

# Differences in traits predict forest phenological responses to photoperiod more than temperature

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Running title: Traits drive photoperiod cues in budburst

## Summary

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

## 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; ?). 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 be promising to 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.

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 of these studies are observational and conducted at the landscape scale (Menzel et al., 2006; ?). In contrast, findings from controlled environment experiments suggest that phenological variation can be consistently decomposed into its cues (Laube et al., 2014; ?). Given the importance of phenology in defining species temporal niches and the environmental conditions of 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.

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 (Sakai and Larcher, 1987; Gotelli and Graves, 1996; Augspurger, 2009) and greater competition later in the season (CITES). Species that varying the timing of leafout, should therefore exhibit traits and growth strategies that allow them to tolerate or avoid these abiotic risks. 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 that are shaped by other traits differences in plant growth strategies.

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 other 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.

We tested whether phenological variation was aligned with existing trait frameworks using data on spring budburst paired with a suite of traits that capture acquisitive to conservative growth strategies (Wright et al., 2004; Reich, 2014). Our study spans across species of temperate deciduous forests in North America and includes both shrubs and tree species. Seasonal differences in environmental conditions between early and late spring create larger gradients in frost risk, soil nutrients, and light availability, in addition to differences in biotic interactions, from herbivory or competition. These seasonal differences in the environment may select for variation in species growth strategies and as a result, correlate with woody plant traits. We predict that early spring species will budburst before canopy closure and have traits we associate with acquisitive growth—particularly shorter heights, small diameters at breast height (DBH), with lower investment in wood structure and leaf tissue—as reflected by low wood specific density (WSD), diffuse-porous wood anatomy, and low leaf mass area—but greater photosynthetic potential as indicated by high leaf nitrogen content (LNC). In contrast, we predict species with later budburst will predominately include canopy species that express more conservative growth strategies—exemplified by their greater investments in long-lived tissue, with ring-porous wood anatomy, taller heights and greater DBH, WSD and LMA, but low LNC.

Here, we decompose high phenological variation in budburst date by estimating phenological cues using experiments, then combine multiple sources of variation using a joint modeling approach. We estimate the three major phenological cues for woody plant budburst: two temperature cues—chilling (associated with cool winter temperatures) and forcing (associated with warm spring temperatures)—and photoperiod. These cues correlate with early to late phenology, with early species (which we predict have acquisitive traits) budbursting with less chilling and lower forcing temperatures (smaller responses to temperature and photoperiod), while later species (which we predict have conservative traits) have larger responses and requiring more chilling, warmer forcing conditions, and longer photoperiods. Using a powerful joint-modeling approach, we estimate the effects of other plant traits on 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. ??). 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 DBH), wood specific density (WSD), leaf mass area (LMA), and the percent leaf nitrogen content (LNC). 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, using a TruePulse 200L rangefinder and used a base height of 1.37 m to measure DBH (?). 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 Canon flatbed scanner (CanoScan Lide 220) and estimated leaf area using the ImageJ software (version 2.0.0).

## 136 Growth chamber study

137 For our growth chamber study, we collected branch cuttings from our highest and lowest latitude pop-  
 138 ulations in each transect, with sampling in our eastern study occurring from 20-28 January 2015 and  
 139 sampling for our western study from 19-28 October 2019. In both our eastern and western controlled  
 140 environment study, we included two temperature treatments and photoperiod, for a total of eight  
 141 distinct treatments. Our treatments included two levels of chilling—with our eastern study having no  
 142 additional chilling or 30 days at 4°C, and our western study 21 days or 56 days of chilling at 4°C, with  
 143 all non-field chilling occurring under dark conditions. Our forcing treatments included either a cool  
 144 regime of 15:5°C or a warm regime of 20:10°C, and our photoperiod treatments consisted of either  
 145 a 8 or 12 hour photoperiod. We recorded budburst stages of each sample every 1-3 days for up to  
 146 four months, defining the day of budburst as the day of budbreak or shoot elongation, defined as code  
 147 07 by Finn et al. (2007). For a more detailed discussion of study sample collection and methods see  
 148 Flynn and Wolkovich (2018) for details on our eastern study and Loughnan and Wolkovich (in prep)  
 149 for details on our western study.

## 151 Statistical Analysis

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

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

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

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

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

$$\quad (4)$$

$$\boldsymbol{\alpha}_{\text{trait}} = \{\alpha_{\text{trait}_1}, \dots, \alpha_{\text{trait}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{trait}} \sim \mathcal{N}(0, \sigma_{\text{trait}}^2) \quad (5)$$

$$\quad (6)$$

164 We include transect as a dummy variable (0/1) and latitude as a continuous variable in our model. We  
 165 modeled traits using natural units, with the exception of LMA, which was rescaled by 100 for numeric  
 166 stability in the model.

167  
 168 Our model also includes partial pooling for species—which controls for variation in the number of trait  
 169 estimates per species and trait variability—using these species-level estimates as predictors for each  
 170 cue ( $\beta_{\text{chilling},j}$ ,  $\beta_{\text{forcing},j}$ ,  $\beta_{\text{photoperiod},j}$ ).

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

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

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

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 ( $\sigma_d^2$ ), as well as the variation in cues not attributed to the trait (using partial pooling).

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

with

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

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

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

We modeled each trait individually, with the exception of ring-porosity, which we compared across species using the posterior estimates of our WSD model, in order 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 converting chilling temperatures to total chill portions, including both the chilling experienced in the field prior to sampling and during the experiment in our 4°C chilling chambers, using local weather station data and used the chillR package to calculate total chill portions (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).

We used weakly informative priors unique to each trait model. 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 ( $n_{\text{eff}}$ ) 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 the 90% uncertainty interval, interpreting parameter estimates with UI that overlap to be statistically similar to each other and intervals 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 traits: height ( $n = 1317$ ), diameter at breast height (DBH,  $n = 1220$ ), wood stem density (WSD,  $n = 1359$ ), leaf mass area (LMA,  $n = 1345$ ), leaf nitrogen content (LNC,  $n = 1351$ ). 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. 1). Leaf nitrogen content was the only trait to vary with latitude alone, with low latitude communities having greater values of LNC than communities at higher latitudes (-0.1, UI: -0.2, -0.06, Table ??). Overall, woody species in our eastern community exhibited greater heights, DBH, and WSD but decreases in LMA with increasing latitude. But in our western communities height and WSD decreased with latitude, while DBH and LMA both increased (Fig. 1). 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. 2).

How our three cues shaped budburst timing varied with traits. In accounting for the effects of traits on budburst, we found that height, DBH, LMA, and LNC all had a strong relationship with photoperiod (Tables ??, ??, ??, ??). For height, DBH, and LNC, species with higher trait values had stronger responses to photoperiod, with species requiring longer photoperiods to budburst (Fig. 2 c, i, o). Species with greater LMA, however, had weaker photoperiod responses, requiring shorter photoperiods to budburst (Fig. 2 f). Despite finding no relationships between temperature cues and other traits, most models estimated chilling as the strongest cue of budburst (Table ??-??). But only our model of height and DBH had strong responses to all three cues (Table ??, ??). Our model of LMA estimated a strong response to only photoperiod (Table ??) and our LNC model a strong response to chilling and photoperiod (Table ??). Our model of WSD estimated strong cue responses in budburst to temperature cues only (Table ??), but we found no clear relationships between cue responses and the different types of wood structure (Fig. ??). These findings suggest that relationships with additional traits can alter the effects and relative importance of cues on budburst. This, paired with large species-level variation, may cause variation in the estimated order of species relative budburst dates across the different models.

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—especially under greater cues—and later budburst estimates for trees (Fig. ??). 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. ??).

## Discussion

Of the six traits we studied, we found budburst responses to one or more phenological cue, but only three of those traits fit within a gradient of acquisitive to conservative growth. Using our joint model-

ing approach, we estimated how these traits interact with cues to shape species budburst, and found that photoperiod—often the weakest cue of budburst (Laube et al., 2014; Zohner et al., 2016; Flynn and Wolkovich, 2018)—may be the most important cue in trait-phenology relationships. In general, we found trait patterns to vary between our eastern and western transects and with latitude, with some traits also varying with community composition. Collectively our results provide new insights into the complexity of the mechanisms that underlie the relationships between traits and environmental cues, while also challenging our existing understanding of these processes.

The large differences in our community assemblages may explain some of the trait variation we observed spatially. Our western sites exhibited lower heights and WSD, expressing a more acquisitive growth strategies on average. Given that our western community is shrub dominated, this suggests these species are more likely to utilize resources early in the season prior to canopy closure. But at the species-level the relationships between traits and budburst cues only partially supported our predictions for how phenology relates to species overall growth strategies. We predicted species with acquisitive traits—particularly small trees with low wood densities, and leaves with low LMA, and high LNC—to have early budburst via small temperature and photoperiod responses. But we found traits to differ in which cues shape phenology. As predicted, acquisitive species with smaller heights and DBH did have smaller photoperiod responses (associated with later budburst). But contrary to our prediction, acquisitive species with low LMA showed larger responses to photoperiod, while leaves with high LNC had strong photoperiod responses. We also did not find any relationships between any of our focal traits and temperature. These results suggest that phenology only partially aligns with trends found in established trait frameworks, but also offer new insight into potential tradeoffs in how varying physiological processes shape species temporal niches.

In comparing our results with a global meta-analysis of tree trait relationships with budburst cues (Loughnan et al., in prep), 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 of LMA and therefore equivalent to low LMA) exhibited large responses to photoperiod (Loughnan et al., in prep). 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. It is possible that the unexpected trends we observed in our results are due to selection on other physiological processes, as many of our traits are associated with one or more ecological function (Wright et al., 2004; Pérez-Harguindeguy et al., 2013; Reich, 2014), such as the relationships between LMA and leaf lifespan or decomposition rates in addition to light capture (De La Riva et al., 2016).

## How traits shape species temporal niches

Individuals’ temporal niches are shaped by numerous—and complex—interactions with local environmental conditions and species assemblages. But studies that focus only on phenology fail to account for interactions between other traits and cues that also contribute to species temporal niches. Previous research that only considered phenology has shown budburst timing to be primarily driven by temperature and only weakly by photoperiod (Chuine et al., 2010; Basler and Körner, 2014; Laube et al., 2014). We, however, found no traits that correlate with responses to temperature, suggesting other cues are impacting leaf and structural traits in temperate forests. Traits like LMA can vary with soil moisture, with variation in leaf area allowing plants to reduce evaporation, selecting for high LMA under dry conditions (De La Riva et al., 2016). As a cue, soil moisture and changes in water use are known to shape 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 LMA and the absence of relationships with temperature. Thus, fully understanding how species growth strategies

correlate with phenology may require the consideration of cues known to shape other plant traits.

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

## Using functional traits to predict climate change responses

Our results offer novel insights into how broader correlations between plant trait syndromes and phenological cues can help predict phenological responses in plant communities with climate change. As temperatures rise, particularly at higher latitudes (Hoegh-Guldberg et al., 2018), these cues will become larger and potentially select for earlier growth in some species, but photoperiod cues will remain fixed. The relationships between photoperiod and other traits we observed have the potential to limit species abilities to track temperatures and constrain the extent to which woody plant phenologies 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 LMA. These constraints could have cascading effects on forest communities, as variable species responses to increasing temperatures further alter species temporal niches 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 its importance as a cue. It is therefore advantageous for photoperiod to still be included as part of a more holistic approach to studying the relationships between phenology and plant traits when forecasting the future impacts of climate change on communities.

## References

- Augspurger, C. K. 2009. Spring 2007 warmth and frost : phenology , damage and refoilation 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.



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

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

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

351 Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. *Science*  
352 329:277–278.

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

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

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

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

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

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

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

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

375 Gross, K. L., M. R. Willig, L. Gough, R. Inouye, and S. B. Cox. 2000. Patterns of species density and  
376 productivity at different spatial scales in herbaceous plant communities. *Oikos* 89:417–427.

377 Hacke, U. G., J. S. Sperry, W. T. Pockman, S. D. Davis, and K. A. McCulloh. 2001. Trends in wood  
378 density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*  
379 126:457–461. Publisher: Springer Science and Business Media LLC.

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

386 Kharouba, H. M., J. Ehrlén, A. Gelman, K. Bolmgren, J. M. Allen, S. E. Travers, and E. M. Wolkovich.  
387 2018. Global shifts in the phenological synchrony of species interactions over recent decades. *Pro-*  
388 *ceedings of the National Academy of Sciences* 115:5211–5216.

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

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

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

394 Loughnan, D., F. A. Jones, G. Legault, C. J. Chamberlain, D. M. Buonaiuto, A. K. Ettinger, M. Gar-  
395 ner, D. S. Sodhi, and E. M. Wolkovich. in prep. Woody plant phenological responses are strongly  
396 associated with key functional traits .

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

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

401 MacFarlane, D. W. 2020. Functional Relationships Between Branch and Stem Wood Density for  
402 Temperate Tree Species in North America. *Frontiers in Forests and Global Change* 3. Publisher:  
403 Frontiers Media SA.

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

407 Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aaasa, R. Ahas, K. Alm-Kübler, P. Bissolli,  
408 O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Don-  
409 nelly, Y. Filella, K. Jatzak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová,  
410 H. Scheffinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Züst. 2006.  
411 European phenological response to climate change matches the warming pattern. *Global Change*  
412 *Biology* 12:1969–1976.

413 Osada, N. 2017. Relationships between the timing of budburst, plant traits, and distribution of 24  
414 coexisting woody species in a warm-temperate forest in Japan. *American Journal of Botany* 104:550–  
415 558.

416 Panchen, Z. A., R. B. Primack, B. Nordt, E. R. Ellwood, A. Stevens, S. S. Renner, C. G. Willis,  
417 R. Fahey, A. Whittemore, Y. Du, and C. C. Davis. 2014. Leaf out times of temperate woody plants  
418 are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytologist* pages  
419 1208–1219.

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

422 Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-  
423 Harte, W. K. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas, P. B. Reich,  
424 L. Poorter, I. J. Wright, P. Ray, L. Enrico, J. G. Pausas, A. C. de Vos, N. Buchmann, G. Funes,  
425 F. Quétier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter Steege, M. G. A. van der Heijden,  
426 L. Sack, B. Blonder, P. Poschlod, M. V. Vaieretti, G. Conti, A. C. Staver, S. Aquino, and J. H. C.  
427 Cornelissen. 2013. New handbook for standardized measurement of plant functional traits worldwide.  
428 *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. Publisher: Wiley.

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 precipitation. *Wood and Fiber Science* 34:96–107.

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.

Wright, J. P., A. S. Flecker, and C. G. Jones. 2003. Local vs. landscape controls on plant species richness in Beaver meadows. *Ecology* 84:3162–3173.

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.

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

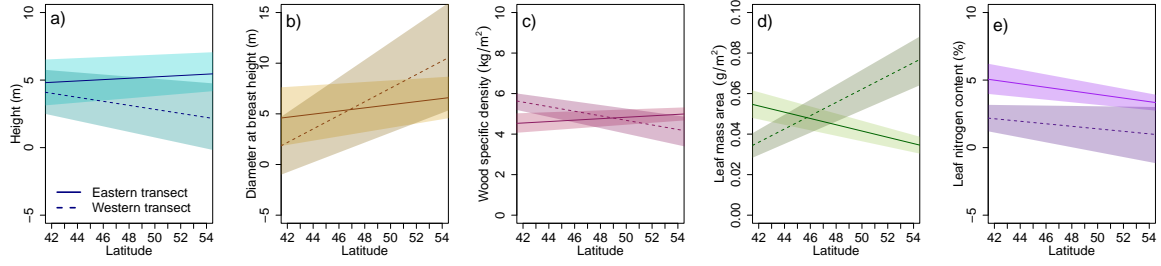


Figure 1: We found geographic differences for only one of our functional traits, the majority exhibiting no differences between latitudes or across transects. Depicted are the spatial trends for, a. height, b. diameter at base height, c. wood specific density, d. leaf mass area, and e. leaf nitrogen content. Dashed lines represent the western transect and solid lines the eastern transect.

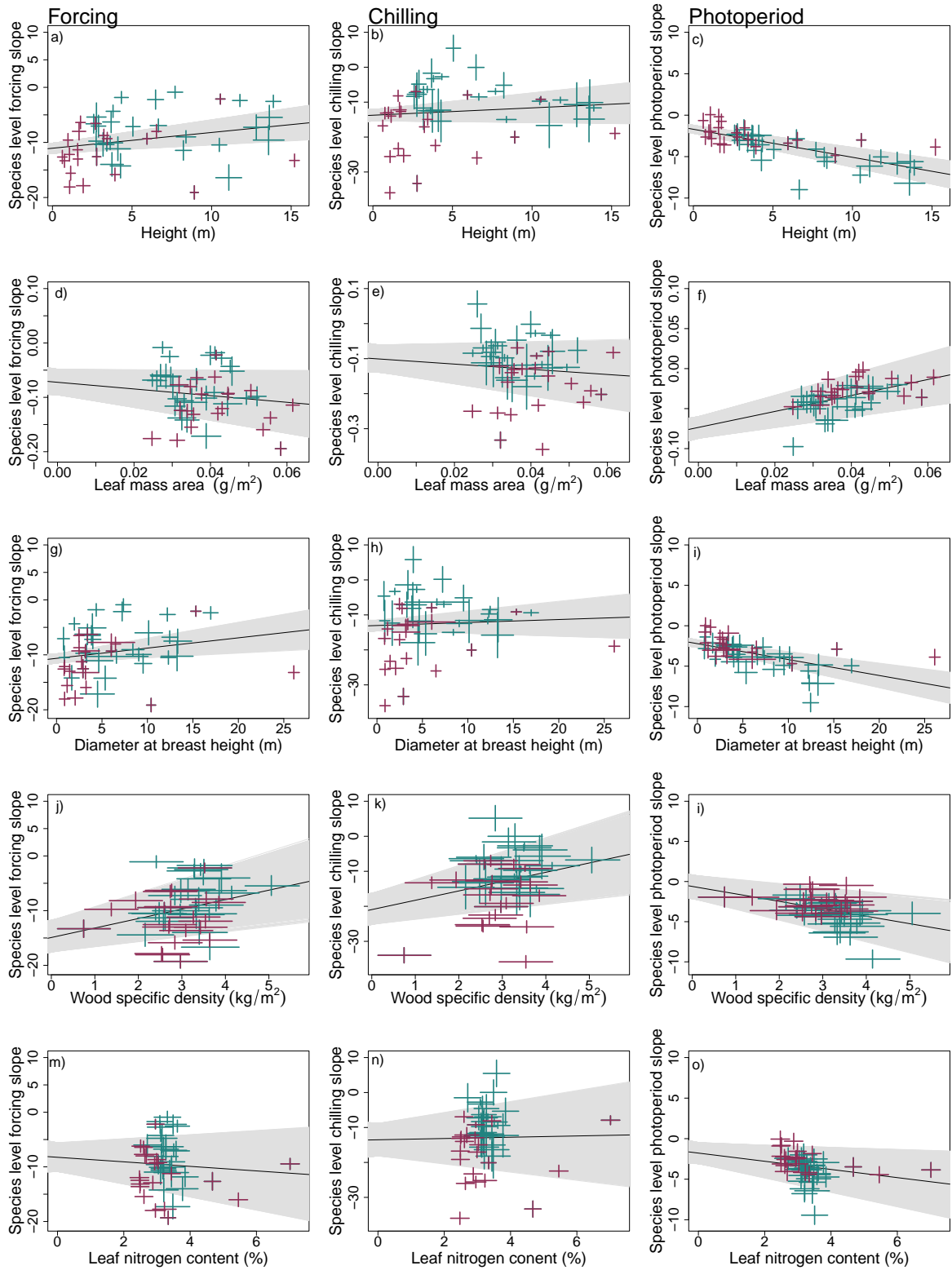


Figure 2: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter at breast height, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species 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.