

Differences in traits predict phenological responses to daylength more than temperature

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Running title: Traits drive photoperiod cues in budburst

Summary

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), posing a challenge to accurate forecasts. In plants, species variation can in part be explained by differences their strategies of growth, 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 the environment (Green et al., 2022), which could be promising to explain species-level variability in phenological responses. Phenology, however, has generally been excluded from plant trait research, 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 local environmental factors, such as temperature, soil moisture, and daylength, that can alter like the rate of plant growth, or leaf development (Menzel et al., 2006). But environmental factors at larger spatial and temporal scales may also drive of 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 species avoid this risk by leafing out later, this variation could also produce greater biotic stress later in the season through a more competitive environment. 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, we can begin to disentangle the environmental cues that shape phenology from those that are shaped by other traits and growth strategies.

Phenology itself is considered a trait with high inter- and intra-specific variability. 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). This variability is often given as justification for excluding phenology from broader functional trait frameworks. But given the importance of phenology in defining species temporal niches and the environmental conditions of growth periods, phenological variation may correlate with other functional traits along the axis of acquisitive to conservative growth strategies.

To understand whether phenology fits within major functional trait frameworks, we must understand the causes of variation within species. Phenological variation is generally observed in natural conditions where considerable differences in the major environmental cues that trigger many phenological events—temperature and daylength (Chuine, 2000; Körner and Basler, 2010)—vary across space and time. However, phenology is often highly predictable when decomposed into these underlying environmental cues (Laube et al., 2014). Within-species variation may also occur across other plant traits (e.g., leaf and wood structure traits), which may vary 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 understanding how phenology and other traits correlate across species will require methods that incorporate variation within species.

Here, we address this challenge 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—including both shrubs and tree species—of temperate deciduous forests in North America. Seasonal differences in environmental conditions create larger gradients in frost risk, soil nutrients, and light availability, in addition to differences in biotic interactions, from herbivory or competition. These differences between early and late season conditions 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 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 predominately 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.

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 daylength. These cues correlate with early to late phenology with early species (which we predict have acquisitive traits) showing smaller responses to temperature and daylength, while later species (which we predict have conservative traits) showing larger responses. 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. This approach represents a considerable advance in how we estimate trait-cue relationships, and may allow us to better estimate species phenological responses from available trait data.

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. ??). For the growth chamber studies on budburst phenology, cuttings were collected from the most southern and northern populations in each transect ($n_{pop}=4$).

Across all eight populations, we measured a diverse assemblage of species from the understory and canopy layers. We selected the angiosperm species that were most abundant, with an aim to maximize the number of closely related species and congeners between our eastern and western communities. We focused on angiosperm species only, as they are more likely to have similar environmental controls to their leafout phenology, and to standardize our leaf trait comparisons by excluding gymnosperms.

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, but before budset. At each population, we measured a total of five traits: height, diameter at breast height (DBH), stem specific density (SSD), leaf mass area (LMA), and the percent leaf nitrogen content (LNC). Each trait was measured for each species present at a population, resulting in us measuring 1-10 healthy adult individuals per species at each 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 stem specific density, we collected a 10 cm sample of branch wood, taken close to the base of 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. Stem 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.

138

139 Growth chamber study

140 For our growth chamber study, we collected branch cuttings from our highest and lowest latitude pop-
 141 ulations in each transect. In both our eastern and western controlled environment study, we included
 142 two temperature treatments and daylength, for a total of eight distinct treatments. Our treatments
 143 included two levels of chilling—with our eastern study having no additional chilling or 30 days at 4°C,
 144 and our western study 30 days or 70 days of chilling at 4°C, with all non-field chilling occurring under
 145 dark conditions. Our forcing treatments included either a cool regime of 15:5°C or a warm regime of
 146 20:10°C, and our photoperiod treatments consisted of either 8 or 12 hour daylengths. We recorded
 147 budburst stages of each sample every 1-3 days for up to four months, defining the day of budburst
 148 as the day of budbreak or shoot elongation (defined as code 07 by (Finn et al., 2007)). For a more
 149 detailed discussion of study sample collection and methods see Loughnan and Wolkovich (in prep).

150

151 Statistical Analysis

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

157

158 Our joint model consists of two parts. The first is a hierarchical linear model, in which we have parti-
 159 tioned the variation of individual observations (i) of a given trait value (Y_{trait}) to account for the effects
 160 of species (j), population-level differences arising from transects (t), latitude, as well as the interaction
 161 between transects and latitude ($\text{transect} \times \text{latitude}$), and finally, residual variation or ‘measurement
 162 error’ (σ_m^2).

163

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

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

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

$$(4)$$

164

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

$$(6)$$

165 Transect was included as a categorical variable and latitude as a continuous variable in our model.
 166 Traits were modeled using natural units, with the exception of LMA, which was rescaled by 100 for
 167 numeric stability in the model. Each of our traits collected *in situ* were modeled individually, but
 168 comparisons across species ring-porosity were made using the posterior estimates of our height model.
 169 This allowed us to best account for inherent differences in wood anatomy across species and growth
 170 form.

171

172 We used partial pooling to uniquely estimate species-level variance ($\alpha_{\text{sp},k}$)—which controls for variation
 173 in the number of trait estimates per species and trait variability—which are then used as predictors of

species-level estimates of each cue ($\beta_{\text{chill},k}$, $\beta_{\text{force},k}$, $\beta_{\text{photo},k}$).

$$\begin{aligned}\beta_{\text{chill}_k} &= \alpha_{\text{chill},k} + \beta_{\text{trait.chill}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{force}_k} &= \alpha_{\text{force},k} + \beta_{\text{trait.force}} \cdot \alpha_{\text{trait},k} \\ \beta_{\text{photo}_k} &= \alpha_{\text{photo},k} + \beta_{\text{trait.photo}} \cdot \alpha_{\text{trait},k}\end{aligned}\tag{7}$$

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

$$Y_{\text{pheno}_{k,g}} \sim \mathcal{N}(\mu_{k,g}, \sigma_d^2)\tag{8}$$

with

$$\mu_{k,g} = \alpha_{\text{pheno},k} + \beta_{\text{chill}_k} \cdot c_g + \beta_{\text{force}_k} \cdot f_g + \beta_{\text{photo}_k} \cdot p_g\tag{9}$$

where α_{pheno_k} , α_{chill_k} , α_{force_k} , and α_{photo_k} are elements of the normal random vectors:

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

We included chilling as chill portions, and each environmental cue as continuous variables. We standardized all cues by z -scoring them, allowing us to make comparisons across cues (see Loughnan and Wolkovich, in prep).

For our model, we used weakly informative priors unique to each trait. 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. Our model estimates are reported as the mean values, with the 90% uncertainty interval. Estimates are given to one decimal place, as this best represents the level of precision we can infer from our data (Gelman et al., 2020).

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 ($n = 1317$), DBH

($n = 1220$), SSD ($n = 1359$), LMA ($n = 1345$), LNC ($n = 1351$). Across our two growth chamber studies, we made observations of 4211 samples, with our observations of budburst spanning 82 and 113 days for our eastern and western studies respectfully.

Most of our traits showed some variation by latitude within each transect (an interactive effect between transect and latitude for which the 90% UI does not cross zero). Leaf nitrogen content (LNC) was the only trait to vary with latitude alone, with low latitude communities having greater values of LNC than communities at higher latitudes (-0.1, UI: -0.2, -0.06, Table ??). Overall, woody species in our eastern community exhibited greater heights, diameters at breast height, and wood specific densities but decreases in leaf mass area (LMA) with increasing latitudes. But in our western communities height and wood specific density declined at higher latitudes, 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 also varied across our traits. For our trait models chilling was the strongest cue of budburst (Table ??, ??, ??, ??). But only our model of height and DBH had strong responses to all three cues (Table ??, ??). Our model of SSD estimated strong cue responses to temperature cues only (Table ??), while our LMA estimated a strong response to photoperiod (Table ??) and our LNC model a strong response to chilling and photoperiod only (Table ??). But in accounting for the effects of traits on budburst, we found that four of our five traits had a strong relationship with photoperiod (Tables ??, ??, ??, ??). 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 (Fig. ??). In particular, we found height to have large correlations between budburst timing and trait values, with earlier estimates of budburst for shrubs—especially under greater cues—and later budburst estimates for trees (Fig. ??). Diameter at breast height showed similar trends as estimates from our height model (results not shown). But this was not the case for our two leaf traits. Leaf nitrogen content, for example, showed no distinct separation between shrub and tree functional groups (Fig. ??).

Discussion

Of the six traits we studied, we found budburst responses to one or more phenological cue, but only three of those traits fit within a gradient of acquisitive to conservative growth. Using our joint modeling approach, we were able to estimate how these traits interact with cues to shape species budburst. We found that photoperiod—often the weakest cue to 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 latitudes, 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 phenotypes 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 SSD, 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 stem densities, and leaves with low LMA, and high LNC—to have early budburst via small temperature and daylength responses. But we found traits to differ in which cues shape phenology. As predicted, conservative species with greater heights and DBH did have larger temperature and photoperiod responses (associated with later budburst), but contrary to our prediction, conservative species with high LMA showed small responses to photoperiod, while leaves with high LNC had strong photoperiod responses. These results suggest that phenology is 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. In addition to also finding relationships between tree height and temperature and photoperiod, we found similar responses in leaf traits, as 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 this result, across these two spatial scales of study, suggest there are alternate underlying mechanisms 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). The trends we observed in LMA, may be the result of other processes than light capture, such as tissue lifespan or decomposition rates (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. In focusing solely on phenology, previous research has shown budburst timing is 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 leaf mass area 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, including radial growth phenology and shoot elongation in woody plants (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 a more holistic consideration of cues known to shape other plant traits.

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. This suggests the relationships between photoperiod and other traits 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 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 their interactions within communities.

Further, our findings of correlations between phenology and other commonly measured traits highlight that accurate forecasts of future changes in phenology may benefit from accounting for the response of other traits to climate change. Across temperature and precipitation gradients, leaf size and shape, for example, 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 suggest its importance as a cue. It is therefore critical that we continue to take a more holistic approach to studying the relationships between phenology and plant traits to accurately forecast the future impacts of climate change on communities.

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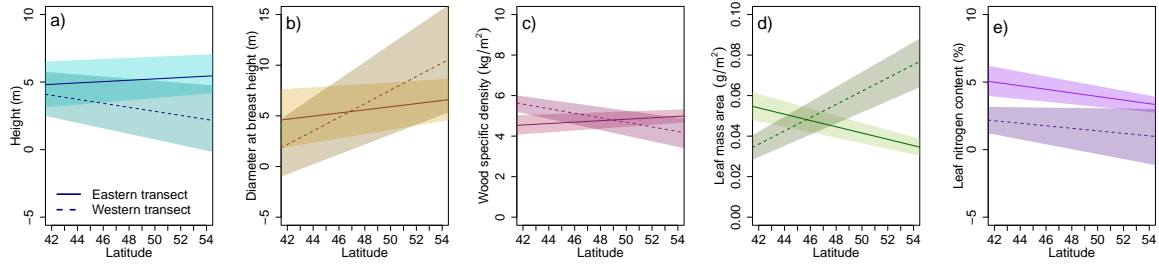


Figure 1: We found geographic differences for only one of our functional traits, the majority exhibiting no differences between latitudes or across transects. Depicted are the spatial trends for, a. height, b. diameter at base height, c. wood specific density, d. leaf mass area, and e. leaf nitrogen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

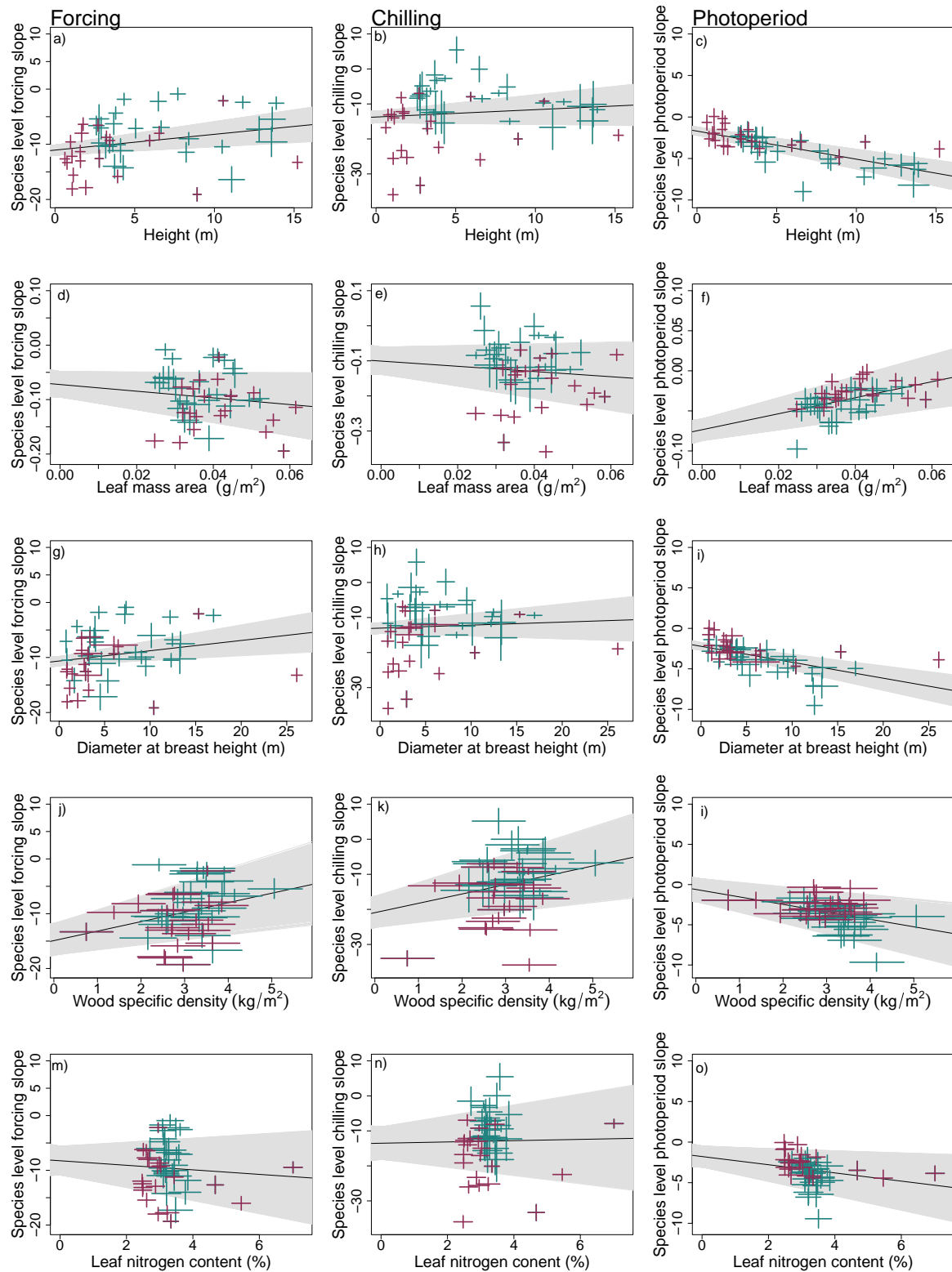


Figure 2: Relationships between species traits and cue responses showed considerable variation across a-c. height, d-f. leaf mass area, g-i. diameter at breast height, j-l. wood specific density, and m-o. the leaf nitrogen content. Point colours representing different species groups, with tree species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