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

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Research questions

1. Do phenological cue-trait relationships change across transects? Populations?

2. How do budburst cues relate to functional traits in temperate woody species?

3. How do shrub and tree species differ in their cue-trait relationships?

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 deciduous forests in North America. Both suites of data were collected from populations that span latitudinal gradient of 4-6° for 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, XXX°W)), Second College Grant, New Hampshire, USA (44.79°N, XXX°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. For the growth chamber studies, 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 in our forest communities, 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 these species are more likely to have similar environmental controls to their leafout phenology, and to standardize our leaf trait comparisons by excluding gymnosperm species with.

Functional traits

We measured all traits in the summer prior to each growth chamber study. For our eastern transect, traits were measured from June 8 to June 25, 2015, and from May 29 to July 30, 2019 for our western transect. 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 populations, resulting in us measuring 1-10 healthy, adult, individuals per species at each population. We also used the WSL xylem database (?) to collected data on species ring-type for the 72.3% of our species represented in the database.

We measured traits in accordance to the methods discusseed by Pérez-Harguindeguy et al. (2013). We calculated tree height using trigonometric methods, using a TruePulse 200L rangefinder and measured DBH 1.42m 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 10cm 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. We measured wood volume 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. We estimated leaf area using the ImageJ software (version X). Upon returning from the field, we dried our leaves for 48h at $70°$ and weighed each leaf using a precision balance. Leaf mass area was calculated as the ratio of the leaf dry mass over it's area.

Growth chamber study

For our growth chamber study, we collected branch cuttings from our highest and lowest latitude populations in each transect. In both our eastern and western controlled environment study, we included two temperature treatments and daylength, 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 30 days or 70 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 of either 8 or 12 hour daylengths. 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 (?)). For a more detailed discussion of study sample collection and methods see Loughnan and Wolkovich (In prep).

Statistical Anlaysis

Our analysis combined our *in situ* trait data with budburst data from the growth chamber studies. 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—allowing us to better partition 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 ($y_{\text{trait}[i]}$) to account for the

82 effects of species (*sp id*), population-level differences arising from transects (*transect id*), as well as
83 the interaction between transects and latitude (*transect × latitude*), and finally, residual variation or
84 'measurement error' (σ_{trait}). Transect was included as a categorical variable and latitude as a contin-
85 uous variable in our model. Traits were modeled using natural units, with the except of LMA, which
86 was rescaled by 100. While each of our traits collected at the individual level were run using separate
87 models, comparisons across species ring-porosity were made using the posterior estimates of our height
88 model. This allowed us to best account for inherent differences in wood anatomy across species and
89 growth form.
90

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

91 The second part of our joint model models the relationship between traits and phenological cues, es-
92 timating their effects on budburst. In this portion of the model, we used partial pooling to uniquely
93 estimate species-level variance ($\alpha_{\text{sp[sp id]}}$)—which controls for variation in the number of trait estimates
94 per species and trait variability—which are then used as predictors of species-level estimates of each
95 cue ($\beta_{\text{force[sp]}}$, $\beta_{\text{chill[sp]}}$, $\beta_{\text{photo[sp]}}$). In addition to the species-level estimates, our model also estimates
96 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
97 how well trait effects explain species-level differences by estimating the the species-level cue variation
98 not explained by traits ($\alpha_{\text{chill[sp]}}$, $\alpha_{\text{force[sp]}}$, $\alpha_{\text{photo[sp]}}$) and individual species responses to cues (C_i,
99 F_i, P_i, respectively). Finally, our model estimates the residual variation across species ($\alpha_{\text{pheno[sp]}}$)
100 and observations (σ_{pheno}). Chilling was included as chill portions, and both forcing and photoperiod
101 as continuous variable, with all cues standardized by *z*-scoring each cue to allow comparisons (see
102 Loughnan and Wolkovich (In prep) for more details).
103

$$\mu_{pheno} = \alpha_{\text{pheno[sp]}} + \beta_{\text{chill[sp]}} \times C_i + \beta_{\text{force[sp]}} \times F_i + \beta_{\text{photo[sp]}} \times P_i \quad (2)$$
$$y_{\text{pheno[i]}} \sim normal(\mu_{pheno}, \sigma_{\text{pheno}})$$

104 trait-cue relationship:

$$\beta_{\text{chill[sp]}} = \alpha_{\text{chill[sp]}} + \beta_{\text{trait.chill}} \times \alpha_{\text{trait sp[sp]}}$$
$$\beta_{\text{force[sp]}} = \alpha_{\text{force[sp]}} + \beta_{\text{trait.force}} \times \alpha_{\text{trait sp[sp]}} \quad (3)$$
$$\beta_{\text{photo[sp]}} = \alpha_{\text{photo[sp]}} + \beta_{\text{trait.photo}} \times \alpha_{\text{trait sp[sp]}}$$

105 Model includes residual variation across species and variation in cues not attributed to the trait
106 (partially pooled):

$$\alpha_{\text{pheno}} \sim normal(\mu_{\alpha_{\text{pheno}}}, \sigma_{\alpha_{\text{pheno}}}) \quad (4)$$
$$\alpha_{\text{force}} \sim normal(\mu_{\alpha_{\text{force}}}, \sigma_{\alpha_{\text{force}}})$$
$$\alpha_{\text{chill}} \sim normal(\mu_{\alpha_{\text{chill}}}, \sigma_{\alpha_{\text{chill}}})$$
$$\alpha_{\text{photo}} \sim normal(\mu_{\alpha_{\text{photo}}}, \sigma_{\alpha_{\text{photo}}})$$

107 For each individually modeled trait, we used weakly informative priors unique to each trait. We vali-
108 dated each models priors using prior predictive checks. We coded our models in the Stan programming

¹⁰⁹ language and fit them using the rstan package. Each model had four chains ran for 6000-8000 total
¹¹⁰ sampling iterations. All our models met basic diagnostic checks, including no divergences, high effec-
¹¹¹ tive sample sizes (n_{eff}) that exceeded 10% of the number of iterations, and $\hat{R}$ values close to 1. Our
¹¹² model estimates are reported as the mean values, with the 90% uncertainty interval. Estimates are
¹¹³ given to one decimal place, as this level of precision reflects the level we can infer from our dataset
¹¹⁴ (Gelman et al., 2020).
¹¹⁵

Results

¹¹⁷ Across our eight populations, we measured 47 species of which 28 were in our eastern transect and 22
¹¹⁸ within our western transect. The species found in both transects include species dominant in both the
¹¹⁹ understory and canopy layer, in our eastern communities we sampled 13 shrubs and 15 trees, while
¹²⁰ we sampled 18 shrubs and 4 trees in our western communities, and three species occurred in both
¹²¹ transects. In total we measured traits of 1428 unique individuals between the two transects across our
¹²² six traits: height ($n = 1317$), DBH ($n = 1220$), SSD ($n = 1359$), LMA ($n = 1345$), LNC ($n = 1351$,
¹²³ ring porosity ($n = 34$)). Across our two growth chamber studies, we made observations of 4211, with
¹²⁴ studies spanning 82 and 113 days for our eastern and western studies respectfully. Using our joint
¹²⁵ modeling approach, we were able to combine our trait data with budburst data from 4211 cuttings
¹²⁶ across the same 47 species we sampled the traits of in the field.
¹²⁷

¹²⁸ Most of our traits showed negligible trait variation across populations, both in terms of differences
¹²⁹ between the two transects (main effect of transect only) or by latitudes within each transect (an in-
¹³⁰ teractive effect between transect and latitude). Only leaf mass area (LMA) differed by latitude within
¹³¹ transects (0.3, UI: 0.2,0.4)—with the LMA of eastern species increasing with latitude—but not west-
¹³² ern species (Fig. 1 d). Similarly, leaf nitrogen content (LNC) showed a weak interaction between
¹³³ latitude and transect (0.3, UI: 0.2,0.4)—with higher latitude populations in eastern transect having
¹³⁴ lower LNC than lower latitude populations and western species (Fig. 1e). Our wood and structural
¹³⁵ traits, however, showed no differences across populations or transects (Table 2 - 3). The differences we
¹³⁶ found across populations were small to negligible, especially in comparison to species-level differences,
¹³⁷ which varied considerably and up to XX fold (Fig. 2.
¹³⁸

¹³⁹ Only a subset of our traits related to at least one budburst cue, but responses were generally weak.
¹⁴⁰ Of our three cues, only photoperiod had relationships with other traits (Fig.). We found similar cue
¹⁴¹ relationships for our two structural traits, finding taller plants with greater DBH to exhibit stronger
¹⁴² photoperiod responses, producing earlier estimates of budburst under longer daylengths (-1.7, UI: -2.9,
¹⁴³ -0.5 for height and -2.3, UI: -3.4, -1.1 for DBH). We, however, found no relationship between cues and
¹⁴⁴ SSD (Table 3) or between cues and species different types of wood porosity 3.
¹⁴⁵

¹⁴⁶ Of our two leaf traits, only one showed a moderate relationship with cues. We found leaf mass area to
¹⁴⁷ relate to photoperiod, with low LMA species advancing their budburst timing with longer photoperiods
¹⁴⁸ (-7.5, UI: -10.9, -4.1). But we found no relationship between cues and LNC.
¹⁴⁹

¹⁵⁰ Which cues had the strongest effects on budburst varied across our trait models, with some models
¹⁵¹ showing stronger responses to photoperiod than temperature (Fig. 4). For most of our trait models,
¹⁵² chilling followed by forcing, were the strongest cues of budburst (Fig. 4). But in accounting for the
¹⁵³ relationship between LMA and cues, our model estimated stronger responses to photoperiod (-7.5,
¹⁵⁴ UI: -10.9, -4.1) that than forcing (-7.1, UI: -13.0, -1.6)—while effects of chilling were weak (90% UI
¹⁵⁵ crossing zero) (Table 4). In contrast, our LNC (Table 5) and SSD models (Table 3) both showed
¹⁵⁶ weak photoperiod effects on budburst (90% UI crossing zero). These finding suggest that additional
¹⁵⁷ traits alter the effects and relative importance of cues on budburst (Fig. 5). This—paired with strong

species-level variation—may cause variation in the estimated responses of species relative budburst dates across the different trait models.

By synthesizing the effects of multiple traits across species, our results allow us to make generalizations across groups of species. Estimates of budburst using our model parameters show clear differences in species timing between trees and shrubs for some traits but not all (Fig. 6). We found height to have strong correlations between budburst timing and trait values, with earlier estimates of budbust for shrubs—especially under stronger cues—and later budburst estimates for trees (Fig. 6). Diameter at breast height showed similar trends, 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. 6).

1. General summary of what we FOUND (with some of what we did)

    (a) Our study = one of the first to combine trait data with phenological cue responses for the same individuals and across species distributions

    (b) We found only three (out of six) traits showed a relationship with phenological traits, with two of those fitting our hypothesized aquis to cons paradigm in the spring.

    (c) Joint modelling approach = use sp-level estimates for traits to understand phenological cue responses and budburst timing suggested photoperiod may be most important to trait-phenology relationships ..

    (d) Includes plant communities in eastern and western deciduous forests of North America, and samples collected from multiple populations—modelling approach that accounts for variation across populations and transects

    (e) We found, however, generally low population-level variation in traits—usually even across the different eastern and western deciduous forests of North America, which was likely driven by species-level variation in traits

2. Population level variation:

    (a) generally traits did not change across population or with latitude

    (b) Only leaf traits varied with transect—patterns are in line with what you would predict given the differences in shrub vs tree spp in our transects

    (c) Predicted shrubs = acquisitive growth strategies = low LMA and high LNC

    (d) Western pop = more shrubs = did have low LMA and high LNC relative to eastern transect

3. Phenology in context of LES

    (a) Summarize whether fits with acquisitive-conservative predictions

        i. Partial support whether phenology = the same acquisitive to conservative gradient in growth commonly found for other traits

        ii. Predicted all traits to correlate with phenological cues = budburst timing—but found relationships with only one of our three cues

        iii. Ht and DBH both in line without prediction that tall, larger trees would have stronger photoperiod cues

        iv. But LMA showed opposite response to photoperiod than predicted—low LMA (acquisitive) spp more responsive to photoperiod

    (b) Interesting similarities with previous studies

        i. Traits have many functions—mitigate abiotic and biotic factors

ii. But trait research has found considerable variation in trait phenotypes across spatial scales (cite Gross 2000, Flecker and Jones 2003)—different responses for different traits

iii. In comparing plant traits across spatial scales, previous studies have found little variation across regional scales (comparing populations or sites) and more within-community variability (Messier et al 2010, Kang et al. 2014, Standen et al. 2023)

iv. But in comparing our results with a global meta-analysis of trait relationships with budburst cues = similar results for some traits

v. Found similar unexpected responses in leaf traits—high specific leaf area (the inverse of LMA) exhibited strong responses to photoperiod—suggests could be alternate underlying mechanisms shaping how species respond to photoperiod cues

vi. But also found strong temperature cues for most traits—not found in our analysis of North American forests

How traits shape species temporal niches

4. Correlations between traits and cues

   (a) Individuals temporal niche = result of numerous and likely complex interactions across abiotic and biotic factors

   (b) Our results suggest focusing on single traits—fails to account for interactions between other traits and cues

   (c) Decades of research on budburst cues = primarily driven by temperature cues—but only photoperiod related to other traits

5. Suggests may be other physiological constraints or trade-offs selecting for other traits and shaping species phenologies

   (a) Temperature—generally thought of as a strong environmental cue—but might not be strongest selective pressure in temperate forests

   (b) Soil moisture = known to select for other types of tree phenology—radial growth and shoot elongation

   (c) LMA can also vary with soil moisture—to reduce evaporation plants can reduce leaf area = high LMA in dry conditions (de la Riva, 2015)—could be driving the unexpected trend in LMA

   (d) Later in the spring—longer photoperiods—less water high LMA would be favorable

   (e) To gain a holistic understanding of species growth strategies and phenotypes require consideration of additional cues

Using functional traits to predict climate change responses

6. Impacts of community dynamics and forecasting

   (a) Community dynamics with climate change

      i. Results = novel insights on how other traits impact phenological sensitivities to environmental cues

      ii. Relationships between budburst and photoperiod could limit the extent of spp advances in spring

      iii. Photoperiod is fixed—unlike temperature cues = increasing with climate change—species ability to track temperature could be constrained

    (b) Forecasting future forests

       i. Our study is one of the first to model the relationship between phenology and other traits—but results simply tell us the associations—need to understand mechanism

      ii. Phenology—cited as finger print of climate change—but other traits have been noted to change as well

     iii. Across temperature and precipitation gradients—leaf size and shape also change—spp shift to conserve water and mitigate effects of transpiration with high high temperatures—cite de le Riva 2016 as example

     iv. trait literature = explored how traits shift across environmental gradients—temp or precip—denoting trends leaf area and height

      v. Important we continue to synthesize across phenology and trait research—better forecast the future impacts of climate change on communities

References

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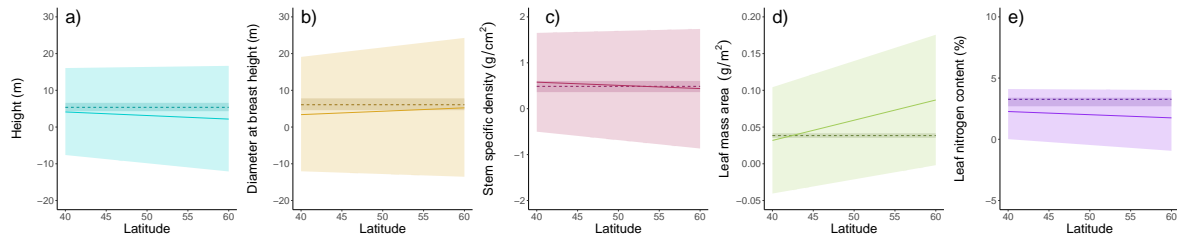
Figures

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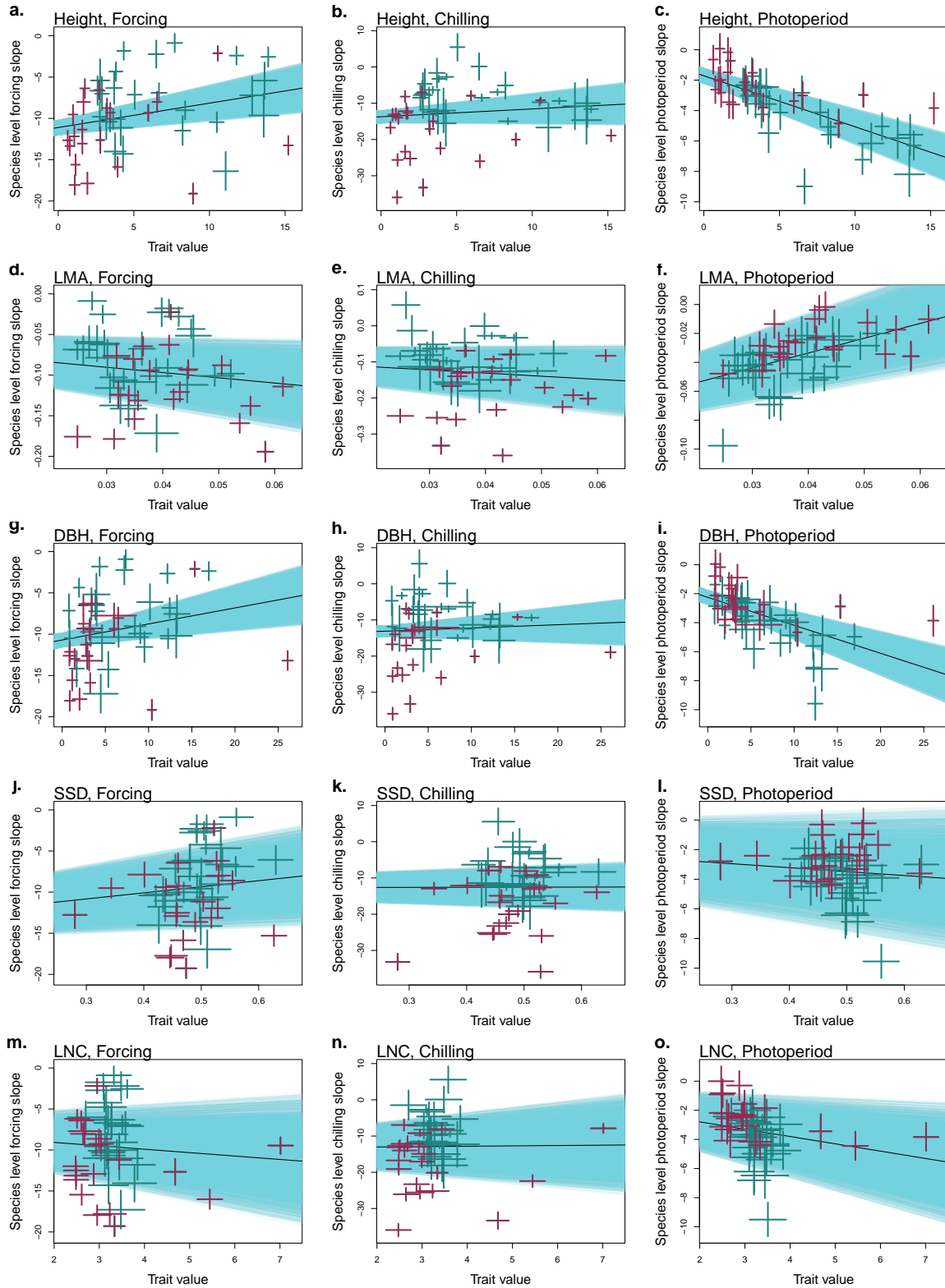
Figure 2: Relationship between species traits and cue responses, for height (a-c), leaf mass area (d-f), diameter at breast height (g-i), stem specific density (j-l), and the leaf nitrogen content (m-o). Point colours representing different species groups, with tree species are depicted in maroon and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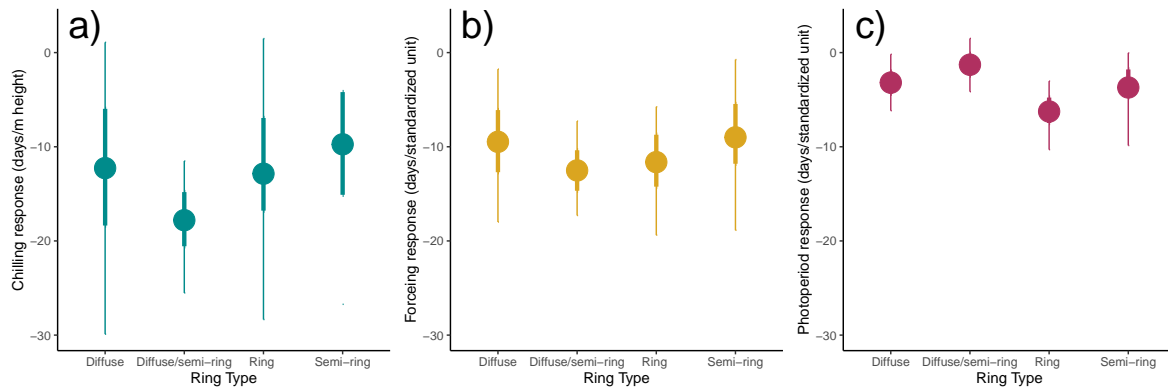
Figure 3: Despite species wood structures causing differing growth strategies, we did not find this trait to correlate with differences in cue responses across species. Thinner lines represent the 90% UI and thicker lines the 50% UI. Here we show the results for height only.
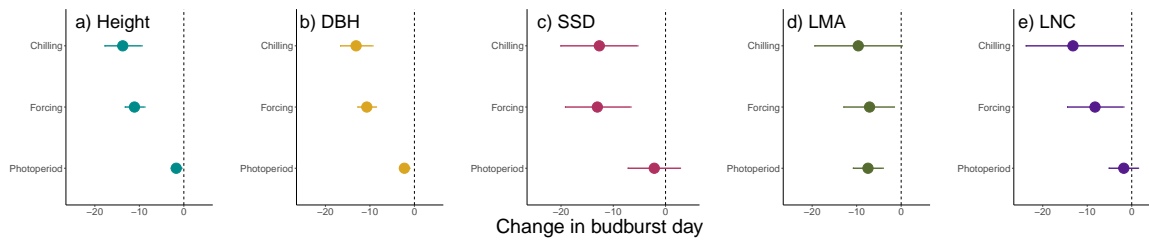

Figure 4: We found fairly consistent estimates for budburst cue responses to chilling, forcing, and photoperiod for each of our trait models: a. height, b. diameter at breast height, c. stem specific density, d. leaf mass area, and e. leaf nitrogen contnet. Lines represent 90% uncertainty intervals.
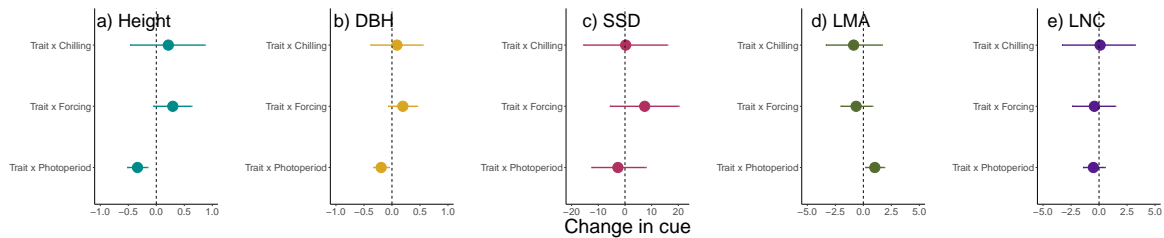

Figure 5: The relationships between traits and cue responses varied considerably across each of our trait models, a. height, b. diameter at breast height, c. stem specific density, d. leaf mass area, and e. leaf nitrogen content, and for individual cues. Lines represent 90% uncertainty intervals. Note the differences in the scale of the x-axis.
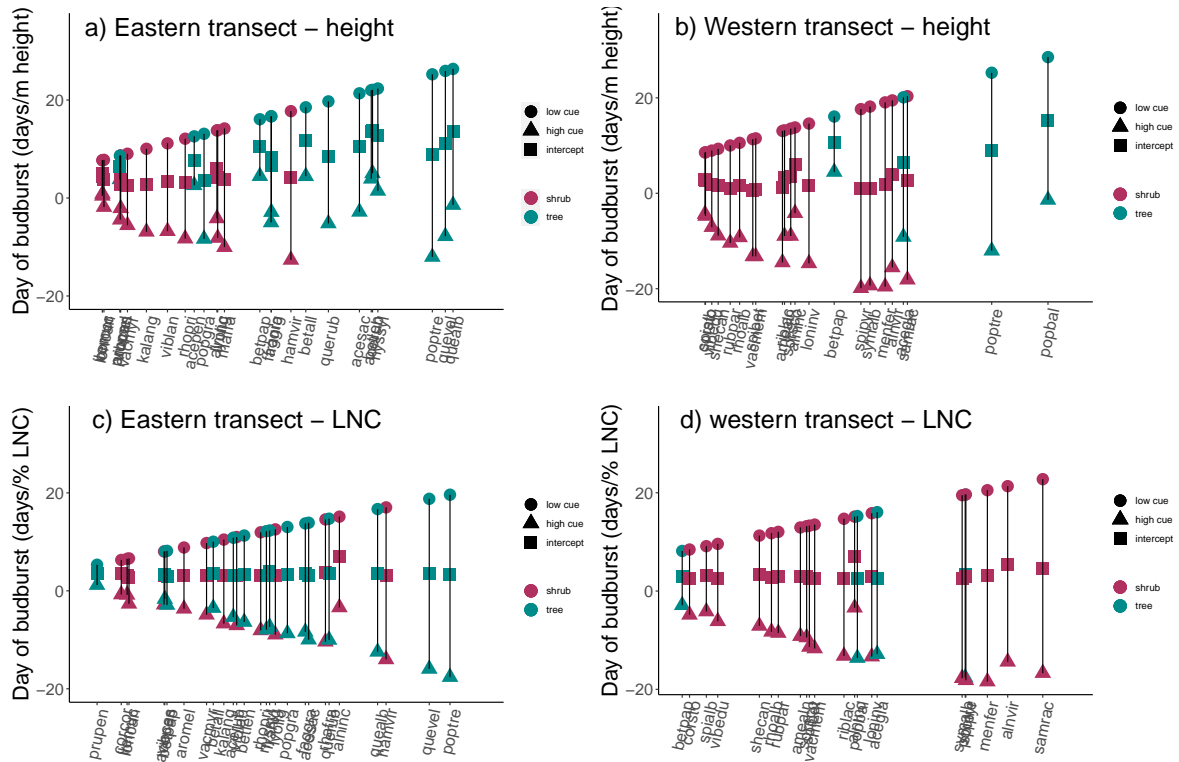
Figure 6: We found budburst estimates differed between our full model (intercept plus cues, depicted as triangles for high cues and as circles for low cues), versus the intercepts only model (without cues, shown as squares). Species are ordered in increasing budburst dates for both the eastern (a and c) and western (b and d) populations, spanning from early budbursting shrubs, in red, to late budbursting trees in blue. For traits such as height (a and b) we found distinct partitioning of budburst across shrub and tree species, but this was not the case for all traits, with our model of leaf nitrogen content showing highly mixed budburst order of shrub and tree species (c and d).

Tables

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

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

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

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

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

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

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

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

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

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