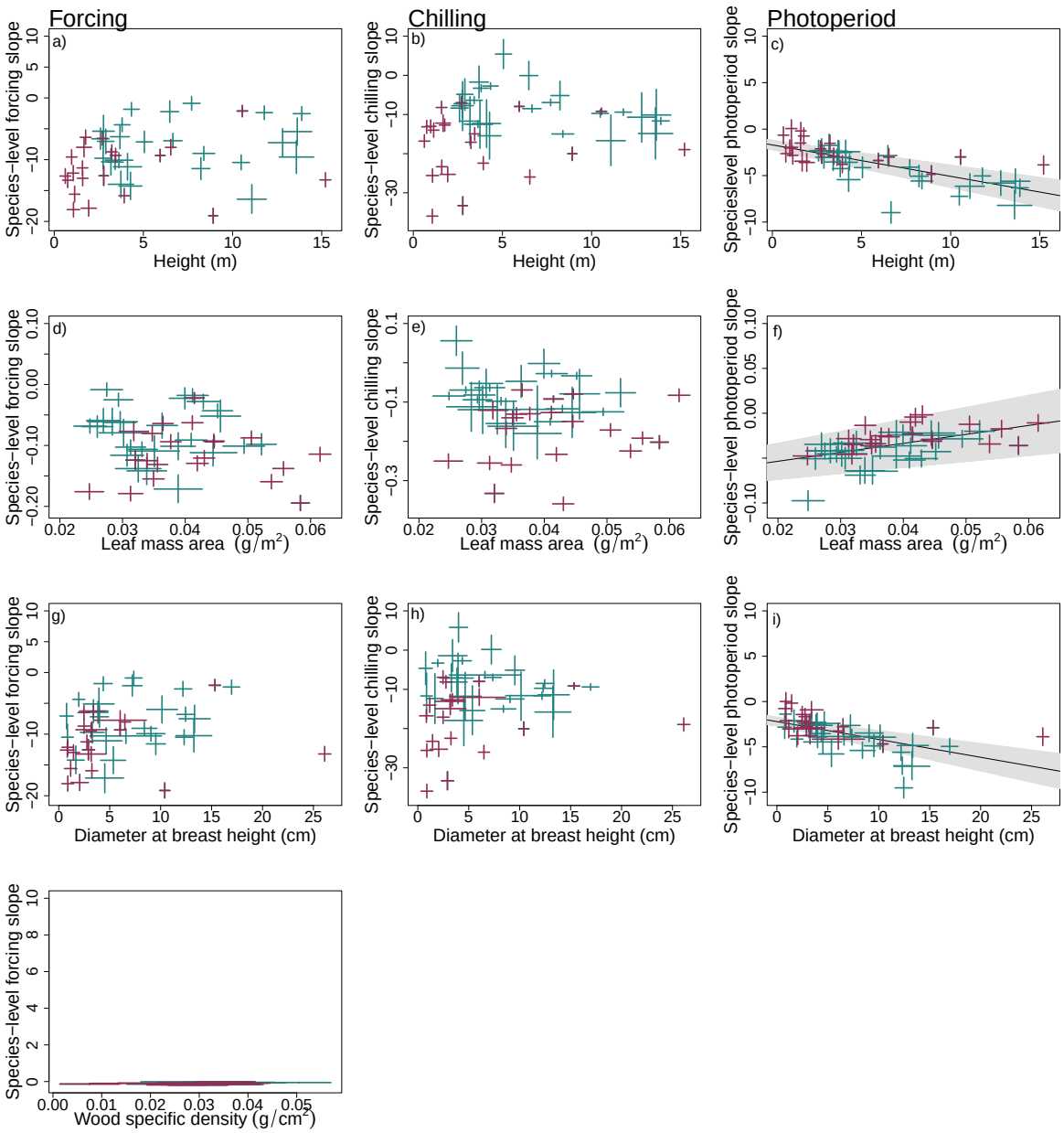

Figure 3: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species shown in red and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

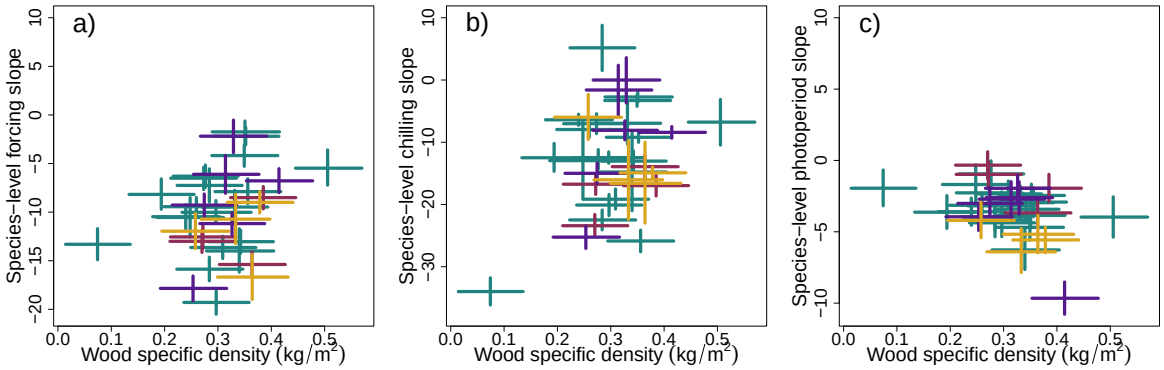

Figure 4: Despite previous studies finding relationships between leaf out timing and species wood xylem structures, we did not find clear differences in species-level estimates of cue responses with wood structure or relative to their wood specific densities. Each cross represents the 50% uncertainty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