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

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Running title: Traits drive photoperiod cues in budburst

Summary

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

Introduction

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

In plants, species variation can be explained, in part, by differences in growth strategies, which are generally inferred from traits (Violle et al., 2007). Decades of research on plant traits have worked to build predictive models of species responses to their environment (Green et al., 2022), which could be promising to explain species-level variability in phenological responses. Phenology, however, has generally be excluded from plant trait research due to its high inter- and intra-specific variability,

making it difficult to leverage existing frameworks to explain phenological variation and predictions future changes.

Previous studies have found high variation in phenology for the same species when observed over different years or sites (Primack et al., 2009; Chuine et al., 2010). But many of these studies are observational and conducted at the landscape scale (**?**Menzel et al., 2006; **?**). In contrast, findings from controlled environment experiments suggest that phenological variation can be consistently decomposed into its cues (Laube et al., 2014; **?**). Given the importance of phenology in defining species temporal niches and the environmental conditions of growth periods, we predict that these phenology-cue relationships may also correlate with other functional traits and vary along an axis of acquisitive to conservative growth strategies.

Correlations between plant traits, growth strategies, and responses to environments have been synthesized into several global frameworks, including the leaf economic spectrum (Wright et al., 2004) and wood economic spectrum (Chave et al., 2009). These frameworks have identified key traits that exhibit distinct gradients, ranging from acquisitive strategies—fast growing plants that produce cheaper tissue —to conservative strategies—with plants that invest in long-lived tissue but slower growth rates (Wright et al., 2004; Díaz et al., 2016). In temperate systems, changes in temperature and frost risk in spring can produce gradients in abiotic stress (Sakai and Larcher, 1987; Gotelli and Graves, 1996; Augspurger, 2009) and greater competition later in the season (CITES). Species that varying the timing of leafout, should therefore exhibit traits and growth strategies that allow them to tolerate or avoid these abiotic risks. Leveraging insights from predictive models of phenology with these well established trait frameworks, we can begin to disentangle the environmental cues that shape phenology from those that are shaped by other traits differences in plant growth strategies.

To determine whether phenology fits within major functional trait frameworks will require a better understanding of the causes of variation within species. Phenological variation is generally observed in natural conditions where considerable differences in the environmental cues that trigger many phenological events—primarily temperature and photoperiod (Chuine, 2000; Körner and Basler, 2010)—vary across space and time. Within-species variation may also occur across other plant traits (e.g., leaf and wood structure traits), and across latitudinal (Wiemann and Bruce, 2002) or environmental gradients (Pollock et al., 2012), though generally to a smaller scale compared to phenology. While our previous growth chamber study found no evidence that phenological cues varied spatially (Loughnan and Wolkovich, in prep), previous work in functional traits has found other traits to exhibit greater spatial variation in response to environmental gradients (Gross et al., 2000; Wright et al., 2003). These results suggest that to better understand how phenology and other traits correlate across species will require methods that incorporate spatial variation within species.

We tested whether phenological variation was aligned with existing trait frameworks using data on spring budburst paired with a suite of traits that capture acquisitive to conservative growth strategies (Wright et al., 2004; Reich, 2014). Seasonal differences in environmental conditions between early and late spring create 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. Here, we decompose high phenological variation in budburst date, using experiments to estimate three major phenological cues for woody plant budburst: chilling (associated with cool winter temperatures), forcing (associated with warm spring temperatures), and photoperiod. We predict that early spring species will budburst before canopy closure—when chilling is lower, forcing temperatures are cooler, and photoperiods shorter (exhibited as smaller responses to temperature and photoperiod). These species should have traits associated 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 high

leaf nitrogen content (LNC) for a greater photosynthetic potential. In contrast, we predict species with later budburst will predominately include canopy species that express more conservative growth strategies and require more chilling, warmer forcing conditions, and longer photoperiods. These species should incur greater investments in long-lived tissue, with ring-porous wood anatomy, taller heights and greater DBH, WSD and LMA, but low LNC. We Use a powerful joint-modeling approach to estimate the relationships between these plant traits and phenological responses to cues, while partitioning the variance from species- and population-level differences.

Materials and Methods

Field sampling

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

Functional traits

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

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

Growth chamber study

For our growth chamber studies, we collected branch cuttings from our highest and lowest latitude populations in each transect, with sampling in our eastern study occurring from 20-28 January 2015 and sampling for our western study from 19-28 October 2019. In both studies, we included a total of

eight distinct treatments consisting of 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, both 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 photoperiods of either 8 or 12 hours. 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 better partitions the drivers of variation in species phenologies

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

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

$$\mu_{i,j} = \alpha_{\text{grand trait}} + \alpha_{\text{trait}_j} + \beta_{\text{transect}} \times transect + \tag{2}$$
$$\beta_{\text{latitude}} \times latitude + \beta_{\text{transect}\times\text{latitude}} \times (transect \cdot latitude) \tag{3}$$
$$\tag{4}$$

$$\boldsymbol{\alpha}_{\text{trait}} = \begin{bmatrix} \{\alpha_{\text{trait}_1} \\ \alpha_{\text{trait}_2} \\ \cdots \\ \alpha_{\text{trait}_n} \end{bmatrix} \text{ such that } \boldsymbol{\alpha}_{\text{trait}} \sim Normal(0, \sigma^2_{\text{trait}}) \tag{5}$$
$$\tag{6}$$

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

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

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

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

with

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

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

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

We modeled each trait individually, with the exception of ring-porosity, which we compared across species using the posterior estimates of our WSD model, in order to account for inherent differences in wood anatomy across species and growth form. We included all three cues (chilling, forcing, and photoperiod) as continuous variables in our model, as well as all two-way interactions between cues and between cues and sites. We converting chilling temperatures to total chill portions, including both the chilling experienced in the field prior to sampling and during the experiment in our 4°C chilling chambers, using local weather station data and used the chillR package to calculate total chill portions (v. 0.73.1, Luedeling, 2020). To account for differences in thermoperiodicity between the two studies (Buonaiuto et al., 2023), we also converted forcing temperatures to mean daily temperatures for each treatment. Finally, we z-scored each cue and site using two standard deviations to allow direct comparisons between results across parameters (Gelman, 2008).

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

Results

Across our eight populations, we measured 47 species of which 28 were in our eastern transect and 22 in our western transect. These include species dominant in both the understory and canopy layer, with our eastern community consisting of 13 shrubs and 15 trees, our western community consisting of 18 shrubs and 4 trees, and three species that occurred in both transects. In total we measured

traits of 1428 unique individuals between the two transects across our five traits: height (n = 1317), diameter at breast height (DBH, n = 1220), wood stem density (WSD, n = 1359), leaf mass area (LMA, n = 1345), leaf nitrogen content (LNC, n = 1351). Across our two growth chamber studies, we made observations of 4211 samples, with our observations of budburst spanning 82 and 113 days for our eastern and western studies respectfully.

Most of our traits showed some variation by latitude within each transect (with a strong interactive effect between transect and latitude, Fig. 1). Leaf nitrogen content was the only trait to vary with latitude alone, with low latitude communities on both our eastern and western transects having greater values of LNC that communities at higher latitudes (-0.1, UI: -0.2, -0.06, Table **??**). The strongest negative interaction was observed for height (-0.2, UI: -0.4, 0), while the strongest positive interaction was observed for LMA (0.5, UI: 0.4, 0.6). 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).

We found that three of our four traits had a strong relationship with photoperiod, but not always in the direction we predicted. Taller species with larger trunk diameters and leaves with high nitrogen content had stronger responses to photoperiod (Table **??**), Fig. 2 c, i, o; Tables **??**, **??**, **??**). Contrary to our expectation, species with denser, high LMA leaves, however, had weaker photoperiod responses, allowing them to potentially budburst under shorter photoperiods (Fig. 2 f).
Temperature cues exhibited no relationships with individual traits ($\beta_{\text{trait.chilling}}$), but by accounting for the effects of leaf or wood traits, we found the importance of our three cues the vary by trait. Our models of height (-13.4, UI: -17.2, -9.9), DBH (-12.5, UI: -16.2, -8.6), WSD (-20.9, UI: -33.2, -9.8), and LNC (-35.1, UI: -68.1, -4.1) all estimated chilling as the strongest cue of budburst (β_{chilling}), with more chilling advancing budburst. Our model of LMA, however, estimated photoperiod as the strongest cue ($\beta_{\text{photoperiod}}$, (-2.7, UI: -30.3, 26). After accounting for the effects of traits, only our height and DBH model found all three environmental cues to drive budburst timing (Tables **??**, **??**). Our models of WSD and LNC in turn found temperature cues alone to shape budburst (Tables **??**, **??**), while our model of LMA found a large response to only photoperiod (Table **??**).
In synthesizing the effects of multiple traits across species, our results can be used to make generalizations across ecologically important groups of species. But only some of our models estimated clear gradients in species timing between trees and shrubs. In particular, we found height to have large correlations between budburst timing and trait values, with earlier estimates of budburst for shrubs (with a mean day of budburst of 10)—especially under greater cues—and later budburst estimates for trees (with a mean day of budburst of 17.3; Fig. **??**). Diameter at breast height showed similar trends as estimates from our height model (results not shown). But this was not the case for our two leaf traits. Leaf nitrogen content, for example, showed no distinct separation between shrub and tree functional groups (Fig. **??**).

Discussion

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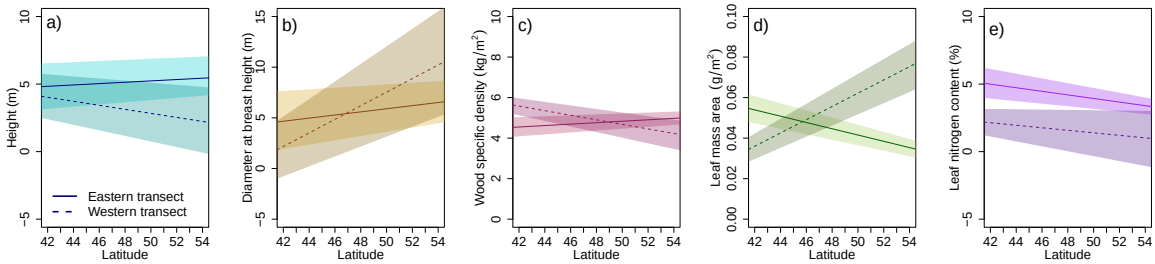

Figure 1: We found geographic differences for only one of our functional traits, the majority exhibiting no differences between latitudes or across transects. Depicted are the spatial trends for, a. height, b. diameter at base height, c. wood specific density, d. leaf mass area, and e. leaf nitrogen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

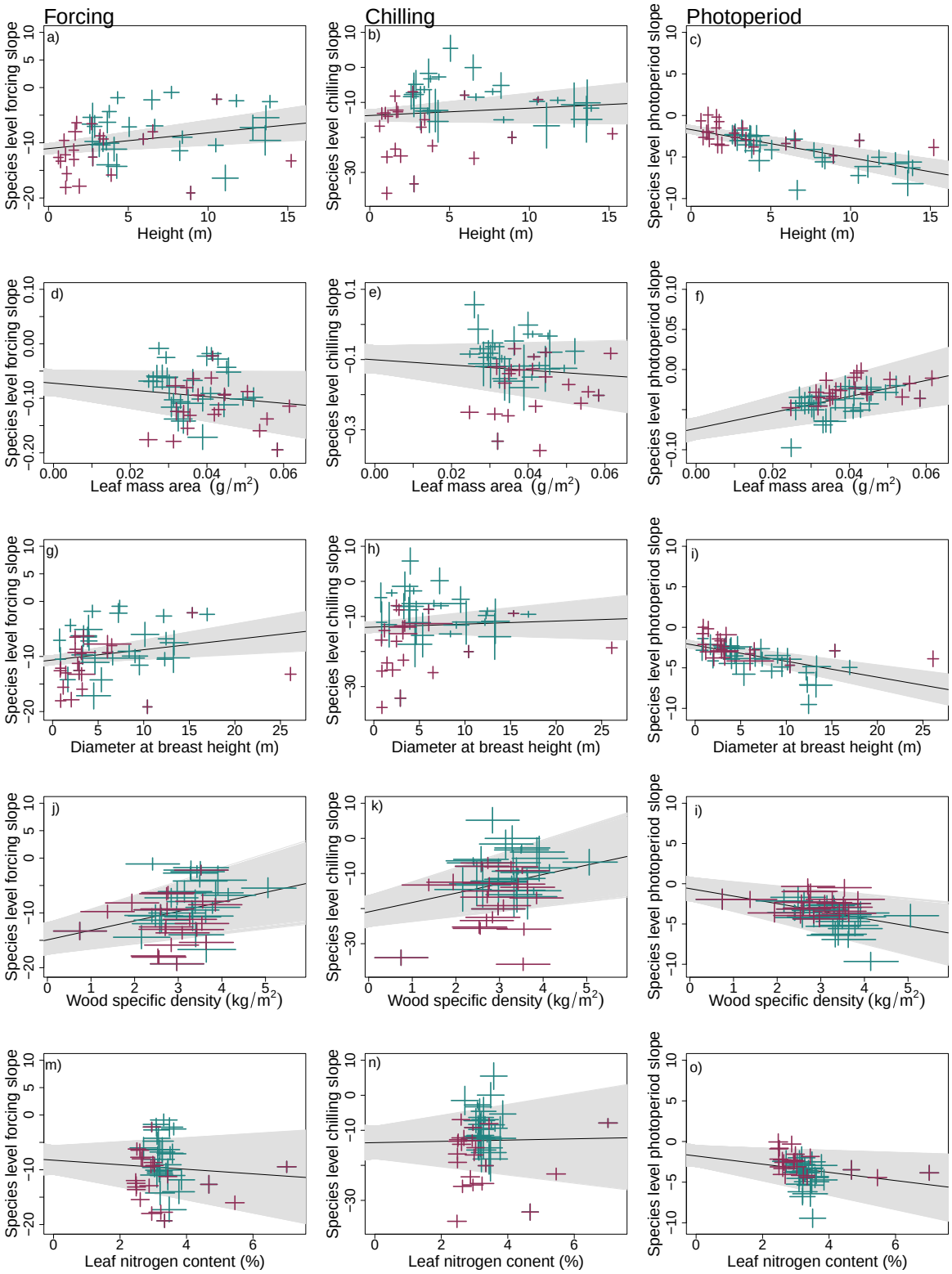

Figure 2: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter at breast height, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species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