

1 How temperature, photoperiod and evolutionary history shape
2 forest leafout

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20

21 Abstract

- 22 1. How species assemble temporally has received growing attention as climate change shifts the timing
23 of major life cycle events across most systems. While theory predicts that plant species should partition
24 time to reduce resource competition—for example by leafing out at different times—few studies have
25 examined this given the complexity of environmental cues that make timings highly variable across
26 years and sites.
- 27 2. We examine species- and community-level responses in budburst across 47 woody plant species
28 across four sites in North America. By manipulating known temperature and photoperiod cues in
29 controlled environments then applying a phylogenetic Bayesian model, we estimate the effects of these
30 cues and evolutionary history in shaping leafout across species.
- 31 3. We found responses from plants sampled at different sites were highly similar, but species var-
32 ied greatly in their timings. Species-specific differences in responses to well-studied temperature and
33 photoperiod cues, however, explained only half this variation, with the remaining variation mostly
34 explained by intrinsic species differences in timing and shared evolutionary history.
- 35 4. This suggests current models of leafout phenology are missing important variation that may struc-
36 ture species assembly within communities. Identifying these unidentified cues or traits is critical to
37 forecasting phenological shifts and understanding their effects on community dynamics.

Introduction

Climate change has led to advances of about three days per decade in the timing of species life history events—phenology (Parmesan, 2007; Thackeray *et al.*, 2016; Cohen *et al.*, 2018). Different types of events, however, are highly variable, with certain events, such as leafout, spanning a period of weeks. Understanding and explaining this variability has become increasingly important as phenology shifts in response to rising temperatures at different rates (Parmesan, 2007; Fitter & Fitter, 2002; Menzel *et al.*, 2006; Yu *et al.*, 2010; Fridley, 2012). Some degree of variability is likely due to differences in climate change itself across space—as some areas warm faster than others and generate larger phenological shifts (Hoegh-Guldberg *et al.*, 2018). Recent research suggests that species-level differences in phenology also drive some of this variation (Vitasse *et al.*, 2009; Wolkovich & Cleland, 2014; Zohner & Renner, 2014; Vitasse *et al.*, 2018). How these differences compare to other potential sources of variation, and what predicts them, is still largely unknown, but has major implications for predicting how changes in phenology will affect community dynamics and ecosystem services.

Differences in species phenologies can impact community structure and dynamics. Community ecology has long posited that species assemble in part through partitioning time, leading to unique temporal niches that allow species to coexist (Chesson *et al.*, 2004; Grime, 1977). For example, earlier germination or leafout may provide understory species early-access to soil and light resources, before larger canopy species leafout (Heberling *et al.*, 2019; Lee & Ibáñez, 2021). These different temporal niches may also trade-off different pressures, with research suggesting that in seasonal systems species that are active earlier experience greater abiotic pressures—such as spring frost—but avoid the larger competitive pressures for resources that occur later in the season when most species are fully active (Sakai & Larcher, 1987; Gotelli & Graves, 1996; Augspurger, 2009; Pau *et al.*, 2011). As climate change variably affects the timing of growth, it may alter the temporal order of species in a community and result in novel interactions between species (Cleland *et al.*, 2012; Rudolf, 2019; Tiusanen *et al.*, 2020), thus changing the competitive landscape and synchrony of interactions within communities.

While recent changes in climate are shaping differences in phenology, for many species their temporal niches may also reflect their evolutionary history. Species traits in communities today are the result of selective pressures acting over evolutionary timescales that include the historical climates and related ancestral phenotypes that were favourable under previous conditions (Wiens *et al.*, 2010). This could produce greater similarity in phenological traits of more closely related species (Davies *et al.*, 2013; Morales-Castilla *et al.*, 2024), which would impact how species respond to future climates.

Spring budburst offers an excellent system to test for species- and community-level patterns in phenology and environmental cues. Budburst of temperate woody plants is well studied and thus known to respond to environmental cues, especially temperatures in the winter and spring—referred to as chilling and forcing, respectively—and daylength or photoperiod (Chuine *et al.*, 2010; Polgar & Primack, 2011; Cooke *et al.*, 2012; Basler & Körner, 2014; Laube *et al.*, 2014). Budburst responses to these cues are generally similar across sites and populations (Zeng & Wolkovich, 2024; Aitken & Bemmels, 2016). Species-level differences, however, are generally much larger than observations of site or

population-level variation (but see Deans, 1996; Sogaard *et al.*, 2008, for examples of population-level differences). Decades of phenological research suggests these unique phenologies are likely due to different responses of species to temperature and photoperiod cues, though they may be also structured by species shared evolutionary history (Lechowicz, 1984; Davies *et al.*, 2013; Gougherty & Gougherty, 2018) and their current environments. For example, research predicts that forest understory species should vary their leafout and budburst early to both gain access to light and soil nutrients prior to canopy closure (Mahall & Bormann, 1978; Muller, 1978), as outlined above, and to reduce competition between species within the understory versus canopy.

Here we test how environmental—temperature and photoperiod—cues and evolutionary relationships shape species-level variation in phenology of forest communities across North America. Leveraging two large-scale growth chamber studies that vary the temperature cues of chilling (cool temperatures in the fall and winter) and forcing (warmer temperatures, usually in the spring) with photoperiod (Fig. 1), we use a Bayesian phylogenetic approach to estimate budburst responses across 47 woody species. We collected samples from plants at four sites, in eastern and western North America (Fig. 1), with pairs of sites on each coast spanning 4 and 6° latitude, respectively. Our dataset includes the diverse assemblages of tree and shrub species found in eastern and western deciduous forests, allowing us to explore differences across both sites and functional groups—including understory shrubs versus canopy trees—in eastern versus western forests.

Materials and Methods

Field sampling

We combined data from two growth chamber studies using dormant branch clippings of North American deciduous woody plants. Such cutting experiments are a common and powerful approach to infer the responses of adult trees to environmental conditions (Vitasse *et al.*, 2014). In our first study, we collected samples from two eastern communities—Harvard Forest, Massachusetts, USA (42.55°N, 72.20°W) and St. Hippolyte, Quebec, Canada (45.98°N, 74.01°W), from 20-28 January, 2015 (previously reported in Flynn & Wolkovich, 2018). The second growth chamber study spanned two western communities—Smithers (54.78°N, 127.17°W) and E.C. Manning Park (49.06°N, 120.78°W), British Columbia, Canada, with sampling from 19-28 October 2019 (not previously published). Combining the datasets from these two experiments allowed us to test for spatial variation in the phenology of woody plant communities at a larger geographic scale and make stronger inferences for how different species vary in their cues.

We selected the dominant deciduous species in each forest community and maximized the number of species occurring across sites. We observed budburst for 47 species spanning eastern and western forest communities, with 28 species at our eastern transect and 22 species at our western transect, of which 3 species occurred at both regions (Fig. 1, Table S1). Of the species in our eastern transect, there were 13 shrubs and 15 trees, while our western transect included 18 shrub and 4 tree species. At all sites, we tagged 15-20 healthy, mature, individuals for each species in the summer prior to sampling.

Depending on the size of the individual, we collected 1-16 cuttings from 6-20 tagged plants, using a pole pruner from the ground. We kept samples cold and immediately placed them in erlenmeyer flasks of water upon returning from the field. We conducted the eastern study at the Arnold Arboretum, Boston, MA, USA, and the western study at the University of British Columbia, BC, Canada. We used daily weather data from local weather stations to calculate the field chilling prior to collection (see Table S2).

Growth chamber study

We used growth chambers with two levels of chilling—with either no additional chilling or 30 days at 4°C for our eastern study, and 21 or 56 days of chilling at 4°C for our western study (all dark)—after which we moved plants to one of two levels of forcing—with day and night temperatures that varied to create a cool regime of 15:5°C and a warm regime of 20:10°C—crossed with two photoperiods of either 8 or 12 hours—for a total of 8 distinct treatments in each study.

Our design was similar for both eastern and western sites (Fig. 1). We had seven to ten replicates per treatment in our eastern study and eight replicates in our western study, with the exception of *Sorbus scopulina*, for which we only had six replicates per treatment. Our eastern and western studies differed only in the timing of sample collection and thermoperiodicity—alternation in day and night temperatures—in forcing treatments. By collecting samples in our eastern study in late January, they experienced considerable field chilling. We collected the western samples in late October, with most chilling occurring under controlled conditions. In our eastern study, we also set the duration of forcing temperatures to correspond with the photoperiod treatments. While this is a widespread and common approach in phenology chamber studies, it leads to a confounding effect in the thermoperiodicity (Buonaiuto *et al.*, 2023). Thus we applied forcing temperatures for 12 hours independent of the duration of the photoperiod treatments in our western study, and controlled for this difference in our statistical approach (see below). Each experiment was conducted across 8 growth chambers. We additionally rotated cuttings within chambers approximately every two weeks to avoid any chamber effects and changed the water and re-cut each cutting to prevent callusing and keep cuttings healthy. We controlled for small differences in the number of replicates across species in our statistical approach using partial pooling (see section on statistical analysis).

We assessed phenological stages of budburst using the BBCH scale, adapted for our specific species (Finn *et al.*, 2007). We also created photographic guides to help define each stage of the BBCH scale for our specific species (Savas *et al.*, 2017; Loughnan & Wolkovich, 2024a). Every 1-3 days, we observed each sample and recorded all phenological stages up to full leaf expansion (defined as code 17 by Finn *et al.*, 2007). Here, we present the response in budburst day, defined as the day of budbreak or shoot elongation (defined as code 07 by Finn *et al.*, 2007) since forcing treatments began. Our eastern study spanned 82 days, with over 19320 phenological observations, while the western study spanned 113 days and 47844 phenological observations.

Statistical Analysis

We tested for differences in budburst cues across species and communities using a phylogenetic mixed effects model with partial pooling ('shrinkage') across species. This approach accounts for both the evolutionary relatedness of our species and estimates the species-level cues and differences across sites. We obtained species phylogenetic relatedness by pruning the Smith & Brown (2018) megatree of angiosperms (Fig. S4).

In our model, we included each of our three cues as continuous variables. To account for the greater amounts of field chilling experienced in our eastern study, we converted our chilling treatments to chill portions for each individual community using local weather station data and the chillR package (v. 0.73.1, Luedeling, 2020). We calculated chill portions for both the chilling experienced in the field prior to sampling and during the experiment in our 4°C chilling chambers. We also converted forcing temperatures to mean daily temperatures in each treatment to account for differences in thermoperiodicity between the two studies (Buonaiuto *et al.*, 2023). Finally, we *z*-scored each cue and site using two standard deviations to allow direct comparisons between results across parameters (Gelman, 2008). In addition to the overall predictors, we included all two-way interactions between cues and between cues and sites.

Our modelling approach allowed us to combine observations of budburst (y_i) across species (sp) to estimate both the effects of species-specific differences in their responses (slope estimates, β) to cues (chilling, forcing and photoperiod) and any remaining species-specific differences in timings (via species-level intercepts, α_{sp_i}). Our full model also estimated effects of sites and all possible two-way interactions between cues, and between cues and sites, to estimate the day of budburst (\hat{y}) relative to the first day of forcing conditions.

$$\begin{aligned}\hat{y}_i = & \alpha_{sp_i} + \beta_{Manning\ park} + \beta_{Harvard\ forest} + \beta_{St.\ Hippolyte} + \\ & \beta_{chilling_{sp_i}} + \beta_{forcing_{sp_i}} + \beta_{photoperiod_{sp_i}} + \\ & \beta_{forcing \times chilling_{sp_i}} + \beta_{forcing \times photoperiod_{sp_i}} + \beta_{chilling \times photoperiod_{sp_i}} + \\ & \beta_{forcing \times Manning\ park_{sp_i}} + \beta_{forcing \times Harvard\ forest_{sp_i}} + \beta_{forcing \times St.\ Hippolyte_{sp_i}} + \\ & \beta_{chilling \times Manning\ park_{sp_i}} + \beta_{chilling \times Harvard\ forest_{sp_i}} + \beta_{chilling \times St.\ Hippolyte_{sp_i}} + \\ & \beta_{photoperiod \times Manning\ park_{sp_i}} + \beta_{photoperiod \times Harvard\ forest_{sp_i}} + \beta_{photoperiod \times St.\ Hippolyte_{sp_i}}\end{aligned}$$

$$y_i \sim \text{normal}(\hat{y}_i, \sigma^2)$$

The slopes were modelled with partial pooling at the species-level:

$$\begin{aligned}\beta_{force_{sp}} &\sim \text{normal}(\mu_{force_{sp}}, \sigma_{force}^2) \\ \dots \\ \beta_{photoperiod \times St.Hippolyte_{sp}} &\sim \text{normal}(\mu_{photoperiod \times St.Hippolyte_{sp}}, \sigma_{photoperiod \times St.Hippolyte_{sp}}^2)\end{aligned}$$

184 We included the phylogenetic effect on species-specific differences in budburst timing (α_{sp}) as a variance
185 covariance matrix (\mathbf{V}) in the parameterization of the normal random vector:

$$\boldsymbol{\alpha}_{sp} = \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \dots \\ \alpha_n \end{bmatrix} \text{ such that } \boldsymbol{\alpha} \sim \text{multi-normal}(\mu_{\alpha}, \mathbf{V}), \quad (1)$$

(2)

186 The timing of budburst ancestrally is represented as the root value of the means of the multivariate
187 normal distribution. For more detail on this method of phylogenetic modeling, see Morales-Castilla
188 *et al.* (2024).

189

190 We used non-informative priors for each of our model parameters (increasing priors three-fold did not
191 demonstrably change our estimates), and validated the model code using test data prior to analysis.
192 Our model produced \hat{R} values close to 1, well mixed chains, and n_{eff} values that exceeded 10% of the
193 model iterations. Our model was fit using the Stan language with the rstan package (v. 2.26.23, Stan
194 Development Team, 2018) in R (v. 4.3.1, R Development Core Team, 2017).

195

196 We present model estimates, relative to baseline or low treatment conditions. This means that we
197 show the average daily temperature for our cooler forcing conditions (which averaged to 8.33°C for our
198 eastern sites and 10°C for our western sites, after accounting for the differences in thermoperiodicity),
199 with a short photoperiod (8 hours photoperiod), and the mean of lowest chill portions from each pop-
200 ulation (which is equivalent to approximately 10 weeks of chilling at 4°C) and—when relevant—our
201 most southern sites. We present results as means and 90% posterior uncertainty intervals from our
202 Bayesian phylogenetic models.

203

204 Results

205 On average, species budburst 30.3 days (uncertainty interval: 25.9, 35.1, all estimates are given as
206 mean \pm 90% uncertainty intervals, henceforth ‘UI,’ and budburst dates given as relative to baseline
207 conditions, see methods for more details) after the start of forcing and photoperiod treatments. Be-
208 tween the earliest and latest budbursting species, the difference in the mean day of budburst was 38.5
209 and 30.7 days for the eastern and western sites respectively. Overall we found species budburst was

moderately phylogenetically structured (λ of 0.4, UI: 0.1, 0.7, estimated on the intercept) and that all cues led to an advance in budburst date. Of the three cues, chilling had the largest effect, with increased chilling advancing budburst (we represent advances with negative numbers, while delays would be positive; -14.8, UI: -16.7, -12.9) and photoperiod the smallest (-3.3, UI: -4.0, -2.7, Fig. 2a, S1). But we found a large, subadditive interaction between forcing and chilling (8.4, UI: 7.0, 9.8, Fig. 2b); meaning that low chilling is offset by high forcing conditions, and vice versa (see Table S3 for model output).

Overall we found small site-level effects compared to differences between cues (Fig. 2). Treatments that received a month less of chilling (low chilling), were 5°C cooler (low forcing), and had shorter photoperiods all budburst later compared to the more chilled, warmer and long photoperiod treatments across all sites and across transects (Fig. S1 a-c, shown for baseline conditions, see Table S3 for model output). Overall budburst dates did not differ between sites, though eastern sites budburst marginally earlier (day 36.0, UI: 28.6, 42.4) compared to the western sites (day 47.8, UI: 40.5, 54.1, see also Table S3 for model output). This could be due to the earlier collection date of our western species, which reduced the field chilling they received relative to our eastern samples (though see corrections for this in the statistical analysis section of our methods).

Budburst of individual species showed distinct differences in their timing and the relative importance of cues. Later budbursting species had slightly larger responses to chilling and forcing (Fig. 3). Despite our expectations that species responses should differ across the canopy layer, with shrubs being less sensitive to cues than trees, we did not find substantial differences across these two functional groups (Fig. S2). Shrubs, like *Cornus stolonifera*, budburst early and showed small responses to chilling and forcing (Fig. 3b, d). But 36.7% of the shrubs, including *Menziesia ferruginea* and *Symphoricarpos alba*, exhibited the opposite response and budburst relatively late (Fig. 4, S2). Similarly for trees, some species did match our predictions, exhibiting stronger cues, but 23.5% of species budburst earlier than expected. While specific tree species, such as *Quercus velutina*, did have larger chilling and photoperiod responses as predicted (Fig. 3a, e), and *Fagus grandifolia* had the largest photoperiod response (Fig. 3e), overall we did not find clear differences between the cues of trees and shrubs across the four forest communities.

Our results provide clear evidence that species-specific differences in their responses to temperature (chilling and forcing) and photoperiod produce species-level differences in budburst timing. But the contribution of these species-specific cue differences to budburst order and timing was small compared to the overall species differences unexplained by cues (represented in the modeling framework as the intercept). Given the major role of chilling, forcing and photoperiod in determining budburst date the exact magnitude of their explanatory power depends on the level of each cue (e.g., forcing has a much larger effect on budburst timing given a constant daytime temperature of 20°C compared to a constant daytime temperature of 15°C), but we found that across the levels of chilling, forcing and photoperiod we studied species-specific differences in responses to cues explained only between 38.4% and 67.6% of variation for eastern species and between 46.6 and 61.9% for western species, with the intercept—which was phylogenetically structured—explaining the rest (Fig. 4).

251

252 We found the rank order of species' budburst timings changed more when estimated using higher
 253 chilling (the average of which is equivalent to approximately 15 weeks chilling at 4°C), forcing (Fig. 1)
 254 and longer photoperiods than under lower chilling and forcing and shorter photoperiods (Fig S3), but
 255 remained fairly consistent. The budburst ranking for the three species that occurred in both transects
 256 remained relatively consistent across the two communities (Fig. 3), with only *Alnus incana* in the
 257 western community experiencing a large change in rank with cues (Fig. S3). In comparing the earliest
 258 and latest budbursting species, we found relatively small differences in cues (Fig. 3). For example, an
 259 early budbursting shrub, *Lyonia ligustrina*, had chilling and forcing cues of -14.8 and -11.5 respectively,
 260 which are comparable to the cue estimates of -16.0 and -11.5 for the much later tree, *Quercus alba*.
 261 Yet the model predicts these species to have a 15.5 day difference in day of budburst, highlighting how
 262 the timing of budburst across species was also strongly related to species level differences independent
 263 of their responses to chilling, forcing and photoperiod (intercept values, see Fig. 4).

264

265 Discussion

266 To accurately forecast shifts in phenology and its impact on ecological communities requires under-
 267 standing which environmental cues are most important at the population-, species-, functional-group
 268 and community-levels. Our results support decades of research finding that budburst timing advances
 269 in response to the well-studied major temperature cues of chilling and forcing (with the greatest re-
 270 sponses to chilling and forcing respectively, see also Ettinger *et al.*, 2020; Flynn & Wolkovich, 2018)
 271 and longer photoperiods while also advancing our understanding how these species-specific responses
 272 to these cues do—or do not—lead to differences in species timings that may structure their temporal
 273 niches within communities. Perhaps surprisingly, we found a large (one-third to one-half) of variation
 274 in species budburst timings was unexplained by different responses to chilling, forcing and photoperiod,
 275 suggesting important unexplained variation. Our results show that some of this variation is due to
 276 species evolutionary history, but not all, suggesting fundamental gaps in our model of one of the best
 277 studied and most important phenological events—woody plant budburst.

278

279 Differences in species responses to temperature and photoperiod were similar across sites and functional
 280 groups, suggesting that understanding the drivers of variation across species may be an important task
 281 to improve forecasting. Our shrub and tree functional groups included a mix of species that budburst
 282 very early or late, suggesting these groups are not inherently different in their timings, at least not
 283 in the North American forest communities we studied. Our results found no detectable site-level
 284 differences across different coasts and over 6° of latitude. This contrasts with research that suggests
 285 latitudinal trends in photoperiod and temperature may impose unique selective pressures, and thus
 286 may drive site-level differences in responses to cues (Keller *et al.*, 2011). Latitudinal gradients in spring
 287 phenological shifts have been found by studies using *in situ* phenological data (Post *et al.*, 2018; Alecrim
 288 *et al.*, 2023). Such work, however, is based on long-term observations in the field, with confounding
 289 differences in study duration and start dates, variable methodologies, and geographic extent. The lack

of site-level effects that we observed—using experiments to estimate responses—suggests budburst cues are not shaped by local conditions, at least at our study scale.

Community composition and interspecific variation in phenology

The variation across species in their responses to environmental cues has the potential to create large differences in species temporal niches and ecological roles. Species ranged from early to late budburst timing in our experimental conditions, spanning a similar period as observed in natural communities (Lechowicz, 1984; Richardson, A.D., O’Keefe, 2009). This suggests our experiment captured a realistic breadth in temperate forest budburst. Furthermore, all our focal species responded to each environmental cue, with large responses to chilling and comparatively small responses to photoperiod—trends consistent with previous studies (Ettinger *et al.*, 2020; Flynn & Wolkovich, 2018). Cues, however, had complex interactions that appear potentially advantageous under warming climates (Heide, 1993; Caffarra & Donnelly, 2011; Flynn & Wolkovich, 2018). The interaction between chilling and forcing may ensure that species budburst even if warmer winters cause insufficient chilling, but will require additional forcing. But despite these differences in species responses to cues, we did not find clear, generalizable trends across functional groups.

Shrubs and trees differ greatly in their physiology, filling different ecological niches. Most of our trees budburst later than our study’s shrubs, a relative order also found by previous studies (Gill *et al.*, 1998; Panchen *et al.*, 2014). But about a quarter of the trees also budburst early, with timing more similar to that of shrubs. Similarly, we found a third of shrubs budburst at similar times as the majority of our trees. These deviations from our expectations for how shrubs and trees partition their budburst timing suggests there is more nuance to these patterns. As tree species advance phenologically—resulting in earlier canopy closure and reduced light availability (Donnelly & Yu, 2019)—shrubs with small cues may have reduced fitness. Our findings suggest, however, that many shrubs will also advance phenologically and have the potential to maintain their relative temporal niche.

Community assembly in responses to cues versus evolutionary history

Our study included the three cues—chilling, forcing and photoperiod—commonly thought to determine budburst timing, but about a third of the total variation was not explained by these cues (Fig. 3), suggesting the general model of budburst may be incomplete. This, paired with the observed phylogenetic structure in budburst timing, hints at unidentified latent traits still missing from our understanding of the processes shaping spring phenology (Webb *et al.*, 2002; Davies *et al.*, 2019).

Latent traits could reflect other cue or trait relationships indicative of species growth strategies or key traits that may facilitate greater resource use, or the greater competitive abilities needed when budbursting later (Grime, 1977). For example, species that budburst early in the season are likely to have faster growth, with traits associated with greater rates of resource acquisition, such as high specific leaf areas or low wood density (Wright *et al.*, 2004; Chave *et al.*, 2009). But our results

suggest that evolutionary history and species ancestral phenotype also have some effect on species timings and cues. Species traits are shaped over ‘deep’ timescales, with previous evolution also influencing responses to the present climate. Phenological trends could thus be an indication of limited evolutionary time to adapt (Lechowicz, 1984), or shaped by selection on other important traits that are not phylogenetically structured. Incorporating both phenology and evolutionary history into a broader trait framework could thus provide insights into traits that correlate with budburst timing, and—ultimately—the current and evolutionary drivers that select for species phenotypes and possibly shape species adaptive potential to future climates.

Predicting budburst under future climates

As climate change leads to greater temperature cues, we are already observing advances in species budburst within diverse ecological communities. The greatest ecological impacts will occur in high latitude communities that are warming the most and the fastest (Hoegh-Guldberg *et al.*, 2018), making species in northern communities most likely to advance their budburst and experience the greatest changes in budburst order. Yet our ability to predict these changes is often limited by the lack of data available. The consistent trends we observed across sites supports forecasting across similar regions with limited local phenological data but similar species assemblages, allowing us to leverage existing research to mitigate the cascading effects that shifted plant phenology could have on ecological communities.

While our findings have applications to plant communities, our analytical approach is widely applicable to forecasting diverse species responses to climate change. The phylogenetic model we used here could be easily applied to other phenological events or suites of species from across the tree of life. By combining species-rich and community-wide approaches with phylogenetic relationships we can better understand the impacts of evolutionary history and current ecological processes in shaping species phenology under a changing climate.

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Competing Interests Statement

The authors have no competing interests.

Author Contribution Statement

Both D.L. and E.M.W. conceived the study, contributed to the analysis and code and contributed to the writing and revision of the manuscript. DL led field and experimental data collection.

³⁶⁸ **Data and code availability statement**

³⁶⁹ All data and Stan code are freely available through the Knowledge Network for Biocomplexity (Lough-
³⁷⁰ nan & Wolkovich, 2024b) and at the Harvard Forest data repository.

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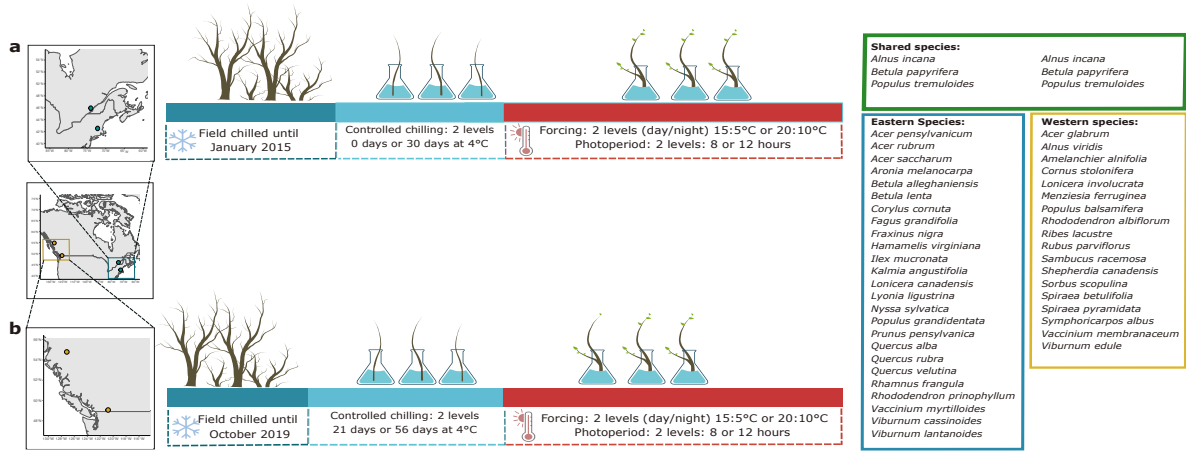


Figure 1: We combined data from two controlled environment studies of temperature and photoperiod cues for budburst in temperate woody species **a**, from two forest communities in eastern North America that span a 4° latitudinal gradient and **b**, two communities in western North America that span a 6° latitudinal gradient. Combined, our dataset includes 28 tree and shrub species from eastern communities and 21 species from western communities, with three species occurring across all four populations. Both studies used a full-factorial design with two levels each of chilling treatments (consisting of a combination of field and different duration of chamber chilling), forcing and photoperiod, for a total of eight unique treatments. Observations of budburst were made during the forcing treatment, using the BBCH scale to classify stages of bud development (see Savas *et al.*, 2017; Loughnan & Wolkovich, 2024a, for guides we made for these species).

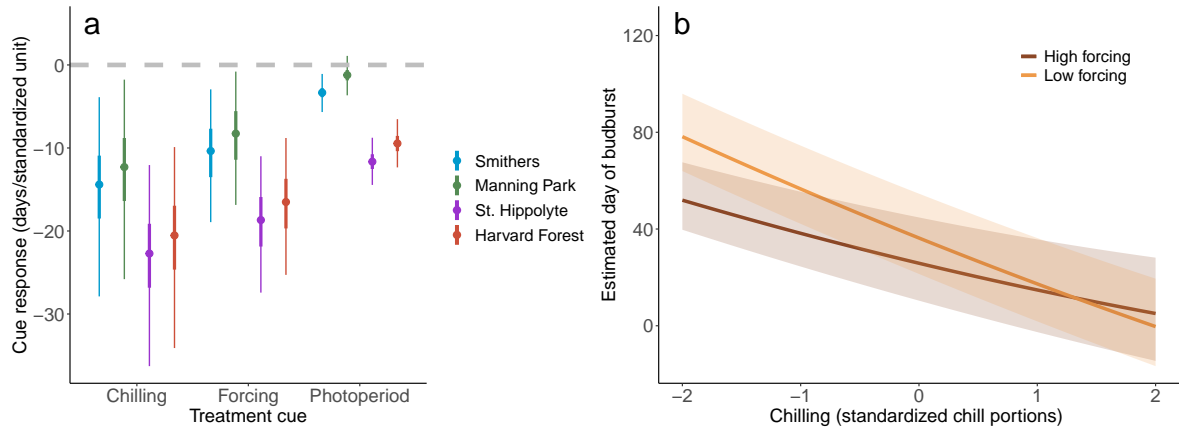


Figure 2: **a**, Posterior distributions of estimated chilling, forcing, and photoperiod responses with individual site-level effects. Points represent the mean, thicker lines the 50% uncertainty interval, and the thin lines the 90% uncertainty interval. **b**, Cues interacted to produce a subadditive effect, where delays in budburst under low chilling was offset by high forcing conditions, and vice versa. To make results comparable across predictors we standardized chilling, forcing, and photoperiod via z -scores using two standard deviations, see methods for further details.

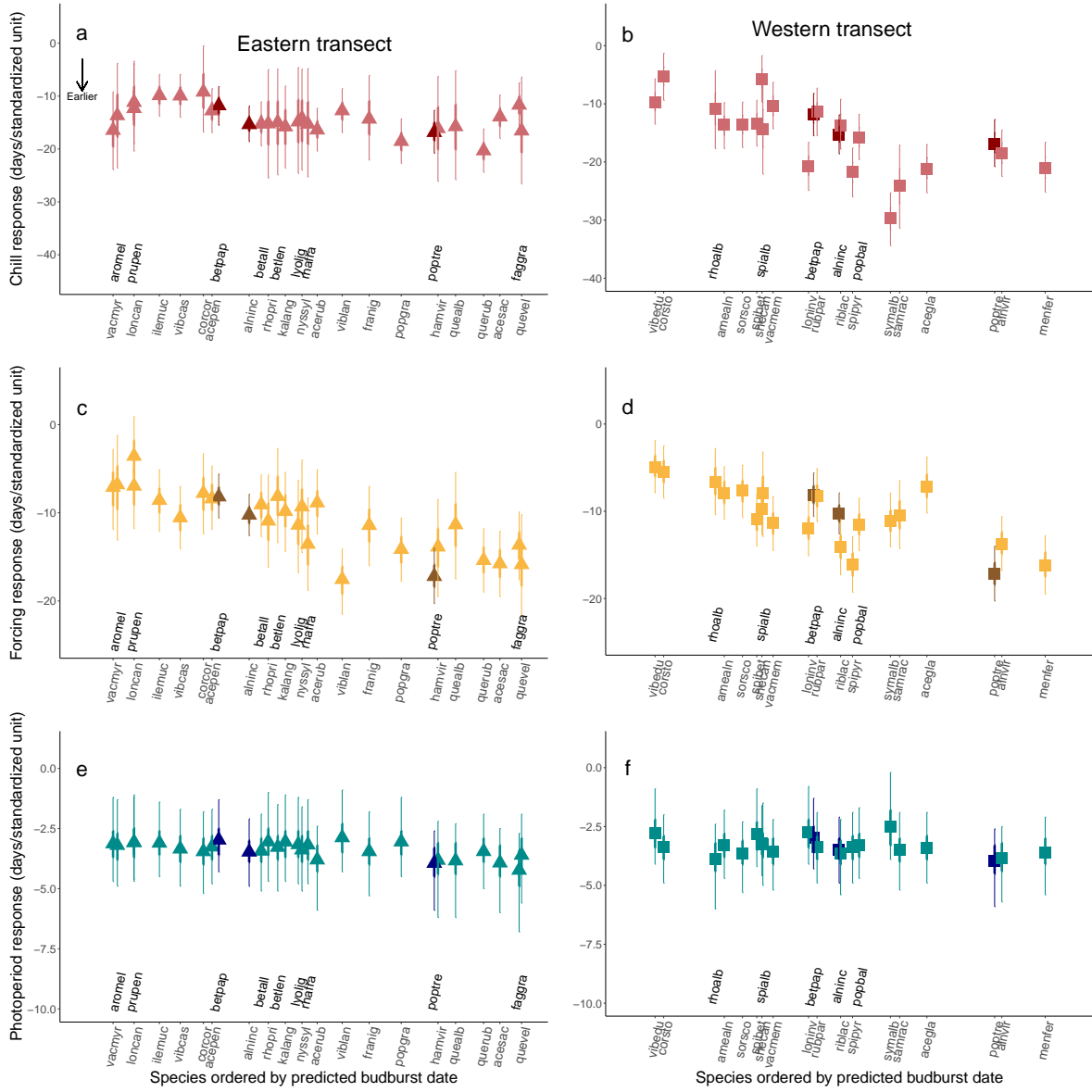


Figure 3: Estimated species **a,b** chilling, **c,d** forcing, and **e,f** photoperiod responses ordered by estimated budburst dates for both the **a,c,e**, eastern and **b,d,f** western sites based on our model estimates. Cues are plotted on differing y-axis scales to better depict species differences across cues. For each species, the points represent the mean, thinner error bars represent the 90% uncertainty interval, and thicker bars represent the 50% uncertainty interval. The three species that occur in both the eastern and western transects are depicted using darker colours. To make the results across cues directly comparable, we standardized predictors (here, chilling, forcing, and photoperiod) via z -scores using two standard deviations, see methods for further details.

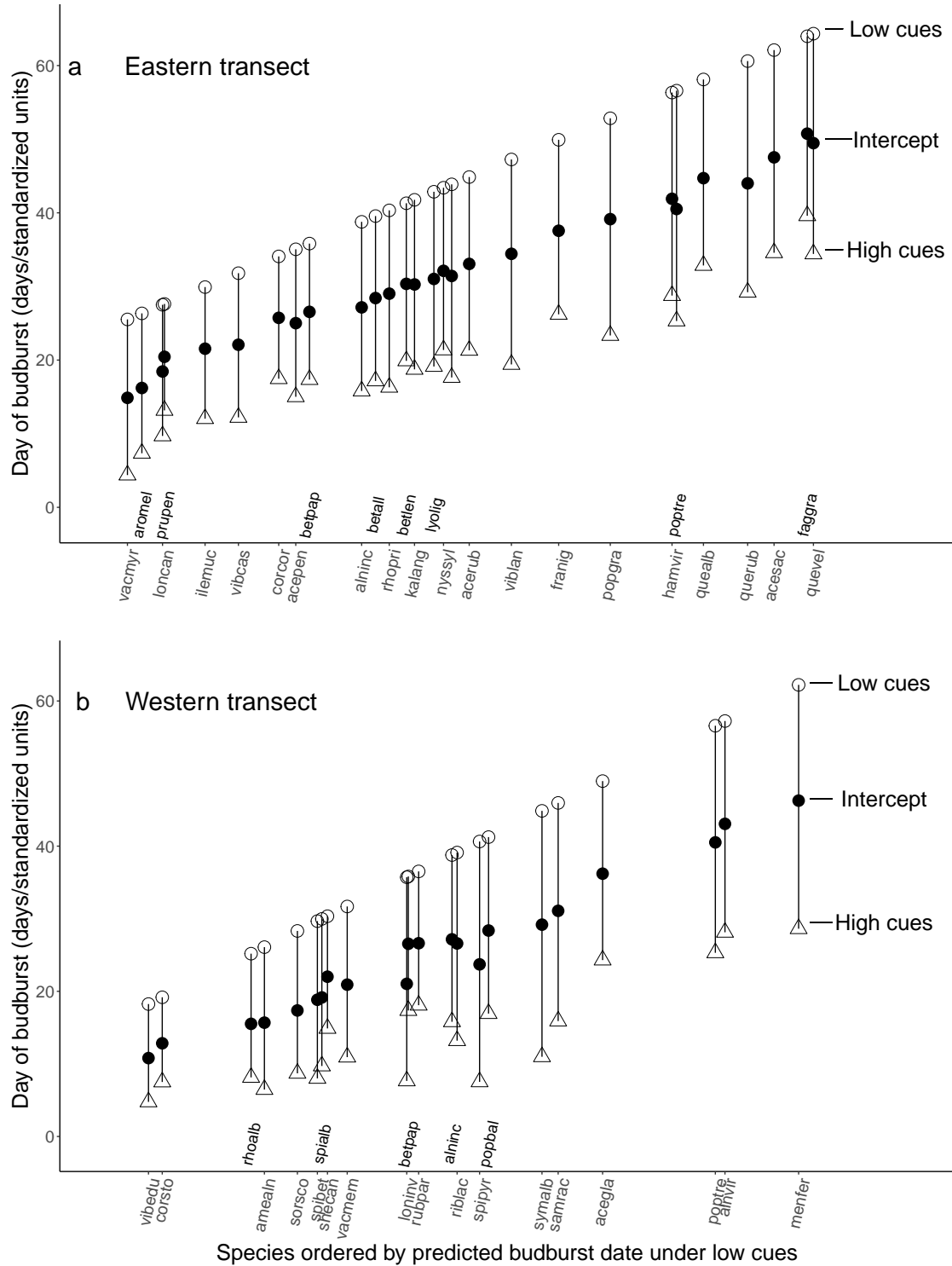


Figure 4: Comparisons of estimated day of budburst based on the full model (intercept plus all cues), shown as white (open) symbols, versus the intercepts only (without effects of chilling, forcing, and photoperiod), shown as black (filled) symbols, ordered according to differences in species estimated budburst dates for both the **a**, eastern **b**, and western sites under low cue conditions, depicted as circles, and high cue conditions, depicted as triangles.