Photoperiod shows strong relationships with leaf and wood traits but not woody plant budburst

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December 22, 2023

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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

1. General pop description
   (a) Combined *in situ* trait data with budburst data from two growth chamber cutting experiments
   (b) Traits were measured across four eastern populations — Harvard Forest, Massachusetts, USA (42.55°N, 72.20°W) and St. Hippolyte, Quebec, Canada (45.98°N, 74.01°W) and four western population — Smithers (54.78°N, 127.17°W) and E.C. Manning Park (49.06°N, 120.78°W)
   (c) Growth chamber study — cuttings collected from the most southern and northern populations in each transect
   (d) Both datasets span latitudinal gradient of 4-6°
2. Describing spp
   (a) Across populations — measured 47 species — 28 eastern transect and 22 western transect
   (b) Selected spp that were most abundant in forest communities
   (c) Eastern transect: 13 shrubs and 15 trees
   (d) Western transect: 18 shrubs and 4 trees
   (e) Three species occurred in both transect

Functional traits

1. General sampling info
    (a) Traits were measured in the summer prior to each growth chamber study.
    (b) Eastern transect: traits measured summer 2015
    (c) Western transect: traits measured May 29 to July 30, 2019
    (d) For each — measured traits for X-10 healthy, adult, individuals of each species
2. Trait sampling — structural/wood traits
    (a) Measured a total of five traits: height (n = 1317), DBH (n = 1220), SSD (n = 1359), LMA (n = 1345), LNC (n = 1351)
    (b) Traits were measured according to recommendations of Perez-Harguindeguy2013.
    (c) Height was measured using a range finder (XX brand etc.).
    (d) Diameter at breast height was measured 1.42 m from the ground.
    (e) Wood volume was measured within 12 hours of collection — 10 cm sample taken from tree branches or shrub primary stems — measured using the water displacement method
    (f) Branch segments were dried at 105°C for 24h and weighted.
3. Trait sampling — leaf traits
    (a) Leaf traits were measured for five haphazardly selected, fully expanded, and hardened leaves
    (b) High resolution scans of leaf area taken using Canon flatbed scanner within 12 hours of collection
    (c) Leaf area was then quantified using the ImageJ software
    (d) Leaves were dried for 48h at 70°C and weighed using a precision balance.

Growth chamber study

1. General information
    (a) To collect branch cuttings for growth chamber study — returned to our highest and lowest latitude populations in each transect
    (b) Eastern transect: Hippolyte and Harvard Forested visited again in 20-28 January for growth chamber study — study conducted at Arnold Arboretum
    (c) Western transect: traits measured May 29 to July 30, 2019 — Smithers and Manning park visited again in 19-28 October, 2019 — study conducted at UBC
2. Treatments and duration
    (a) For both growth chamber studies — 8 distinct treatments:
    (b) two levels of chilling — no additional chilling or 30 days at 4°C = eastern study, and 30 days or 70 days of chilling at 4°C for our western study — all dark
    (c) two levels of forcing—a cool regime of 15:5°C and a warm regime of 20:10°C
    (d) two photoperiods of either 8 or 12 hours
    (e) For detailed disucssion of study differences see Loughnan et al. (phenology paper)
3. Data collection — BBCH
    (a) Phenological stages were based on BBCH scale adapted for our specific species

   (b) Observations made every 1-3 days for each sample
   (c) stages were recorded up to full leaf expansion — limited our analysis to budburst
   (d) Eastern study lasted for 82 days, 19320 observations—add Sexpr obj
   (e) Western study lasted for 113 days, 47844 observations

Statistical Anlaysis

1. Introduce approach and why it is useful:
   (a) Our analysis combined the trait data with the budburst data from the growth chamber study
   (b) Built joint model for each trait—directly models the relationship between leaf and structural traits and budburst
   (c) Approach carries through uncertainty between trait and phenology data—combines observational trait data with experimental phenology data
2. Begin to describe the model:
   (a) hierarchical linear model—partitioning variation of individual observations (i) of a given trait value ($y_{\text{trait}[i]}$) to the effects of species (*sp id*), and population-level differences arising from transects (*transect id*) or the interaction between transects and latitude (*transect* $\times$ *latitude*), and residual variation (σ_{trait}), sometimes called 'measurement error').
   (b) Transect included as a dummy variable and latitude as a continuous variable
   (c) Latitude values z-scored
   (d) Most traits were modeled using their natural units—except LMA was rescaled by 100
3. describe trait part of model
   (a) Model give unique estimates for each species ($\alpha_{\text{sp[sp id]}}$) and estimate of variance—partial pooling—controls for variation in the number of trait estimates per spp and trait variability
   (b) Estimate for differences between transect ($\beta_{transect}$) and the interaction between transects and latitude ($\beta_{transect \times latitude}$)
   (c) These species-level estimates of traits become predictors of species-level estimates of each cue— ($\beta_{\text{force[sp]}}$, $\beta_{\text{chill[sp]}}$, $\beta_{\text{photo[sp]}}$)

   Trait model:

$$\begin{aligned} \mu_{trait} &= \alpha_{\text{grand trait}} + \alpha_{\text{sp[sp id]}} + \beta_{\text{transect}} + \beta_{\text{transect}\times\text{latitude}} \\ \beta_{transect} &\sim normal(\mu_{transect}, \sigma_{\text{transect}}) \\ \beta_{\text{transect}\times\text{latitude}} &\sim normal(\mu_{\text{transect}\times\text{latitude}}, \sigma_{\text{transect}\times\text{latitude}}) \end{aligned} \tag{1}$$

   Cue part:

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

4. Explain phenology part of model
   (a) Across each spp—get esti of overall effect of each trait on cue ($\beta_{\text{trait.chill}}$, $\beta_{\text{trait.force}}$, $\beta_{\text{trait.photo}}$)

   (b) and estimate of species-level cue variation not explained by traits ($\alpha_{\text{chill}[sp]}$, $\alpha_{\text{force}[sp]}$, $\alpha_{\text{photo}[sp]}$) = estimate of how well trait effects explain species-level differences
   (c) Also get estimates of species responses to cues (C_i, F_i, P_i, respectively—z-scored)—with residual variation across species ($\alpha_{\text{pheno[sp]}}$) and observations ($\sigma_{\text{pheno}}$)
   (d) Partial pooling for residual variation across species and variation in cues not attributed to the trait

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

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

5. General info about model checks etc.:
   (a) weakly informative priors
   (b) validated model priors using prior predictive checks
   (c) model was coded in the Stan programming language and fit using the rstan package cite rstan2018
   (d) Four chains (4000-6000 total sampling iterations), and all models met basic diagnostic checks, including no divergences, high effective sample size (n_{eff}), and $\hat{R}$ close to 1—LMA model still has low ESS—issue with neff—otherwise this is true
   (e) 90% UI given in text

Results

1. Our study = one of the first to combine trait data with phenological cue responses for the same individuals and across species distributions.
   (a) Includes plant communities in eastern and western deciduous forests of North America
   (b) Samples collected from multiple populations—modelling approach that accounts for variation across populations and transects
   (c) Joint modelling approach = use sp-level estimates for traits to understand phenological cue responses and budburst timing
   (d) Taking a community-level approach—with woody tree and shrub species = different growth strategies and presumably suites of traits
2. Traits differed in their population-level variation
   (a) Most of our traits varied across populations—changing both between the two transects and with latitude
   (b) Height (-0.6, UI: -1.4,0.2), DBH (2.7, UI: 1.2,4.2), and LMA (1.4, UI: 1.0,1.8)—strong interactions between latitude and transect

   (c) We found tree height to decline with increasing latitude, while tree DBH and LMA both increased
   (d) LNC differed between the two transects (0.1, UI: -0.5,0.6—greater in western transect
   (e) But no population-level variation in SSD
   (f) Fig. 1

3. All traits related to at least one budburst cue—but responses were generally weak
   (a) Of our three cues—photoperiod strongest relationship with other traits
   (b) Our two structural traits = similar cue relationships—taller plants with greater DBH = stronger photoperiod responses = earlier bb under longer daylengths (-1.7, UI: -2.9, -0.5 for height and (-0.2, UI: -0.3, -1 for DBH)
   (c) But no correlation between between ring porosity of wood with cues 3.

4. leaf traits varied more in the direction of cue responses
   (a) LMA showed strong responses to photoperiod with low LMA species advancing in bb with longer photoperiods (-7.5, UI: 0.2, 1.9)
   (b) In contrast—LNC strong responses to forcing but not chilling or photoperiod—high LNC species responded more to warmer spring temperatures (-0.9, UI: -2.7, 0.9)

5. Regardless of trait effects—our joint modeling approach still estimated phenological cue responses in line with previous work.
   (a) All models showed earlier budburst in response to all three cues
   (b) Individual spp varied in both their timing and cue responses—but for most models responses were strongest for chilling and weakest for photoperiod.
   (c) Only our LMA produced unique cue estimates—estimating photoperiod cues (-7.5, UI: -11.0, -4.1) stronger than forcing cues (-6.8, UI: -13.1, -0.9) (Table 4)
   (d) ref Fig. 4 and Fig. 5

6. Including trait effects better informed spp level estimates of phenology
   (a) Estimates bb using our model parameters show clear differences in bb timing between tree and shrub spp for some traits (Fig. 6)
   (b) Height showed strong correlations between bb timing and trait values—shrub spp were estimated to bb earlier—especially under stronger cues—tree spp were later
   (c) But this was not case for leaf traits—LNC showed no distinct separation between species functional groups (Fig. 6)

Figures

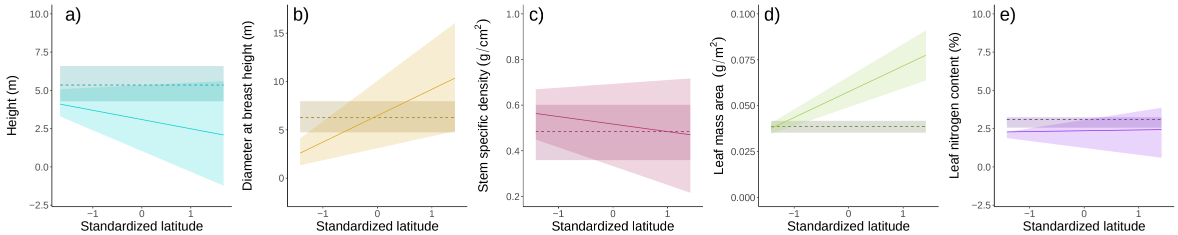

Figure 1: We only found biogeographic differences for four of our functional traits, with the direction of the relationship varying across traits. Both height a. height and b. diameter at base height showed strong interactions between latitude and trait values, while c. leaf mass area has the weakest response, and d. stem specific density, and e. carbon:nitrogen moderate interactive effects.

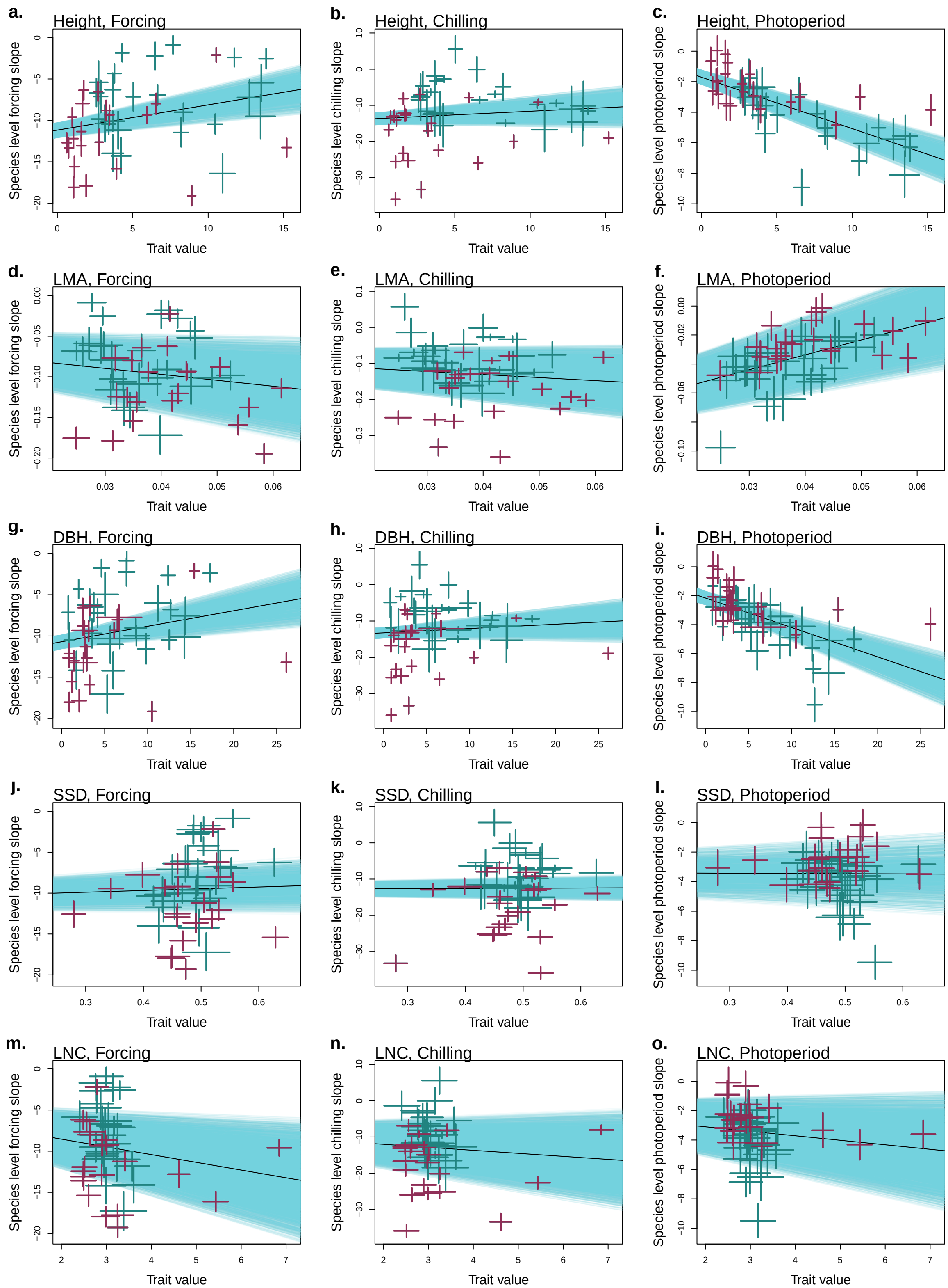

Figure 2: Relationship between species traits and cue responses, for height (a-c), leaf mass area (d-f), diameter at breast height (g-i), stem specific density (j-l), and the carbon to nitrogen ratio (m-o). Point colours representing different species groups, tree species are depicted in maroon and shrub species in teal.

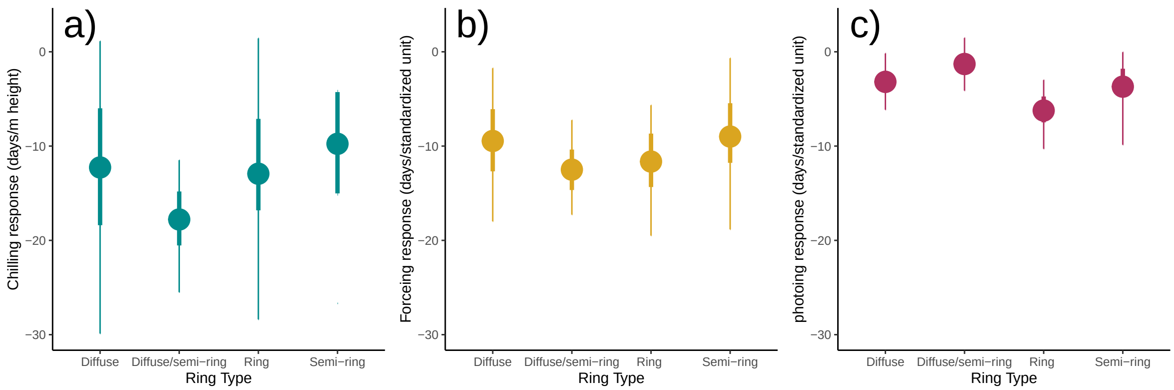

Figure 3: Despite differing in their wood structures and growth strategies, we did not find this trait to correlate with differences in cue responses across species. Thinner lines represent the 90% UI and thicker lines the 50% UI. Here we show the results for height only, see supplementary material for additional trait estimates.

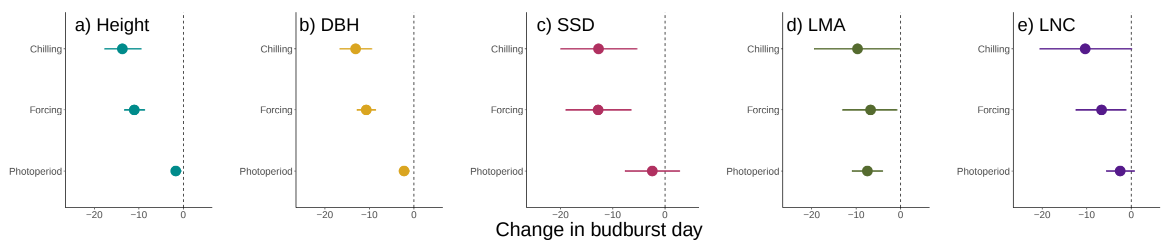

Figure 4: We found consistent estimates for budburst cue responses to chilling, forcing, and photoperiod for each of our trait models: a. height, b. diameter at breast height, c. stem specific density, d. leaf mass area, and e. carbon:nitrogen. Lines represent 90% uncertainty intervals.

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. carbon:nitrogen, and for individual cues. Lines represent 90% uncertainty intervals. Note the differences in the scale of the x-axis.

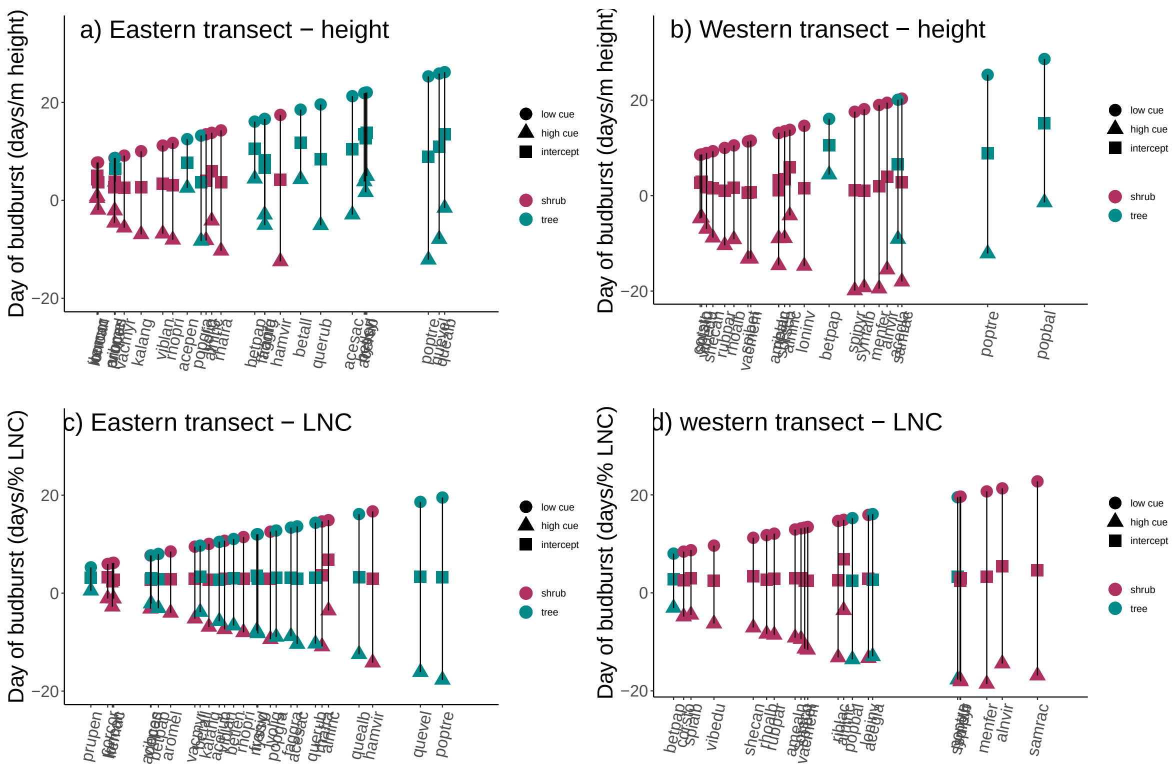

Figure 6: We found budburst estimates differed between our full model (intercept plus cues, depicted as triangles for high cues and circles for low cues), versus the intercepts only model (without cues, shown as squares). Species are ordered in increasing budburst dates for both the eastern (a and b) and western (c and d) populations, spanning from early budbursting shrubs, in red, to late budbursting trees, in blue.

163 # Tables

Table 1: Summary output from a joint Bayesian model of height and budburst phenology in which species are partially pooled and ..... The model includes photoperiod and forcing as continuous variables.

	mean	5%	25%	75%	95%
Transect	-2.30	-3.20	-2.60	-1.90	-1.30
Transect x latitude	-0.60	-1.30	-0.90	-0.30	0.10
Forcing	-11.00	-13.30	-11.90	-10.10	-8.70
Chilling	-13.70	-17.70	-15.40	-12.10	-9.50
Photoperiod	-1.70	-2.90	-2.20	-1.20	-0.50
Trait x forcing	0.30	-0.10	0.10	0.40	0.60
Trait x chilling	0.20	-0.50	-0.10	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 and ..... The model includes photoperiod and forcing as continuous variables.

	mean	5%	25%	75%	95%
Transect	0.30	-1.60	-0.50	1.00	2.20
Transect x latitude	2.80	1.20	2.10	3.40	4.30
Forcing	-10.70	-12.80	-11.60	-9.90	-8.60
Chilling	-13.10	-16.70	-14.60	-11.60	-9.50
Photoperiod	-2.20	-3.30	-2.70	-1.80	-1.00
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	-0.30	-0.10	-0.10

Table 3: Summary output from a joint Bayesian model of SSD and budburst phenology in which species are partially pooled and ..... The model includes photoperiod and forcing as continuous variables.

	mean	5%	25%	75%	95%
Transect	0.00	-0.00	0.00	0.10	0.10
Transect x latitude	-0.00	-0.10	-0.10	-0.00	0.00
Forcing	-12.80	-19.00	-15.40	-10.30	-6.50
Chilling	-12.70	-20.00	-15.70	-9.70	-5.40
Photoperiod	-2.40	-7.70	-4.50	-0.40	2.80
Trait x forcing	6.90	-6.20	1.90	12.20	19.70
Trait x chilling	0.30	-15.30	-5.90	6.80	15.60
Trait x photoperiod	-2.10	-12.70	-6.40	2.20	8.70

Table 4: Summary output from a joint Bayesian model of LMA and budburst phenology in which species are partially pooled and ..... The model includes photoperiod and forcing as continuous variables.

	mean	5%	25%	75%	95%
Transect	1.90	1.40	1.70	2.10	2.40
Transect x latitude	1.40	1.00	1.20	1.60	1.80
Forcing	-6.80	-13.10	-9.20	-4.20	-0.90
Chilling	-9.70	-19.50	-13.60	-5.70	-0.20
Photoperiod	-7.50	-11.00	-8.90	-6.10	-4.10
Trait x forcing	-0.70	-2.20	-1.40	-0.10	0.90
Trait x chilling	-0.80	-3.30	-1.80	0.20	1.60
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 and ..... The model includes photoperiod and forcing as continuous variables.

	mean	5%	25%	75%	95%
Transect	-0.70	-1.30	-1.00	-0.50	-0.20
Transect x latitude	0.10	-0.50	-0.20	0.30	0.60
Forcing	-6.70	-12.50	-8.90	-4.30	-1.20
Chilling	-10.30	-20.60	-14.60	-6.00	0.10
Photoperiod	-2.50	-5.60	-3.80	-1.20	0.70
Trait x forcing	-0.90	-2.70	-1.70	-0.20	0.90
Trait x chilling	-0.80	-4.20	-2.20	0.50	2.40
Trait x photoperiod	-0.30	-1.30	-0.70	0.10	0.70