Differences in leaf and wood traits predict phenological sensitivity to daylength more than temperature

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January 25, 2024

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Introduction

Climate change is having profound effects on ecological communities, influencing species fitness, interactions, and the structure of ecological communities. Recent shifts in species phenologies—or timing of life history events—has been cited as the strongest evidence of climate change impacts, with widespread advances being observed across the tree of life (Root et al., 2003; Parmesan and Yohe, 2003). Across species we find high variability in phenological responses (Thackeray et al., 2016; Cohen et al., 2018; Kharouba et al., 2018), but overall we have a poor understanding of the physiological mechanisms or specific environmental factors driving the observed variation across species and populations.

Phenology is just one of many traits that are shaped by environmental cues. Our understanding of the interdependence between phenological events and species overall growth strategies—which we infer from other traits (?)—are relatively poor. It is critical to identify these relationships to better understand the mechanisms that are driving species phenological and trait variation, especially if we are to accurately predict future changes in community dynamics and ecosystem services, including pollination and carbon sequestration (Cleland et al., 2007).

Trait variation can arise from differences in environmental drivers at both the proximate and ultimate scale. Proximate phenological drivers include local environmental factors, such as temperature, soil moisture, and daylength. At this scale, variation in temperatures can alter the timing of plant growth (Menzel et al., 2006) or select for organisms body size (Audzijonyte et al., 2020). But the environmental factors at the ultimate scale also change across spatial and temporal gradients. Within a growing season, this can produce greater abiotic stress early in the season through high risks of frost events, while also producing greater biotic stress later in the season through a more competitive environment. These ultimate drivers determine how species respond to environmental cues and the effects of biotic interactions to shape species ecological niche and local species assemblages. Collectively how these proximate and ultimate drivers act on a given species are what shape their overall phenotype. Decades of trait ecology has illustrated the ways in which species phenotypes correlate with their growth strategies and responses to environments. The consistency in these relationships across communities allows trait values to provide inferences of growth strategies and community processes, independent of species identity (McGill et al., 2006). In plants this has led to the development of frameworks such as the leaf economic spectrum (Wright et al., 2004) and wood economic spectrum (Chave et al., 2009). Under these frameworks, trait values are shown to follow distinct gradients that range from acquisitive

growth strategies—with plants producing cheaper tissue and overall faster growth—to conservative strategies—under which plants invest resources in long-lived tissue but grow at slower rates (Wright et al., 2004; Díaz et al., 2016). These traits serve as proxies for difficult to measure physiological processes and responses to biotic interactions (Shipley et al., 2016), but provide considerable insights into the mechanisms shaping plant communities globally.

Drawing on the relationships between traits and species growth strategies, we can further our understanding of how plant communities assemble and the promote species coexistence. To date, many of of these studies have focused on community-level responses, using metrics of functional diversity or community weighted means **?**. But these methods fail to account for the high degrees of intraspecific variation that have been recorded across traits (Albert et al., 2010) and are limited in their ability to account for the diversity of factors that lead to trait variation. To best understand the processes that define species growth strategies and ecological niche, we much account for variation at multiple scales and use analytical methods that can accurately partition variance across its multiple sources.

Phenology itself is considered a trait with high inter and intraspecific variability. Previous studies have demonstrated the high degrees of individual species variation in the relative importance of cues (Laube et al., 2014). It is this variability that is often given as justification for excluding phenology from broader functional trait frameworks. But given the importance of phenology in defining species temporal niche and determining what environmental conditions growth occurs under, we predict phenological variation to correlate with other functional traits and for similar cues to promote acquisitive versus conservative growth strategies.

But species-level differences are not the only source of variation, as there is the potential for spatial variation to also select for species traits and overall phenotypes. Across the distribution of a species there can be considerable differences in temperatures and daylength. Additionally, plant traits may also vary across latitudinal gradients, with differences in woody plant leaf and structural traits. While our previous growth chamber study found no evidence that phenological cues varied spatially (Loughnan and Wolkovich, in prep), previous work in functional traits suggests other traits may exhibit stronger spatial variation in response to gradients in environmental cues (**??**). Through these differences in the competitive landscape and species assemblages, there is the potential for local adaptation in traits across populations. While our previous growth chamber study found no evidence that phenological cues varied spatially (Loughnan and Wolkovich, in prep), previous work in functional traits suggests other traits may exhibit stronger spatial variation in response to gradients in environmental cues.

In our study, we use spring budburst and trait data from woody plants to study the relationship between cues and traits. Environmental conditions across the spring can create strong gradients in frost risk, soil nutrients, and light availability, in addition to differences in biotic interactions, such as decreased herbivore apparency and increased competition. We predict that these differences between early and late season conditions will select for variation in species growth strategies and as a result, correlate with woody plant traits. We predict that species that grow early in the spring 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 density and leaf tissue (low stem specific density and leaf mass area), but greater photosynthetic potential (high leaf nitrogen content (LNC)). In contrast, we predict species with later budburst will include canopy species that express more conservative growth strategies—exemplified by their greater investments in tissue, with taller heights, large DBH, greater SSD and LMA, but low LNC. Similarly, we would predict this variation in species traits to correlate with budburst cues, with species with acquisitive traits showing weaker budburst responses to temperature and daylength cues, but species with conservative growth strategies showing stronger budburst responses to each of cue.

By combining commonly measured plant traits—with known associations with variable growth strategies across environments—with experimental budburst data, we were able to directly test the relationships between species trait phenotypes and the environmental cues that drive phenology. We paired individual-level measurements of woody plant traits with observed budburst data from a controlled environment experiment. Taking a community-wide approach, our work explores budburst-trait relationships across functional groups in both the understory and canopy layers of temperate deciduous

94 forests in North America. Measuring six leaf and structural traits and three budburst cues—chilling,
95 forcing, and photoperiod—we tested for correlation between budburst cues and traits, and how these
96 relationships vary spatially. Using a powerful joint-modeling approach, we were able to estimate the
97 effects traits on phenological responses to cues, while partitioning the variance from species-level and
98 population-level differences. This approach represents a considerable advance in how we estimate trait-
99 cue relationships, and may allow us to better estimate species phenological responses from available
100 trait data.

Research questions

Materials and Methods

Field sampling

104 We combined *in situ* trait data with budburst data from two growth chamber cutting experiments con-
105 ducted across eastern and western temperate deciduous forests in North America. Both suites of data
106 were collected from populations that span latitudinal gradient of 4-6° for eastern and western commu-
107 nities respectively. Our trait measurements were taken across eight populations, of which there were
108 four eastern populations—Harvard Forest, Massachusetts, USA (42.55°N, 72.20°W), White Mountains,
109 New Hampshire, USA (44.11°N, 52.14°W)), Second College Grant, New Hampshire, USA (44.79°N,
110 50.66°W), and St. Hippolyte, Quebec, Canada (45.98°N, 74.01°W) and four western population—E.C.
111 Manning Park (49.06°N, 120.78°W), Sun Peaks (50.88°N, 119.89°W), Alex Fraser Research Forest
112 (52.14°N, 122.14°W), and Smithers (54.78°N, 127.17°W), British Columbia (BC), Canada (Fig. 1).
113 For the growth chamber studies on budburst phenology, cuttings were collected from the most southern
114 and northern populations in each transect (n_{pop}=4).
115
116 Across all eight populations, we measured a diverse assemblage of species from the understory and
117 canopy layers. We selected the angiosperm species that were most abundant in our forest communities,
118 with an aim to maximize the number of closely related species and congeners between our eastern and
119 western communities. We focused on angiosperm species only, as these species are more likely to have
120 similar environmental controls to their leafout phenology, and to standardize our leaf trait comparisons
121 by excluding gymnosperm species.
122

Functional traits

124 We measured all traits in the summer prior to each growth chamber study. For our eastern transect,
125 traits were measured from 8-25 June 2015, and from 29 May 29 to 30 July 2019 for our western transect.
126 At each population, we measured a total of five traits: height, diameter at breast height (DBH), stem
127 specific density (SSD), leaf mass area (LMA), and the percent leaf nitrogen content (LNC). Each trait
128 was measured for each species present at a population, resulting in us measuring 1-10 healthy adult
129 individuals per species at each population. We also used the WSL xylem database (Schweingruber
130 and Landolt, 2010) to collect data on species ring-type for the 72.3% of our species represented in the
131 database.
132
133 We measured traits in accordance to the methods discussed by Pérez-Harguindeguy et al. (2013). We
134 calculated tree height using trigonometric methods, using a TruePulse 200L rangefinder and measured
135 DBH 1.42 m from the ground. For shrub heights, we measured the distance from the ground to the
136 height of the top foliage and measured stem diameters at approximately 1 cm above ground-level. To
137 measure stem specific density, we collected a 10 cm sample of branch wood, taken close to the base of
138 the stem. All samples were kept cool during transport and measurements of stem volume taken within

¹³⁹ 12 hours of sample collection. We measured wood volume using the water displacement method. We
¹⁴⁰ dried our stem samples upon returning from the field at 105°C for 24h, and weighed their dry mass.
¹⁴¹ Stem specific density was calculated as the dry mass of the sample over its fresh volume.

¹⁴²
¹⁴³ For our two leaf traits, we haphazardly selected five, fully expanded, and hardened leaves, avoiding
¹⁴⁴ leaves with considerable herbivory damage. We kept leaves cool during sampling and transport. For
¹⁴⁵ each leaf, we took high resolution scans using a Canon flatbed scanner (CanoScan Lide 220) within 12
¹⁴⁶ hours of collection. We estimated leaf area using the ImageJ software (version 2.0.0). Upon returning
¹⁴⁷ from the field, we dried our leaves for 48 h at 70°C and weighed each leaf using a precision balance.
¹⁴⁸ Leaf mass area was calculated as the ratio of the leaf dry mass over its area.

¹⁴⁹

Growth chamber study

¹⁵¹ For our growth chamber study, we collected branch cuttings from our highest and lowest latitude pop-
¹⁵² ulations in each transect. In both our eastern and western controlled environment study, we included
¹⁵³ two temperature treatments and daylength, for a total of eight distinct treatments. Our treatments
¹⁵⁴ included two levels of chilling—with our eastern study having no additional chilling or 30 days at 4°C,
¹⁵⁵ and our western study 30 days or 70 days of chilling at 4°C, with all non-field chilling occurring under
¹⁵⁶ dark conditions. Our forcing treatments included either a cool regime of 15:5°C or a warm regime of
¹⁵⁷ 20:10°C, and our photoperiod treatments consisted of of either 8 or 12 hour daylengths. We recorded
¹⁵⁸ budburst stages of each sample every 1-3 days for up to four months, defining the day of budburst
¹⁵⁹ as the day of budbreak or shoot elongation (defined as code 07 by (Finn et al., 2007)). For a more
¹⁶⁰ detailed discussion of study sample collection and methods see Loughnan and Wolkovich (in prep).

¹⁶¹

Statistical Anlaysis

¹⁶³ Our analysis combined our *in situ* trait data with budburst data from the growth chamber studies.
¹⁶⁴ For each trait, we developed a joint Bayesian model, in which the relationship between traits and cues
¹⁶⁵ is used to estimate budburst. This statistical approach improves upon previous analyses of multiple
¹⁶⁶ traits, as it allows us to carry through uncertainty between trait and phenology data—allowing us to
¹⁶⁷ better partition the drivers of variation in species phenologies

¹⁶⁸
¹⁶⁹ Our joint model consists of two parts. The first is a hierarchical linear model, in which we have par-
¹⁷⁰ titioned the variation of individual observations (i) of a given trait value ($y_{\text{trait}[i]}$) to account for the
¹⁷¹ effects of species (*sp id*), population-level differences arising from transects (*transect id*), as well as
¹⁷² the interaction between transects and latitude (*transect* × *latitude*), and finally, residual variation or
¹⁷³ 'measurement error' (σ_{trait}).

¹⁷⁴

$$\mu_{trait} = \alpha_{\text{grand trait}} + \alpha_{\text{sp[sp id]}} + \beta_{\text{transect}} \times transect + \beta_{\text{transect}\times\text{latitude}} \times (transect \times latitude) \quad (1)$$
$$\alpha_{sp} \sim normal(0, \sigma_{sp})$$
$$y_{trait} \sim normal(\mu_{trait}, \sigma_{trait})$$

¹⁷⁵ Transect was included as a categorical variable and latitude as a continuous variable in our model.
¹⁷⁶ Traits were modeled using natural units, with the exception of LMA, which was rescaled by 100 for
¹⁷⁷ numeric stability in the model. While each of our traits collected at the individual level were run using
¹⁷⁸ separate models, comparisons across species ring-porosity were made using the posterior estimates of
¹⁷⁹ our height model. This allowed us to best account for inherent differences in wood anatomy across

180 species and growth form.

181

182 We used partial pooling to uniquely estimate species-level variance ($\alpha_{\text{sp[sp id]}}$)—which controls for
183 variation in the number of trait estimates per species and trait variability—which are then used as
184 predictors of species-level estimates of each cue ($\beta_{\text{chill[sp]}}$, $\beta_{\text{force[sp]}}$, $\beta_{\text{photo[sp]}}$).

185

$$\begin{aligned}
\beta_{\text{chill[sp]}} &= \alpha_{\text{chill}[sp]} + \beta_{\text{trait.chill}} \times \alpha_{\text{trait sp[sp]}} \\
\beta_{\text{force[sp]}} &= \alpha_{\text{force}[sp]} + \beta_{\text{trait.force}} \times \alpha_{\text{trait sp[sp]}} \\
\beta_{\text{photo[sp]}} &= \alpha_{\text{photo}[sp]} + \beta_{\text{trait.photo}} \times \alpha_{\text{trait sp[sp]}}
\end{aligned} \tag{2}$$

186 In addition to the species-level estimates, the second part of our model estimates the overall effect of
187 each trait on each cue ($\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$). From this we can estimate how well traits
188 explain species-level differences—by estimating the the species-level cue variation not explained by
189 traits ($\alpha_{\text{chill}[sp]}$, $\alpha_{\text{force}[sp]}$, $\alpha_{\text{photo}[sp]}$) and individual species responses to cues (C_i, F_i, P_i, respectively).
190 Finally, our model estimates the residual budburst variation across species ($\alpha_{\text{pheno[sp]}}$) and observations
191 (σ_{pheno}). Our model estimates the residual variation across species as well as the variation in cues not
192 attributed to the trait (partial pooling).

$$\begin{aligned}
\mu_{pheno} &= \alpha_{\text{pheno[sp]}} + \beta_{\text{chill[sp]}} \times C_i + \beta_{\text{force[sp]}} \times F_i + \beta_{\text{photo[sp]}} \times P_i \\
y_{\text{pheno[i]}} &\sim normal(\mu_{pheno}, \sigma_{\text{pheno}})
\end{aligned} \tag{3}$$

193

$$\begin{aligned}
\alpha_{\text{pheno}} &\sim normal(\mu_{\alpha_{\text{pheno}}}, \sigma_{\alpha_{\text{pheno}}}) \\
\alpha_{\text{force}} &\sim normal(\mu_{\alpha_{\text{force}}}, \sigma_{\alpha_{\text{force}}}) \\
\alpha_{\text{chill}} &\sim normal(\mu_{\alpha_{\text{chill}}}, \sigma_{\alpha_{\text{chill}}}) \\
\alpha_{\text{photo}} &\sim normal(\mu_{\alpha_{\text{photo}}}, \sigma_{\alpha_{\text{photo}}})
\end{aligned} \tag{4}$$

194 Chilling was included as chill portions, and both forcing and photoperiod as continuous variables. We
195 standardized all cues by z-scoring them, allowing us to make comparisons across cues (see Loughnan
196 and Wolkovich (in prep) for more details).

197

198 For model, we used weakly informative priors unique to each trait. We validated our choice in priors
199 using prior predictive checks. We coded our models in the Stan programming language and fit them
200 using the rstan package. Each model had four chains, with models run for 6000-8000 total sampling
201 iterations. All our models met basic diagnostic checks, including no divergences, high effective sample
202 sizes (n_{eff}) that exceeded 10% of the number of iterations, and $\hat{R}$ values close to 1. Our model esti-
203 mates are reported as the mean values, with the 90% uncertainty interval. Estimates are given to one
204 decimal place, as it best represents the level of precision we can infer from our data (Gelman et al.,
205 2020).

206

Results

208 Across our eight populations, we measured 47 species of which 28 were in our eastern transect and 22
209 in our western transect. These include species dominant in both the understory and canopy layer, with
210 our eastern community consisting of 13 shrubs and 15 trees, and our western community consisting of
211 18 shrubs and 4 trees. There were three species that occurred in both transects. In total we measured
212 traits of 1428 unique individuals between the two transects across our five traits: height ($n = 1317$),

DBH ($n = 1220$), SSD ($n = 1359$), LMA ($n = 1345$), 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 negligible variation across populations, both in terms of differences between the two transects (main effect of transect only) or by latitude within each transect (an interactive effect between transect and latitude). Only leaf mass area (LMA) differed by latitude within transects (0.3, UI: 0.2,0.4)—with the LMA of eastern species increasing with latitude—but not western species (Fig. 2 d). Similarly, leaf nitrogen content (LNC) showed a weak interaction between latitude and transect (0, UI: 0.0,0)—with higher latitude populations in our eastern transect having lower LNC than lower latitude populations and western species (Fig. 2e). Our wood and structural traits, however, showed no differences across populations or transects (Table 2 - 3). The differences we found across populations were small to negligible, especially in comparison to species-level differences, which varied considerably and up to 33 fold (Fig. 3.

Only a subset of our traits related to at least one budburst cue, but responses were generally weak, with the exception of trait-specific relationships to photoperiod. We found similar cue relationships for our two structural traits, with tall plants with larger DBH exhibiting stronger photoperiod responses and producing earlier estimates of budburst under longer daylengths (-1.7, UI: -2.9, -0.5 for height and -2.3, UI: -3.4, -1.1 for DBH). But we found no relationship between cues and SSD (Table 3) or between cues and species different types of wood porosity (Fig. 4). Of our two leaf traits, only LMA showed a relationship with photoperiod, with low LMA species advancing their budburst timing more in response to longer photoperiods compared to high LMA species(-7.5, UI: -10.9, -4.1). But we found no relationship between LNC and any of our three cues.

How our three cues shaped budburst timing also varied across our trait models. For most of our trait models, chilling followed by forcing, were the strongest cues of budburst (Fig. 5). But in accounting for the correlations between LMA and cues, our model estimated stronger responses to photoperiod (-7.5, UI: -10.9, -4.1) than forcing (-7.1, UI: -13.0, -1.6), and a relatively weak effect of chilling (90% UI crossing zero) (Table 4). In contrast, our LNC (Table 5) and SSD models (Table 3) both showed negligible relationships between photoperiod and budburst timing (90% UI crossing zero). These findings suggest that relationships with additional traits can alter the effects and relative importance of cues on budburst (Fig. 6). This—paired with strong species-level variation—may cause variation in the estimated responses of species relative budburst dates across the different trait 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 (Fig. 7). In particular, we found height to have strong correlations between budburst timing and trait values, with earlier estimates of budbust for shrubs—especially under stronger cues—and later budburst estimates for trees (Fig. 7). Diameter at breast height showed similar trends as estimates from the 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. 7).

Discussion

Our study is one of the first to combine trait data with phenological cue responses for the same individuals and across a large area. Of the six traits we studied, we found only three that related to phenological cues. But only two of those traits fit within our hypothesized paradigm of acquisitive to conservative growth strategies in the spring. Using our joint modeling approach, we were able to

estimate how these traits interact with cues to shape species budburst timing, but contrary to our expectations our model suggested photoperiod may be the most important cue in trait-phenology relationships. In general, these patterns were consistent across our populations and between our eastern and western transects, despite the differences latitudes and community composition. Collectively our results provide new insights into the complexity in the mechanisms that underlie the relationships between phenotypes and environmental cues, while also challenging our existing understanding of these processes.

Across our eight forest populations, only our two leaf traits varied between our eastern and western communities or with latitude. Overall these patterns of variation were in line with our predictions, based on the transect differences in species composition. Since our western community consists of a greater number of shrub species, we predicted these populations to express more acquisitive growth strategies on average. This was confirmed by the lower LMA and high LNC we observed in our western transect. As a result of these trait differences, our western deciduous forests are likely to differ in their resource partitioning nutrient cycles, as the dominant shrubs species are more likely to utilize resources prior to canopy closure.

While the strong differences in our community assemblages explained some of the trait variation we observed spatially, 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. Only three of our six traits depicted cue responses that followed our predicted correlation with the variation in other traits across a gradient of acquisitive to conservative growth. While we predicted species with acquisitive traits—particularly large trees with high stem densities, and leaves with high LMA, and low LNC—to have weak temperature and daylength cues, we only found traits to correlate with the effects of photoperiod on budburst. As predicted, conservative species with greater heights and DBH did have stronger photoperiod responses, but contrary to our prediction, conservative species with high LMA also showed weak responses to photoperiod. 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 niche.

Despite our study spanning forest communities across North America, we only specific traits to vary spatially. This was surprising, as we expected the inherent variation in temperature and daylengths to impose local adaptation in species traits. However, research using the similar plant traits have also found little variation in trait values across regional scales (**??**Standen and Baltzer, 2023). But most of our predictions for how traits pertain to species growth strategies are based on globally distributed species. These findings stress the importance of studying ecological processes across spatial scales as the ultimate and proximate drivers selecting species phenotypes can vary considerably across scales.
In comparing our results with a global meta-analysis of tree trait relationships with budburst cues, however, we found similar trait-cue relationships for several of our traits. In addition to also finding relationships between tree height and photoperiod, we found similar responses in leaf traits, with high specific leaf area (the inverse of LMA) exhibiting strong responses to photoperiod (Loughnan and Wolkovich, in prep). The consistency of this result across these two disparate spatial scales suggests there are alternate, underlying mechanisms shaping how species respond to photoperiod cues. Several of our traits are associated with one or more physiological process or ecological functions, and associated with species ability to mitigate both abiotic and biotic factors (Wright et al., 2004; Pérez-Harguindeguy et al., 2013; Reich, 2014). The unexpected trends we observed in LMA suggests that selection on this trait does not pertain to leaves light capturing abilities, but rather other processes.

How traits shape species temporal niches

Individuals temporal niche are shaped by numerous, and complex, interactions with local environmental conditions and species assemblages. Our results suggest, however, that focusing only on phenology

fails to account for interactions between other traits and cues that may equally contribute to species temporal niche. In focusing solely on phenology data, previous research has shown budburst cues are primarily driven by temperature cues, with photoperiod being weakest cue (Chuine et al., 2010; Basler and Körner, 2014; Laube et al., 2014). This suggests there may be other physiological constraints or trade-offs selecting for other traits, which also shape species phenologies. But we did not find strong temperature cues—despite temperature generally being thought of as a strong environmental cue— suggesting other selective pressure are more important in temperate forests. This may relate to the importance of environmental cues known to select for other tree phenological events. Soil moisture and changes in water use and cell turgor are known to shape radial growth and shoot elongation in woody plants (Cabon et al., 2020; Peters et al., 2021). Leaf mass area can also vary with soil moisture, with variation in leaf area allowing plants to reduce evaporation, as high LMA is advantageous under dry conditions (De La Riva et al., 2016). If decreases in soil moisture correlate with long photoperiod conditions, it may be contributing to the unexpected trends we observed in LMA and the absence of relationships with temperature. To gain a holistic understanding of species growth strategies and phenotypes will therefore require the consideration of additional cues, such as soil moisture, that are known to shape other plant traits.

Using functional traits to predict climate change responses

Our results offer novel insights to how broader plant traits impact phenological sensitivities to environmental cues. While temperatures are becoming stronger with climate change, particularly at higher latitudes (Hoegh-Guldberg et al., 2018), photoperiod is fixed. This suggests the relationships between photoperiod and other traits have the potential to limit species abilities to track temperatures and may constrain how much woody plant phenologies will advance with climate change. These effects are likely to be strongest on larger 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 interactions within communities.

Our study is one of the first to jointly model the relationship between phenology and other commonly measured traits. But our results simply tell us the associations between cues and traits, and not the underlying mechanism per se. While phenological traits are often cited as the finger print of climate change, our results suggest other traits may also mediate budburst timing. To accurately forecast future changes in phenology, we need to account 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 temperatures (De La Riva et al., 2016). These changes have the potential to impact species photosynthesis and ultimately ecosystem services, such as carbon sequestration. While phenological research has focused on forecasting responses to temperature, the selection by other traits for photoperiod suggest it is still an important cue. It is therefore critical that we continue to take a more holistic approach to studying the relationships between phenology and traits to accurately forecast the future impacts of climate change on communities.

References

Albert, C. H., W. Thuiller, N. G. Yoccoz, A. Soudant, F. Boucher, P. Saccone, and S. Lavorel. 2010. Intraspecific functional variability: extent, structure and sources of variation. Journal of Ecology 98:604–613.

Audzijonyte, A., S. A. Richards, R. D. Stuart-Smith, G. Pecl, G. J. Edgar, N. S. Barrett, N. Payne, and J. L. Blanchard. 2020. Fish body sizes change with temperature but not all species shrink with warming. Nature Ecology & Evolution 4:809–814.

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.

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

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. Trends in Ecology and Evolution 22:357–365.

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.

Gelman, A., J. Hill, and A. Vehtari. 2020. Regression and other stories. Cambridge University Press.

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 1.5ºC 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.

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.

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

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

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

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.

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

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

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

Shipley, B., F. De Bello, J. H. C. Cornelissen, E. Laliberté, D. C. Laughlin, and P. B. Reich. 2016. Reinforcing loose foundation stones in trait-based plant ecology. Oecologia 180:923–931.

Standen, K. M., and J. Baltzer. 2023. Greater variation in boreal plant community composition and community-level traits at local-than regional-scale. Journal of Vegetation Science 34:1–14.

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.

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.
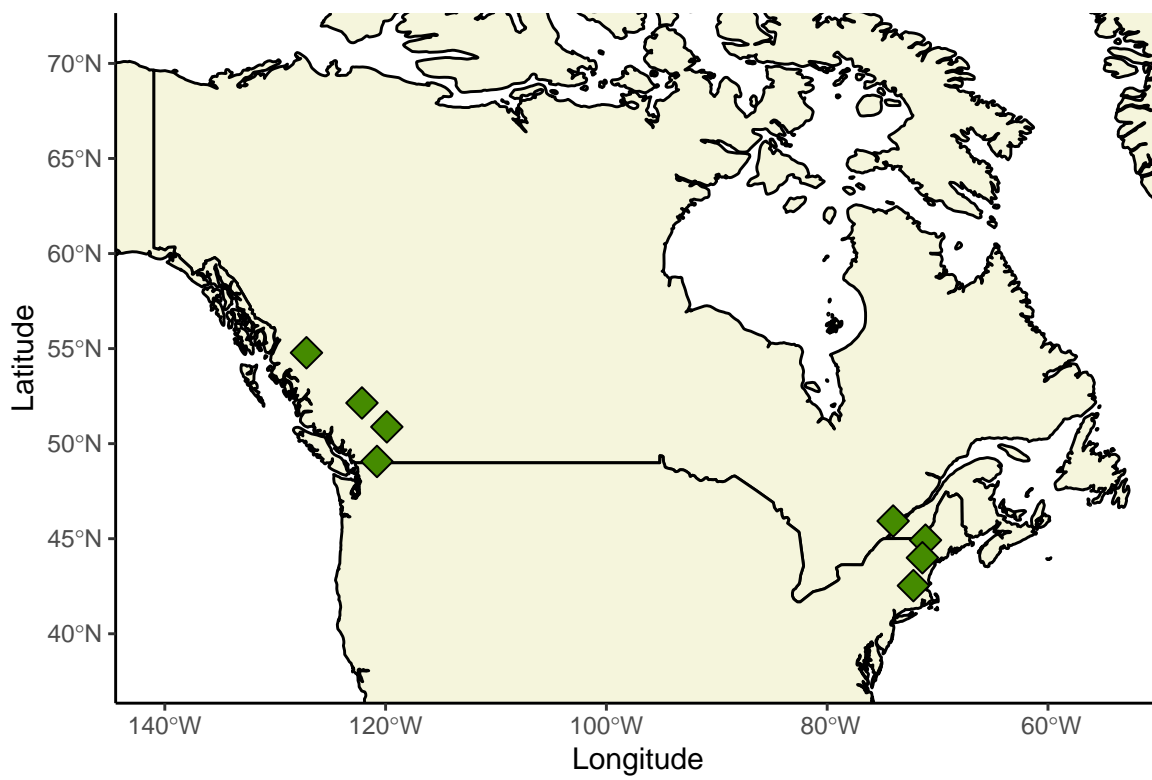
435 # Figures

Figure 1: We measured our trait in eight temperate deciduous forests, with four eastern populations and four western population that spanned 4-6° latitude. The branch clippings used in our two growth chamber experiments were taken from the most northern and most southern populations in each transect.
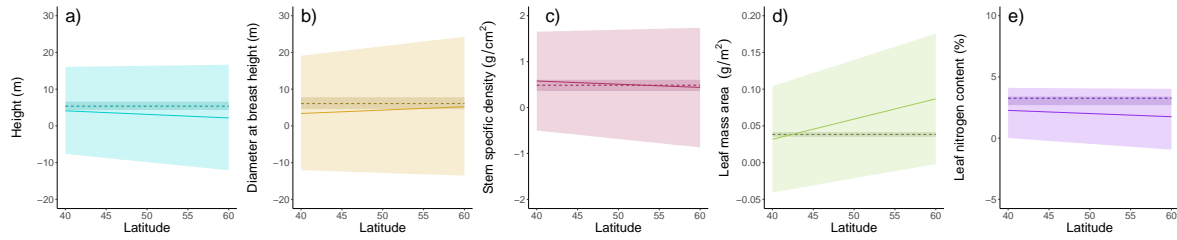
Figure 2: We found geographic differences for four of our functional traits, with the direction of the relationship varying across traits. Of our traits a. height, b. diameter at base height, c. leaf mass area, and e. leaf nitrogen content showed strong interactions between latitude and transect, while d. stem specific density showed no effects of geography. Dashed lines represent the western transect and solid lines the eastern transect.
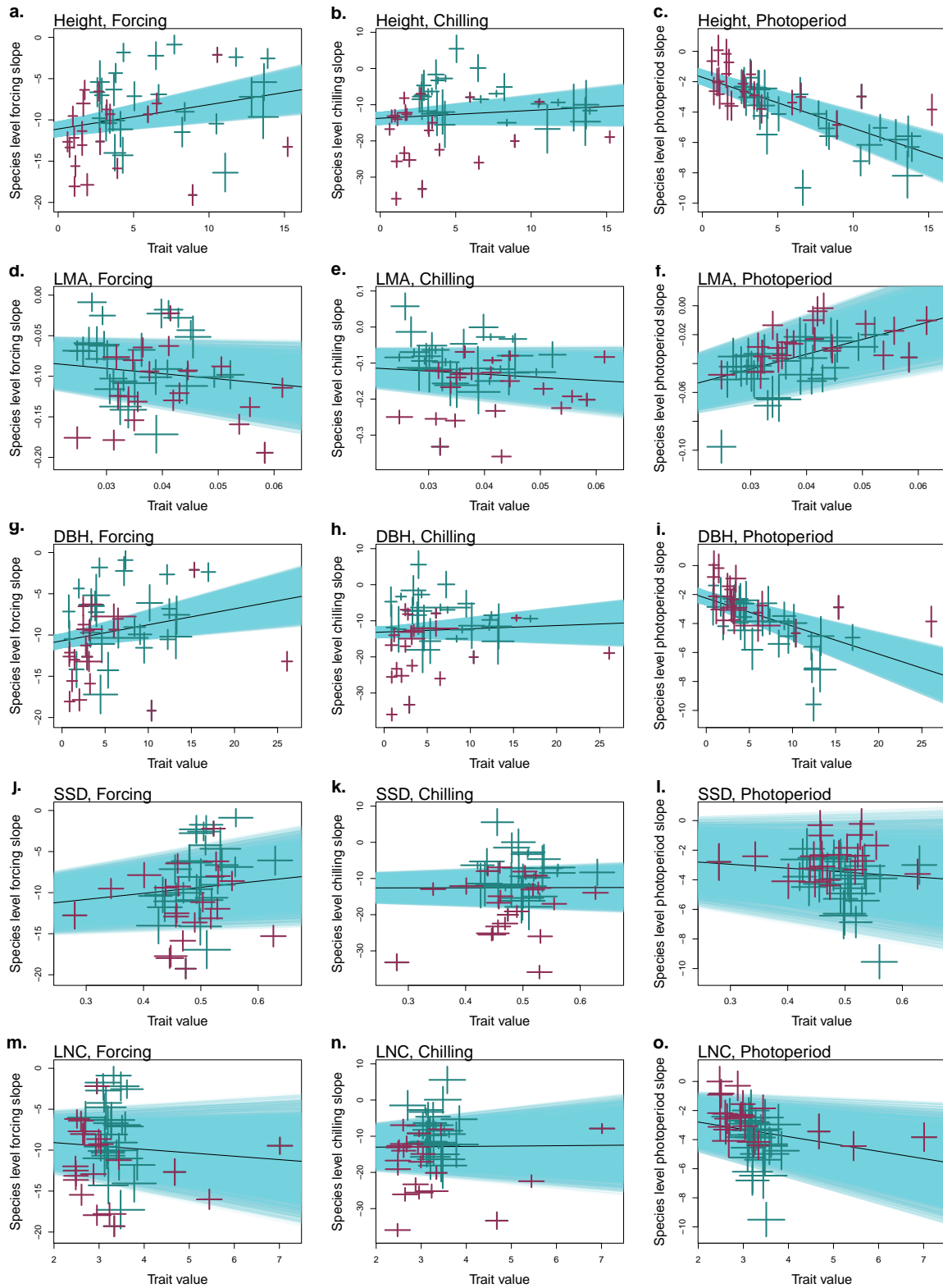
Figure 3: Relationship between species traits and cue responses, for height (a-c), leaf mass area (d-f), diameter at breast height (g-i), stem specific density (j-l), and the leaf nitrogen content (m-o). Point colours representing different species groups, with tree species are depicted in maroon and shrub species in teal.
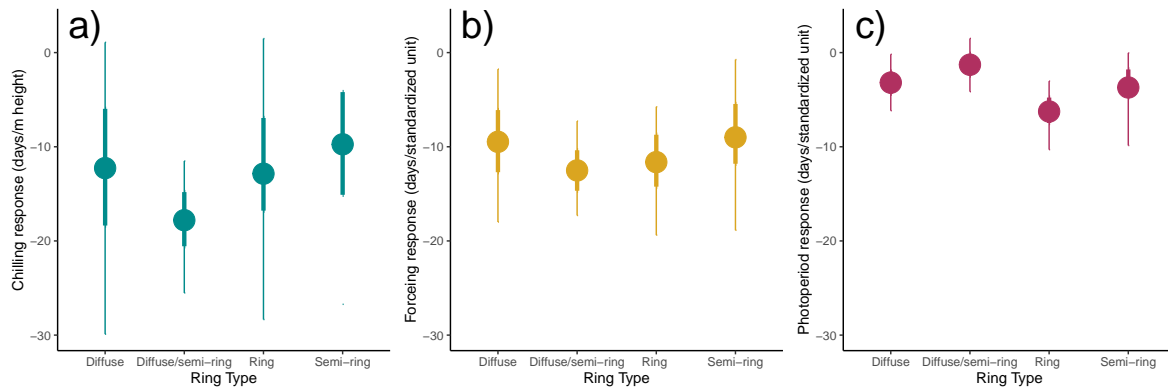
Figure 4: Despite species wood structures causing differing growth strategies, we did not find this trait to correlate with differences in cue responses across species. Thinner lines represent the 90% UI and thicker lines the 50% UI. Here we show the results for height only.
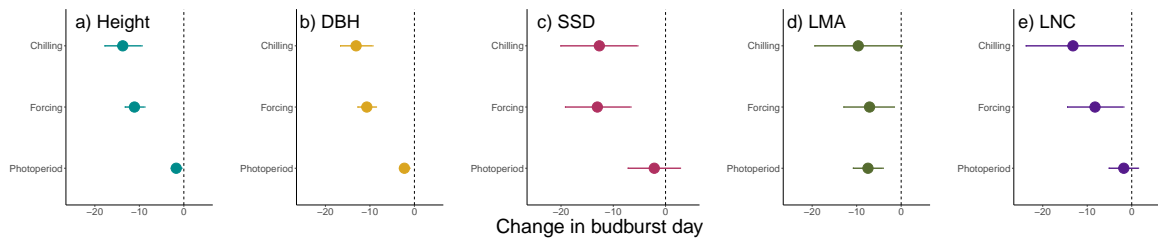

Figure 5: We found fairly consistent estimates for budburst cue responses to chilling, forcing, and photoperiod for each of our trait models: a. height, b. diameter at breast height, c. stem specific density, d. leaf mass area, and e. leaf nitrogen contnet. Lines represent 90% uncertainty intervals.
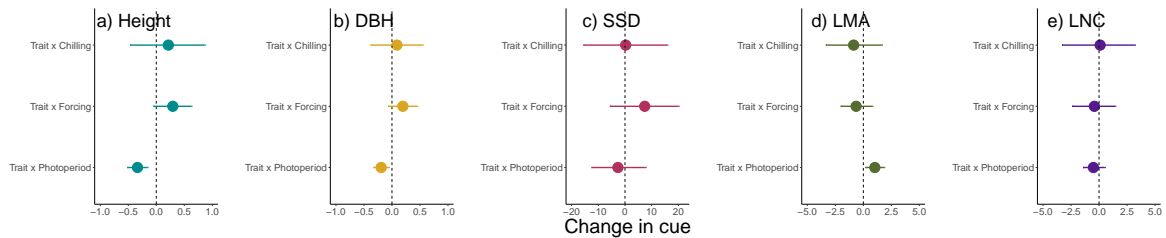

Figure 6: The relationships between traits and cue responses varied considerably across each of our trait models, a. height, b. diameter at breast height, c. stem specific density, d. leaf mass area, and e. leaf nitrogen content, and for individual cues. Lines represent 90% uncertainty intervals. Note the differences in the scale of the x-axis.
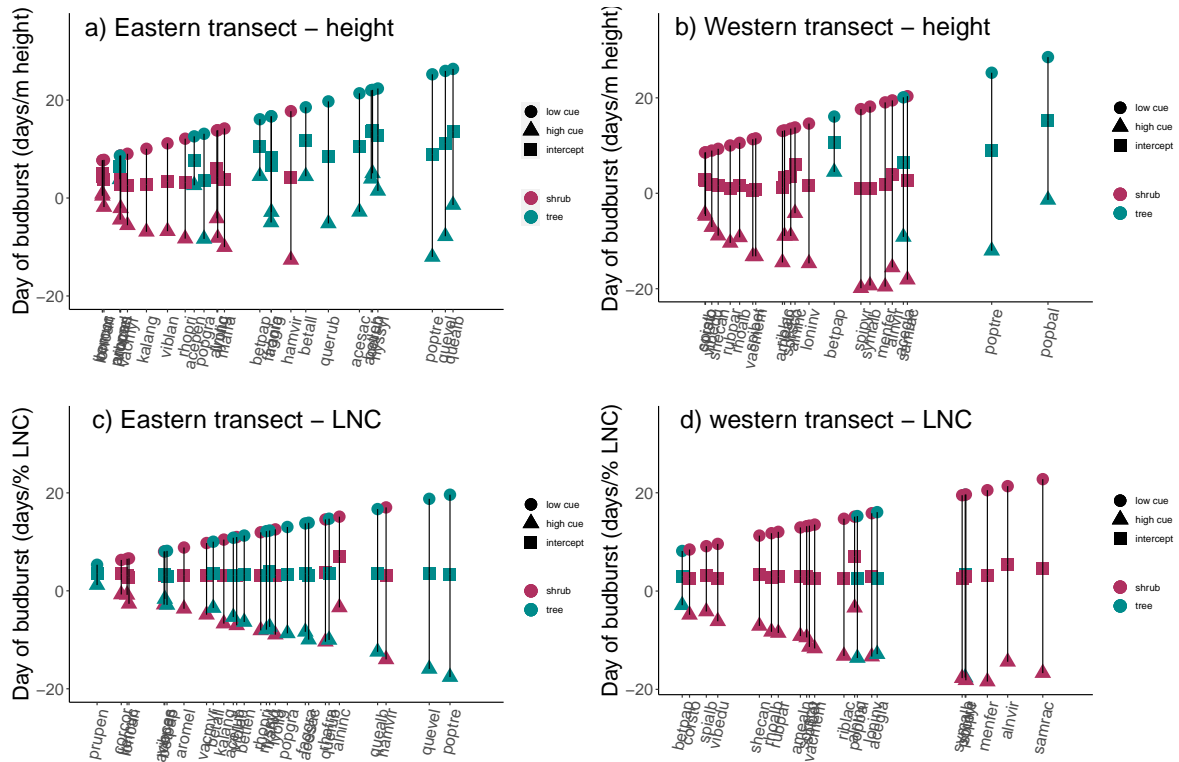
Figure 7: We found budburst estimates differed between our full model (intercept plus cues, depicted as triangles for high cues and as circles for low cues), versus the intercepts only model (without cues, shown as squares). Species are ordered in increasing budburst dates for both the eastern (a and c) and western (b and d) populations, spanning from early budbursting shrubs, in red, to late budbursting trees in blue. For traits such as height (a and b) we found distinct partitioning of budburst across shrub and tree species, but this was not the case for all traits, with our model of leaf nitrogen content showing highly mixed budburst order of shrub and tree species (c and d).

436 # Tables

Table 1: Summary output from a joint Bayesian model of height and budburst phenology in which species are partially pooled. The effect of transect is modeled as a categorical variable and latitude as continuous in interaction term with transect. The model includes photoperiod and forcing as continuous variables, with all three cues z-scored to allow comparisons across cues.

	mean	5%	25%	75%	95%
Transect	2.60	-3.00	0.40	4.90	8.30
Transect x latitude	-0.10	-0.20	-0.10	-0.00	0.00
Forcing	-11.10	-13.30	-12.00	-10.20	-8.80
Chilling	-13.70	-17.80	-15.50	-12.10	-9.50
Photoperiod	-1.70	-2.90	-2.20	-1.20	-0.50
Trait x forcing	0.30	-0.10	0.20	0.40	0.60
Trait x chilling	0.20	-0.50	-0.00	0.50	0.90
Trait x photoperiod	-0.30	-0.50	-0.40	-0.30	-0.20

Table 2: Summary output from a joint Bayesian model of DBH and budburst phenology in which species are partially pooled. The effect of transect is modeled as a categorical variable and latitude as continuous in interaction term with transect. The model includes photoperiod and forcing as continuous variables, with all three cues z-scored to allow comparisons across cues.

	mean	5%	25%	75%	95%
Transect	-6.40	-13.70	-9.40	-3.40	1.00
Transect x latitude	0.10	-0.10	0.00	0.20	0.30
Forcing	-10.70	-12.80	-11.60	-9.90	-8.60
Chilling	-13.10	-16.70	-14.60	-11.60	-9.40
Photoperiod	-2.30	-3.40	-2.70	-1.80	-1.10
Trait x forcing	0.20	-0.10	0.10	0.30	0.40
Trait x chilling	0.10	-0.40	-0.10	0.30	0.50
Trait x photoperiod	-0.20	-0.30	-0.20	-0.10	-0.10

Table 3: Summary output from a joint Bayesian model of SSD and budburst phenology in which species are partially pooled. The effect of transect is modeled as a categorical variable and latitude as continuous in interaction term with transect. The model includes photoperiod and forcing as continuous variables, with all three cues z-scored to allow comparisons across cues.

	mean	5%	25%	75%	95%
Transect	0.40	-0.10	0.20	0.60	0.90
Transect x latitude	-0.00	-0.00	-0.00	-0.00	0.00
Forcing	-13.00	-19.30	-15.70	-10.50	-6.70
Chilling	-12.70	-20.10	-15.60	-9.70	-5.40
Photoperiod	-2.20	-7.20	-4.20	-0.00	2.80
Trait x forcing	7.40	-5.70	2.00	13.00	20.10
Trait x chilling	0.30	-15.60	-5.90	6.50	15.90
Trait x photoperiod	-2.70	-12.60	-7.00	1.50	7.80

Table 4: Summary output from a joint Bayesian model of LMA and budburst phenology in which species are partially pooled. The effect of transect is modeled as a categorical variable and latitude as continuous in interaction term with transect. The model includes photoperiod and forcing as continuous variables, with all three cues z-scored to allow comparisons across cues.

	mean	5%	25%	75%	95%
Transect	-11.70	-15.30	-13.20	-10.20	-8.00
Transect x latitude	0.30	0.20	0.20	0.30	0.40
Forcing	-7.10	-13.00	-9.30	-4.80	-1.60
Chilling	-9.60	-19.50	-13.50	-5.70	0.20
Photoperiod	-7.50	-10.90	-8.90	-6.00	-4.10
Trait x forcing	-0.60	-2.00	-1.20	-0.10	0.80
Trait x chilling	-0.90	-3.40	-1.90	0.10	1.70
Trait x photoperiod	1.00	0.20	0.70	1.40	1.90

Table 5: Summary output from a joint Bayesian model of LNC and budburst phenology in which species are partially pooled. The effect of transect is modeled as a categorical variable and latitude as continuous in interaction term with transect. The model includes photoperiod and forcing as continuous variables, with all three cues z-scored to allow comparisons across cues.

	mean	5%	25%	75%	95%
Transect	0.00	-0.80	-0.30	0.40	0.90
Transect x latitude	-0.00	-0.00	-0.00	-0.00	-0.00
Forcing	-8.20	-14.50	-10.80	-5.80	-1.80
Chilling	-13.20	-23.80	-17.70	-8.80	-2.00
Photoperiod	-1.80	-5.20	-3.10	-0.40	1.40
Trait x forcing	-0.40	-2.40	-1.20	0.40	1.40
Trait x chilling	0.10	-3.30	-1.20	1.50	3.20
Trait x photoperiod	-0.50	-1.40	-0.90	-0.10	0.50