Differences in traits predict 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. This variation could reflect differences in species growth strategies. In plants, such differences correlate with 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. Using data of woody plant budburst, for which temperature and photoperiod cues are known, we decomposed the sources of variation that underlie the timing of spring growth and identified the shared trait-cue relationships for six commonly measured traits. Working across eight forest communities, we collected *in situ* trait measurements from 1428 individuals of 48 species. Trait data was paired 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 (Root et al., 2003; Parmesan and Yohe, 2003). These general phenological response, however, average over high variability across species (Thackeray et al., 2016; Cohen et al., 2018; Kharouba et al., 2018), and pose a challenge to accurate forecasts. In plants, species variation can be explained in part by differences in their 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 be excluded from plant trait research, making it difficult to leverage this important framework to explain

phenological variation and improve predictions.

Research on trait ecology has shown species traits to correlate with growth strategies and responses to environments. Gradients in traits can arise from differences in local environmental factors, such as temperature, soil moisture, and nutrients, that can alter the rate of plant growth (Wright and Westoby, 1999; Moles et al., 2014; Laughlin et al., 2021). But environmental factors at larger spatial and temporal scales may also drive variation. In temperate systems, changes in temperature in spring can produce gradients in abiotic stress through the decreasing risk of frost events later in the season (Sakai and Larcher, 1987; Gotelli and Graves, 1996; Augspurger, 2009). If some species avoid this risk by leafing out later, this variation could also produce greater biotic stress through a more competitive environmental later in the season. These relationships have proven to be consistent across communities, allowing trait values to infer growth strategies and community processes independent of species identity (McGill et al., 2006). In plants this has been synthesized into several frameworks, including the leaf economic spectrum (Wright et al., 2004) and wood economic spectrum (Chave et al., 2009), under which trait values follow distinct gradients that range 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). 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.

Phenology itself is considered a trait with high inter- and intra-specific variability, with previous studies finding high variation in phenology for the same species when observed over different years or sites (Primack et al., 2009; Chuine et al., 2010). This variability is often given as justification for excluding phenology from broader functional trait frameworks. But many of these studies are observational and conducted at the landscape scale. In contrast, experiments in which phenology is observed under controlled environments 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.

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 address the challenges of incorporating phenological variation in a broader trait framework by using the phenological event of spring budburst alongside a suite of traits that can 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. Both suites of data were collected from populations that span a latitudinal gradient of 4-6° for the eastern and western communities respectively. Our trait measurements were taken 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. S1). For the two growth chamber studies on budburst phenology, cuttings were collected 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. For our eastern transect, traits were measured from 8-25 June 2015, and from 29 May to 30 July 2019 for our western transect, following full leafout but before budset. At each population, we measured a total of five traits: 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). Each trait was measured for 1-10 healthy adult individuals for each species present at a population. We also used the WSL xylem database (Schweingruber and Landolt, 2010) to collect data on species ring-type for the 72.3% of our species represented in the database.

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 measured DBH 1.37 m from the ground. 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. 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. All samples were kept cool during transport and measurements of stem volume taken within 12 hours of sample collection using the water displacement method. We dried our stem samples upon returning from the field at 105°C for 24h, and weighed their dry mass. Wood specific density was calculated as the dry mass of the sample over its fresh volume.

For our two leaf traits, we haphazardly selected five, fully expanded, and hardened leaves, avoiding leaves with considerable herbivory damage. We kept leaves cool during sampling and transport. For each leaf, we took high resolution scans using a Canon flatbed scanner (CanoScan Lide 220) within 12 hours of collection, and estimated leaf area using the ImageJ software (version 2.0.0). Upon returning from the field, we dried our leaves for 48 h at 70°C and weighed each leaf using a precision balance. Leaf mass area was calculated as the ratio of the leaf dry mass over its area. To measure the percent leaf nitrogen content, leaf samples were ground to a fine powder and encapsulated for combustion elemental analysis.

Growth chamber study

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

Statistical Analysis

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

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

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

4

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

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

$$\tag{4}$$

180

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

$$\tag{6}$$

181 Transect was included as a dummy variable and latitude as a continuous variable in our model. Traits
182 were modeled using natural units, with the exception of LMA, which was rescaled by 100 for numeric
183 stability in the model. Each of our traits collected *in situ* were modeled individually, but comparisons
184 across species ring-porosity were made using the posterior estimates of our WSD model. This allowed
185 us to better account for inherent differences in wood anatomy across species and growth form.

186

187 We used partial pooling to uniquely estimate species-level variance—which controls for variation in
188 the number of trait estimates per species and trait variability—which are then used as predictors of
189 species-level estimates of each cue ($\beta_{\text{chilling,j}}$, $\beta_{\text{forcing,j}}$, $\beta_{\text{photoperiod,j}}$).

190

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

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

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

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

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

198 with

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

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

$$\boldsymbol{\alpha}_{\text{pheno}} = \{\alpha_{\text{pheno}_1}, ..., \alpha_{\text{pheno}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{pheno}} \sim \mathcal{N}(\mu_{\text{pheno}}, \sigma^2_{\text{pheno}}) \tag{10}$$

$$\boldsymbol{\alpha}_{\text{chilling}} = \{\alpha_{\text{chilling}_1}, ..., \alpha_{\text{chilling}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{chilling}} \sim \mathcal{N}(\mu_{\text{chilling}}, \sigma^2_{\text{chilling}})$$

$$\boldsymbol{\alpha}_{\text{forcing}} = \{\alpha_{\text{forcing}_1}, ..., \alpha_{\text{forcing}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{forcing}} \sim \mathcal{N}(\mu_{\text{forcing}}, \sigma^2_{\text{forcing}})$$

$$\boldsymbol{\alpha}_{\text{photo}} = \{\alpha_{\text{photo}_1}, ..., \alpha_{\text{photo}_n}\}^T \text{ such that } \boldsymbol{\alpha}_{\text{photo}} \sim \mathcal{N}(\mu_{\text{photo}}, \sigma^2_{\text{photo}})$$

200 We included all three cues as continuous variables in our model. We converted chilling temperatures
201 to total chill portions, including both the chilling experienced in the field prior to sampling and during
202 the experiment in our 4°C chilling chambers. For this we used local weather station data from each of

5

the four populations where samples were collected, and calculated total chill portions using the chillR package (v. 0.73.1, Luedeling, 2020). To account for differences in thermoperiodicity between the two studies (Buonaiuto et al., 2023), we 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). In addition to the overall predictors, we included all two-way interactions between cues and between cues and sites.

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_{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.

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 (an interactive effect between transect and latitude for which the 90% UI does not cross zero, Fig. 1). Leaf nitrogen content was the only trait to vary with latitude alone, with low latitude communities having greater values of LNC that communities at higher latitudes (-0.1, UI: -0.2, -0.06, Table S5). 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 S1, S2, S4, S5). 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 S1-S5). But only our model of height and DBH had strong responses to all three cues (Table S1, S2). Our model of LMA estimated a strong response to only photoperiod (Table S4) and our LNC model a strong response to chilling and photoperiod (Table S5). Our model of WSD estimated strong cue responses in budburst to temperature cues only (Table S3), but we found no clear relationships between cue responses and the different types of wood structure (Fig. S2). 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. S3). 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. S3).

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 modeling 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 by 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.

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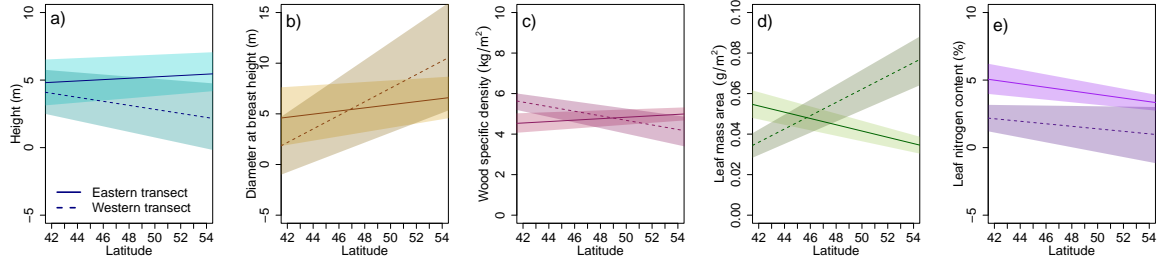
Figure 1: We found geographic differences for only one of our functional traits, the majority exhibiting no differences between latitudes or across transects. Depicted are the spatial trends for, a. height, b. diameter at base height, c. wood specific density, d. leaf mass area, and e. leaf nitrogen content. Dashed lines represent the western transect and solid lines the eastern transect.
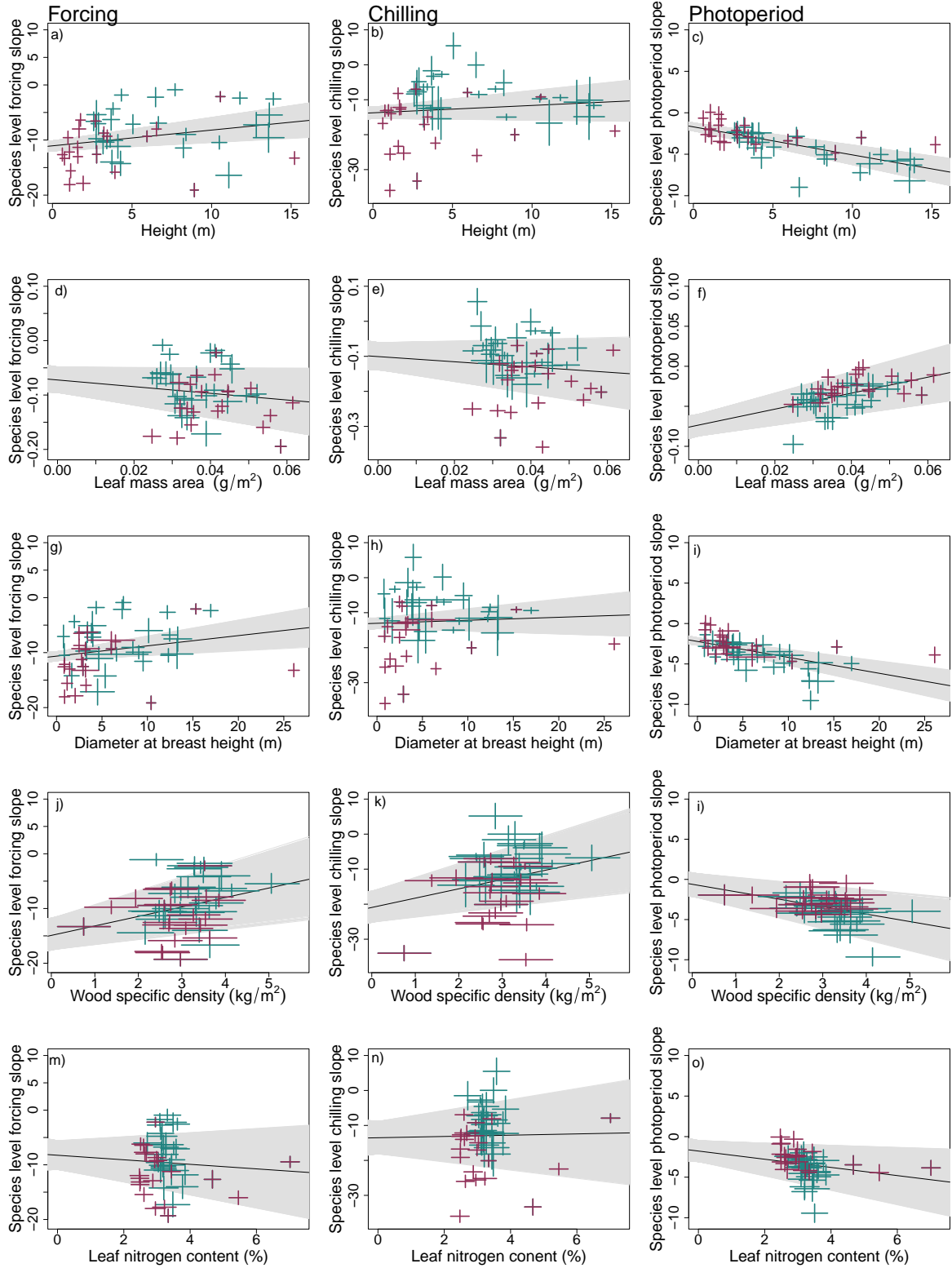
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Figure 2: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter at breast height, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing 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.

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