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

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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; **?**). 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 (**?**). 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 (**?**) and wood economic spectrum (**?**). 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 (**??**). These traits serve as proxies for difficult to measure physiological processes and responses to biotic interactions (**??**), 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 (**?**) 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 (**?**). 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 forests in North America. Measuring six leaf and structural traits and three budburst cues—chilling,

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

Research questions

Materials and Methods

Field sampling

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

Functional traits

123 We measured all traits in the summer prior to each growth chamber study. For our eastern transect,
124 traits were measured from 8-25 June 2015, and from 29 May 29 to 30 July 2019 for our western transect.
125 At each population, we measured a total of five traits: height, diameter at breast height (DBH), stem
126 specific density (SSD), leaf mass area (LMA), and the percent leaf nitrogen content (LNC). Each trait
127 was measured for each species present at a population, resulting in us measuring 1-10 healthy adult
128 individuals per species at each population. We also used the WSL xylem database (Schweingruber
129 and Landolt, 2010) to collect data on species ring-type for the 72.3% of our species represented in the
130 database.
131
132 We measured traits in accordance to the methods discussed by Pérez-Harguindeguy et al. (2013). We
133 calculated tree height using trigonometric methods, using a TruePulse 200L rangefinder and measured
134 DBH 1.42 m from the ground. For shrub heights, we measured the distance from the ground to the
135 height of the top foliage and measured stem diameters at approximately 1 cm above ground-level. To
136 measure stem specific density, we collected a 10 cm sample of branch wood, taken close to the base of
137 the stem. All samples were kept cool during transport and measurements of stem volume taken within
138 12 hours of sample collection. We measured wood volume using the water displacement method. We

139 dried our stem samples upon returning from the field at 105°C for 24h, and weighed their dry mass.
140 Stem specific density was calculated as the dry mass of the sample over its fresh volume.
141
142 For our two leaf traits, we haphazardly selected five, fully expanded, and hardened leaves, avoiding
143 leaves with considerable herbivory damage. We kept leaves cool during sampling and transport. For
144 each leaf, we took high resolution scans using a Canon flatbed scanner (CanoScan Lide 220) within 12
145 hours of collection. We estimated leaf area using the ImageJ software (version 2.0.0). Upon returning
146 from the field, we dried our leaves for 48 h at 70°C and weighed each leaf using a precision balance.
147 Leaf mass area was calculated as the ratio of the leaf dry mass over its area.
148

Growth chamber study

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

Statistical Anlaysis

162 Our analysis combined our *in situ* trait data with budburst data from the growth chamber studies.
163 For each trait, we developed a joint Bayesian model, in which the relationship between traits and cues
164 is used to estimate budburst. This statistical approach improves upon previous analyses of multiple
165 traits, as it allows us to carry through uncertainty between trait and phenology data—allowing us to
166 better partition the drivers of variation in species phenologies
167
168 Our joint model consists of two parts. The first is a hierarchical linear model, in which we have par-
169 titioned the variation of individual observations (i) of a given trait value ($y_{\text{trait}[i]}$) to account for the
170 effects of species (*sp id*), population-level differences arising from transects (*transect id*), as well as
171 the interaction between transects and latitude (*transect × latitude*), and finally, residual variation or
172 'measurement error' (σ_{trait}).
173

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

174 Transect was included as a categorical variable and latitude as a continuous variable in our model.
175 Traits were modeled using natural units, with the exception of LMA, which was rescaled by 100 for
176 numeric stability in the model. While each of our traits collected at the individual level were run using
177 separate models, comparisons across species ring-porosity were made using the posterior estimates of
178 our height model. This allowed us to best account for inherent differences in wood anatomy across
179 species and growth form.
180

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

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

185 In addition to the species-level estimates, the second part of our model estimates the overall effect of
186 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
187 explain species-level differences—by estimating the the species-level cue variation not explained by
188 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).
189 Finally, our model estimates the residual budburst variation across species ($\alpha_{\text{pheno[sp]}}$) and observations
190 (σ_{pheno}). Our model estimates the residual variation across species as well as the variation in cues not
191 attributed to the trait (partial pooling).

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

192

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

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

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

Results

207 Across our eight populations, we measured 47 species of which 28 were in our eastern transect and 22
208 in our western transect. These include species dominant in both the understory and canopy layer, with
209 our eastern community consisting of 13 shrubs and 15 trees, and our western community consisting of
210 18 shrubs and 4 trees. There were three species that occurred in both transects. In total we measured
211 traits of 1428 unique individuals between the two transects across our five traits: height ($n = 1317$),
212 DBH ($n = 1220$), SSD ($n = 1359$), LMA ($n = 1345$), LNC ($n = 1351$). Across our two growth chamber
213 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 re-

lationships. 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 (?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 (**???**). 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 (**?**). 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 (**?**). 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.

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₄₀₀ # Figures
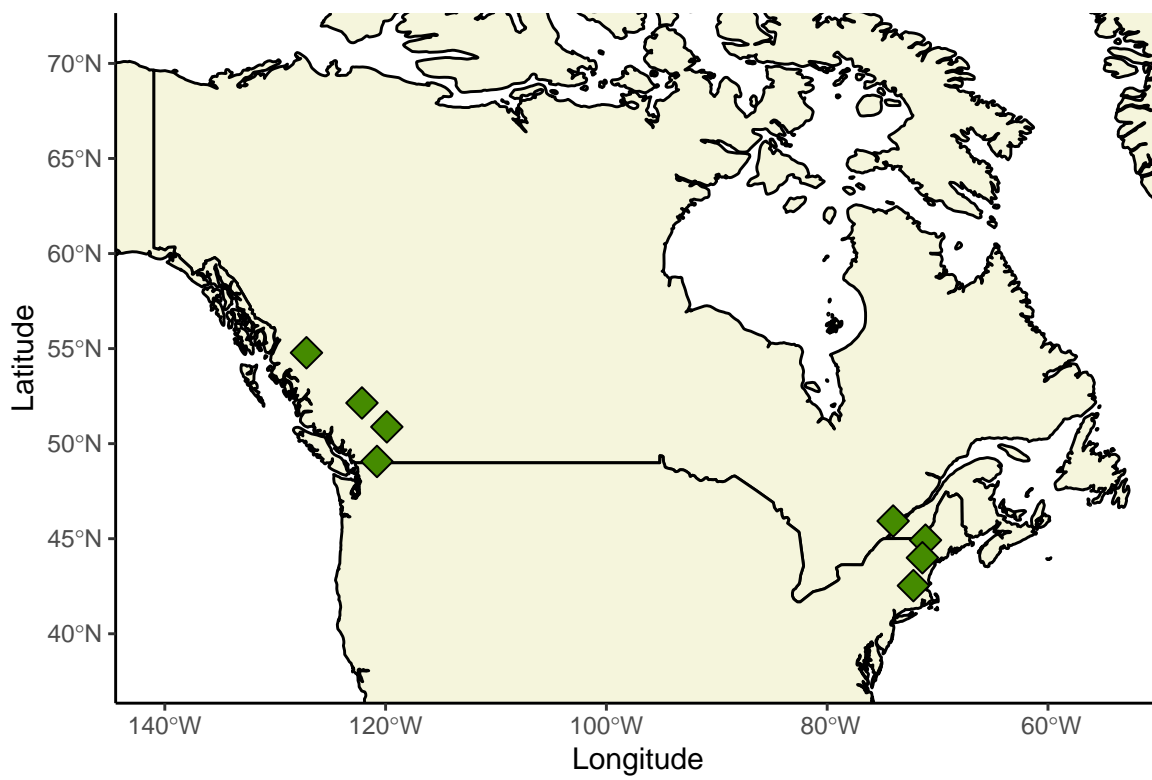
Figure 1: We measured our trait in eight temperate deciduous forests, with four eastern populations and four western population that spanned 4-6° latitude. The branch clippings used in our two growth chamber experiments were taken from the most northern and most southern populations in each transect.
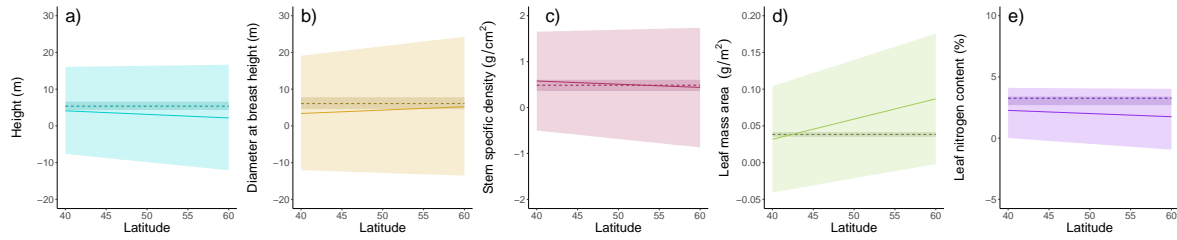
Figure 2: We found geographic differences for four of our functional traits, with the direction of the relationship varying across traits. Of our traits a. height, b. diameter at base height, c. leaf mass area, and e. leaf nitrogen content showed strong interactions between latitude and transect, while d. stem specific density showed no effects of geography. Dashed lines represent the western transect and solid lines the eastern transect.
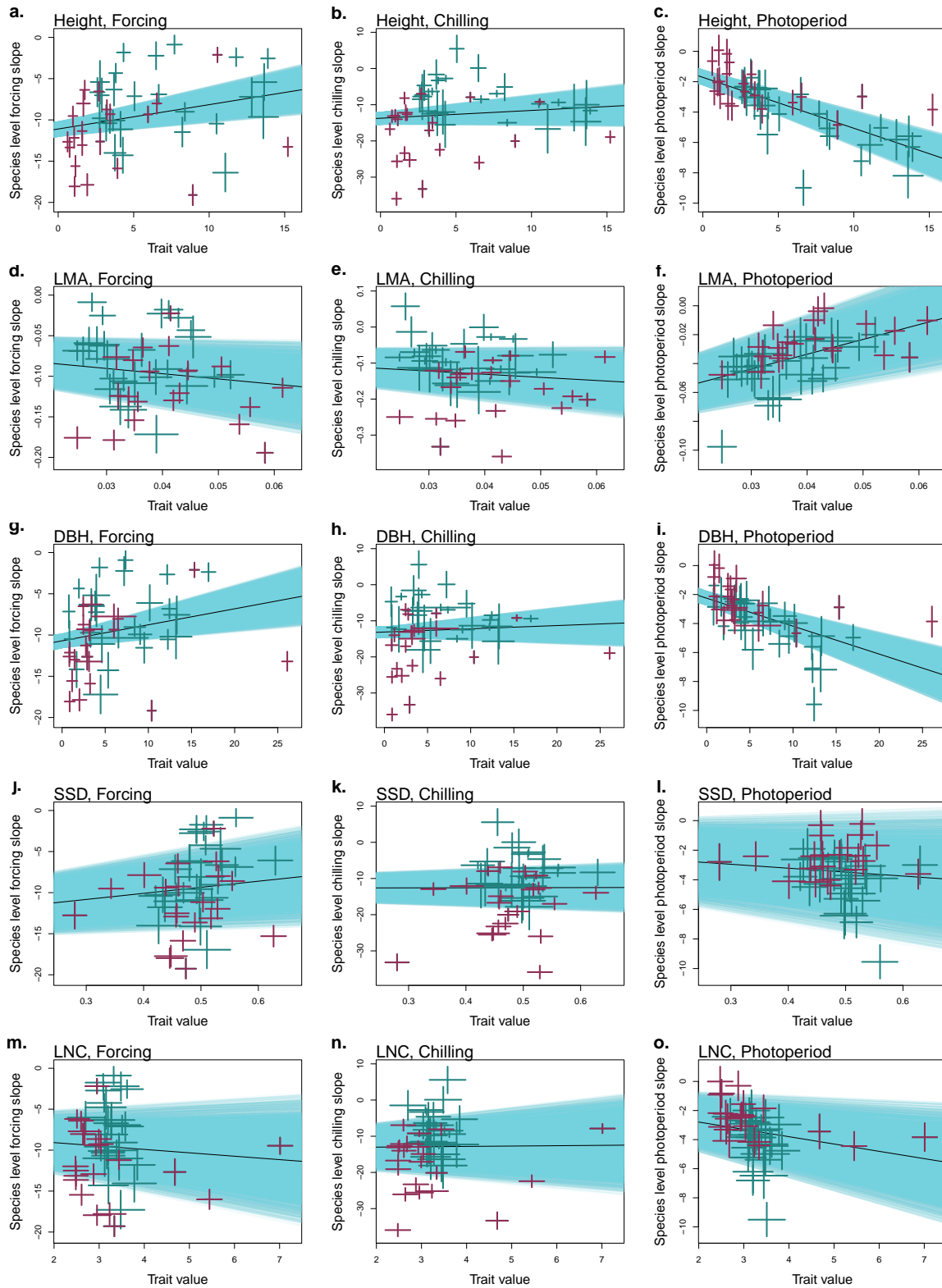
Figure 3: Relationship between species traits and cue responses, for height (a-c), leaf mass area (d-f), diameter at breast height (g-i), stem specific density (j-l), and the leaf nitrogen content (m-o). Point colours representing different species groups, with tree species are depicted in maroon and shrub species in teal.
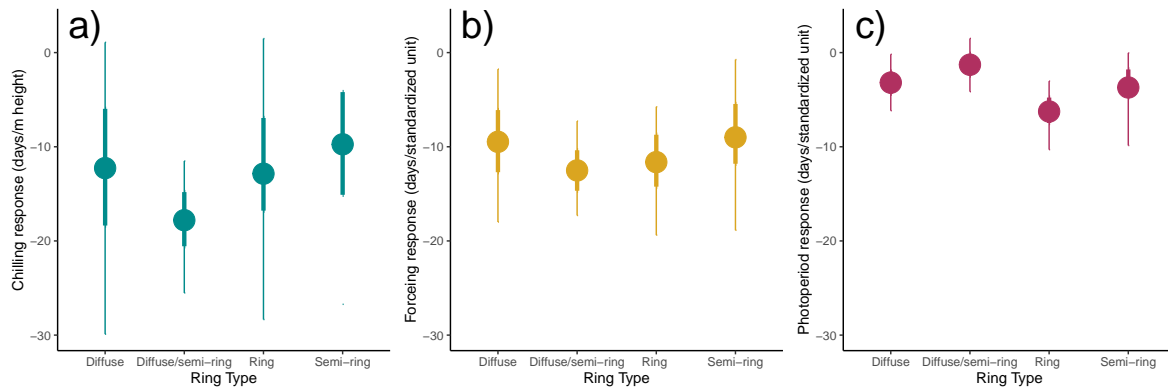
Figure 4: Despite species wood structures causing differing growth strategies, we did not find this trait to correlate with differences in cue responses across species. Thinner lines represent the 90% UI and thicker lines the 50% UI. Here we show the results for height only.
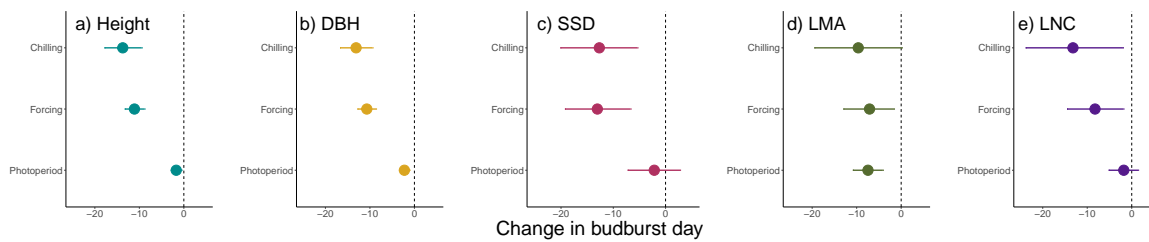

Figure 5: We found fairly consistent estimates for budburst cue responses to chilling, forcing, and photoperiod for each of our trait models: a. height, b. diameter at breast height, c. stem specific density, d. leaf mass area, and e. leaf nitrogen contnet. Lines represent 90% uncertainty intervals.

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.
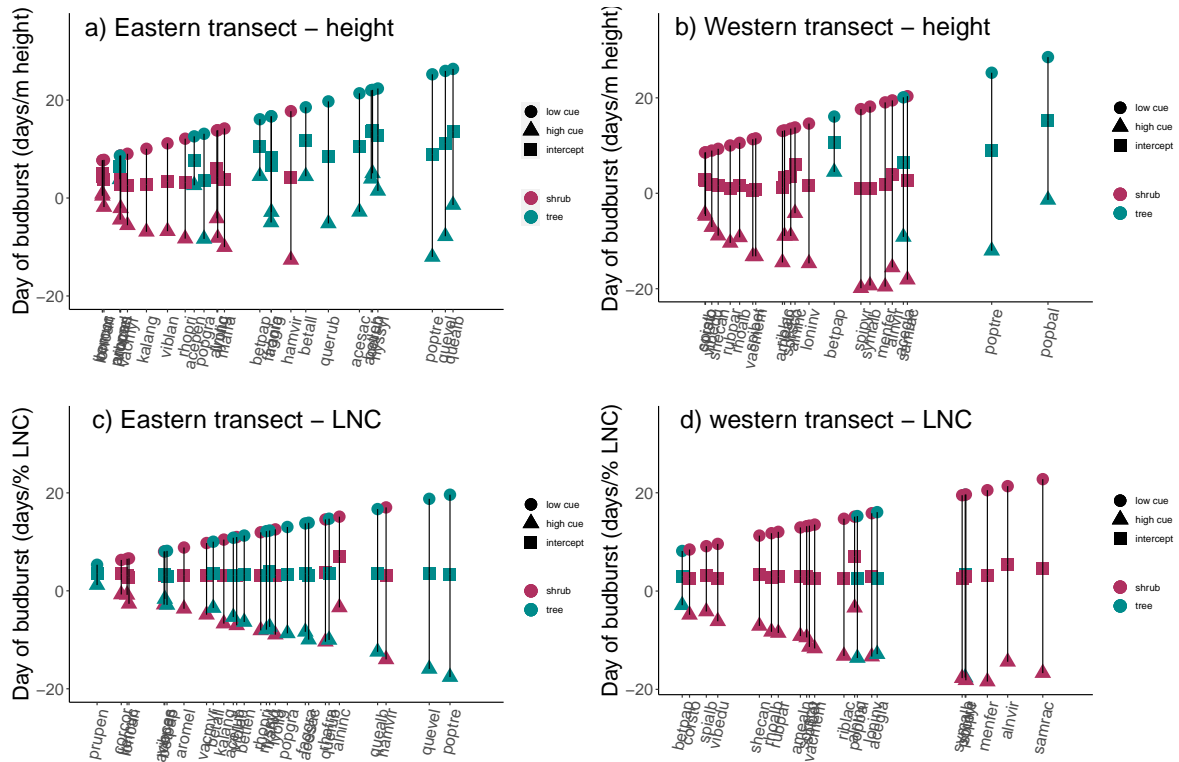
Figure 7: We found budburst estimates differed between our full model (intercept plus cues, depicted as triangles for high cues and as circles for low cues), versus the intercepts only model (without cues, shown as squares). Species are ordered in increasing budburst dates for both the eastern (a and 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).

Tables

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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