Current environments and evolutionary history shape forest temporal assembly

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Abstract

The timing of major life history events, such as the start of growth or reproduction, often span weeks or months within a community due to species differences in their timing. Theory suggests this variation comes from species partitioning time to reduce competition for resources. But shared evolutionary history may moderate such potential effects. Adding to this complexity, timings vary across environments as they are often controlled by responses to cues like temperature and daylength. To understand these drivers of variability, we examined community-level responses to environmental cues across 47 species from eastern and western North America. We focused on woody plant budburst, where the underlying cues—temperature and daylength—are well known and can be manipulated in controlled environments. Using a Bayesian phylogenetic model, we found little variation across sites, but strong variation by species. Budburst advanced in response to temperature and daylength, with these cues explaining 38.4 and 67.6% of variation. The remaining variation was partially ascribed to intrinsic differences in species that were phylogenetically structured ($\lambda = 0.4$). These phylogenetic effects suggest an role of additional traits that determine woody plant budburst, and could improve predictions of future phenological shifts and 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 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. Understanding the drivers of species-level variation could help address these gaps and predict

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), and may trade-off different pressures. Increasing research suggests that species with early temporal niches 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 species-level 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 those 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 will 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), though some research has documented differences (Deans, 1996; Sogaard *et al.*, 2008). Species-level differences, however, are generally much larger. Decades of work have found that species have unique phenologies, which may structure their positions within communities. For example, forest understory species may budburst early to gain access to light and soil nutrients (Mahall & Bormann, 1978; Muller, 1978) before canopy species become active. These unique phenologies may be structured by species shared evolutionary history (Lechowicz, 1984; Davies *et al.*, 2013; Gougherty & Gougherty, 2018).

Here we test how environmental cues and evolutionary relationships shape species-level variation in phenology of forest communities in North America. Leveraging two growth chamber studies that vary chilling, forcing and photoperiod, 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, with pairs of sites on each coast spanning 4 and 6° latitude. 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 (e.g., 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 fist 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 of 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 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 (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 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 30 or 70 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 species. 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 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). Further details regarding the re-cutting of samples, water changes, and rotation through chambers are presented in Flynn & Wolkovich (2018). We controlled for 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, 2024). 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 date, defined as the day of budbreak or shoot elongation (defined as code 07 by Finn *et al.*, 2007). Our eastern study spanned 82 days, with over 19320 phenological observations, while the western study spanned 113 days and 47844 phenological observations.

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Statistical Analysis

We tested for differences in budburst cues across species and communities using a phylogenetic mixed effects model with partial pooling ('shrinking') 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 a species-level intercept (α_{sp_i}) and slope estimates (β) for individual cues, sites, and all possible two-way interactions between cues (chilling, forcing and photoperiod) and between cues and sites to estimate the day of budburst ($\hat{y}$) relative to the first day of forcing conditions.

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

$$y_i \sim \text{normal}(\hat{y}_i, \sigma_y^2)$$
$$\epsilon_i \sim \text{normal}(0, \sigma_y^2)$$

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

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

We included the phylogenetic effect of budburst timing (α_{sp}) as a variance covariance matrix ($\boldsymbol{V}$) in the parameterization of the normal random vector:

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

$$\tag{2}$$

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

We used semi-informative priors for each of our model parameters, validating the model code using test data prior to analysis. Our model produced $\hat{R}$ values close to 1, well mixed chains, and n_{eff} values that exceeded 10% of the model iterations. Our model was fit using the Stan language with the rstan package (v. 2.26.23, Stan Development Team, 2018) in R (v. 4.3.1, R Development Core Team, 2017).

We present model estimates, relative to baseline conditions of low chilling, low forcing, and short photoperiod treatments, and—when relevant—for the Smithers community. We present results as means and 90% posterior uncertainty intervals from our Bayesian phylogenetic models.

Results

On average, species budburst 30.3 days (uncertainty interval: 25.9, 35.1, all estimates are given as mean ± 90% uncertainty intervals, henceforth 'UI,' and budburst dates given as relative to baseline conditions, see methods for more details) after the start of forcing and photoperiod treatments. The empirical observations on which this modelled mean is based, span budburst days as early as 13.6 for *Aronia melanocarpa*, and as late as day 52.1 for *Quercus velutina*. Between the earliest and latest budbursting species, the difference in the mean day of budburst was 38.5 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 (-14.8, UI: -16.7, -12.9) and photoperiod the smallest (-3.3, UI: -4.0, -2.7, Fig. 1a, S1). But we found a large, positive interaction between forcing and chilling (8.4, UI: 7.0, 9.8, 1b); this subadditive effect means that low chilling is offset by high forcing conditions, and vice versa (Fig. **??** and see Table S3 for model output).

Overall we found small site-level effects compared to differences between cues. Across all species, there was considerable overlap in the responses of the four sites to each cue (Fig. 1). As such, low forcing, chilling, and shorter photoperiods all produced later estimated budburst dates compared to higher temperature and longer 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 (36.0, UI: 28.6, 42.4) compared to the western sites (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. 2). 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*, showed small responses to chilling and forcing (Fig.

2b, d). But 36.7% of the shrubs, including *Menziesia ferruginea* and *Symphoricarpos alba*, exhibited the opposite response and budburst relatively late (Fig. 3,S2). Similarly for trees, some matched our predictions for their cues, but 23.5% budburst earlier than expected. Specific tree species, such as *Quercus velutina*, did have larger chilling and photoperiod responses as predicted (Fig. 2a, e), and *Fagus grandifolia* had the largest photoperiod response (Fig. 2e). But overall we did not find clear differences between the cues of trees and shrubs across the four forest communities.

Our results depict the relative importance of phenological cues to variation across species, but we found the contribution of cues to budburst order and timing to be dependent on the magnitude of the cue, and to be small compared to the overall species differences unexplained by cues (represented in the modeling framework as the intercept). The rank order of species estimated budburst changed more under high cue conditions than under low cues (Fig S3). The budburst ranking for the three species that occurred in both transects remained relatively consistent across the two communities (Fig. 2), with only *Alnus incana* in the western community experiencing a large change in rank with cues (Fig. S3).

In comparing the earliest and latest budbursting species, we found relatively small differences in cues (Fig. 2). For example, an early budbursting shrub, *Lyonia ligustrina*, had chilling and forcing cues of -14.8 and -11.5 respectively, which are comparable to the cue estimates of -16.0 and -11.5 for the much later tree, *Quercus alba*. Yet the model predicts these species to have a 15.5 day difference in day of budburst. This highlights how the timing of budburst across species was also strongly related to species level differences outside of cues (intercept values, see Fig. 3). Across the range of cue values, 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. 3).

Discussion

We found that species temporal niches were partly explained by differences in environmental cues, but did not vary predictably by functional groups. Similar to other studies, the timing of budburst generally advanced in response to each cue, with the greatest responses to chilling and forcing respectively (Ettinger *et al.*, 2020; Flynn & Wolkovich, 2018). Some of the variability in the importance of cues across species was driven by their evolutionary history, but this alone did not explain that considerable variation observed in species budburst timing. These findings highlight that while it is important to account for evolutionary history, there remains other unidentified cues or traits that contribute to the processes shaping phenology.

Species responses to temperature and daylength were similar across sites suggesting no detectable site-level differences, across different coasts and over 6° of latitude. This contrasts with research that suggests latitudinal trends in photoperiod and temperature may impose unique selective pressures, and thus may drive site-level differences in responses to cues (Keller *et al.*, 2011). Latitudinal gradients in spring phenological shifts have been found by studies using *in situ* phenological data (Post *et al.*, 2018; Alecrim *et al.*, 2023). But, this work is based on long-term observations in the field, with confounding differences in study duration and start dates, variable methodologies, and geographic extent. The lack of site-level effects that we observed suggests budburst cues are not shaped by local conditions, at least at our study scale.

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Community composition and interspecific variation in phenology

The variation across species in their responses to environmental cues creates large potential differences in their 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. Despite these differences in species responses to cues, however, 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. 2), 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 (Webb *et al.*, 2002; Davies *et al.*, 2019).

Latent traits could reflect environmental cues or additional traits that mitigate such cues. Theories of how plants vary in their growth strategies predict phenology should correlate with other key traits, including those that facilitate greater resource use and earlier spring growth, or the greater competitive abilities needed when budbursting later (Grime, 1977). For example, early successional species are predicted to budburst early in the season and have traits associated with faster growth rates and resource acquisition, such as high specific leaf areas or low wood density (Wright *et al.*, 2004; Chave *et al.*, 2009). Incorporating phenology into a broader trait framework could thus provide insights into traits that correlate with budburst timing, and—ultimately—the drivers selecting for species phenotypes.

Our results suggest that evolutionary history and species ancestral phenotypee have some effect on species adaptive potential to future climates, but they explain only part of the variability observed. Species traits are shaped over 'deep' timescales, with previous evolution influencing responses to the present climate. While phylogenetic trends could thus be an indication of limited evolutionary time to adapt—as is believed to be the case for temperate species, like *Nyssa* and *Fagus* that had shorter geological time frames to respond to their local temperatures (Lechowicz, 1984)—there are other important traits that are not phylogenetically structured.

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Predicting budburst under future climates

To accurately forecast shifts in phenology and its impact on ecological communities will require an understanding of what environmental cues are most important at the population-, species-, and community-level. As climate change leads to greater temperature cues, we are already observing advances in species budburst within diverse ecological communities. But the greatest ecological impacts will occur in high latitude communities that are warming fastest and to a greater extent (Hoegh-Guldberg *et al.*, 2018). This makes species in northern communities most likely to advance their budburst and experience the greatest changes in budburst order, but our knowledge of these systems is 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. Our ability to do so would allow us to better mitigate the cascading effects changes in species temporal niche and interactions—such as with pollinators or herbivores—could have on ecological communities and their competitive landscapes and critical ecosystem services.

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 our changing climate.

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Author Contribution Statement

Both D.L. and E.M.W. conceived the study, led the collection of the data for the Western and Eastern experiments respectively, contributed to the analysis and code and contributed to the writing and revision of the manuscript.

Competing Interests Statement

The authors have no competing interests.

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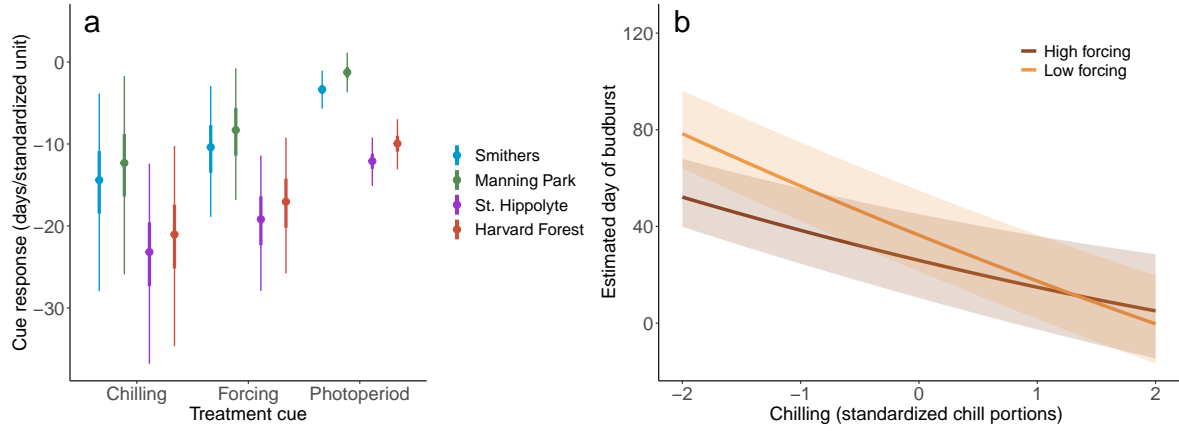
Figure 1: **a,** Posterior distributions of estimated chilling, forcing, and photoperiod responses with site level effects for individual sites. Points represent the mean, thicker lines the 50% uncertainty interval, and the thin lines the 90% uncertainty interval. **b,** Cues interacted to produce a subadditive effect that promoted budburst under either low forcing or low chilling conditions. variable responses that promote budburst when individual cues are not met. We standardized predictors (chilling, forcing, and photoperiod) via z-scores using two standard deviations, see methods for further details.
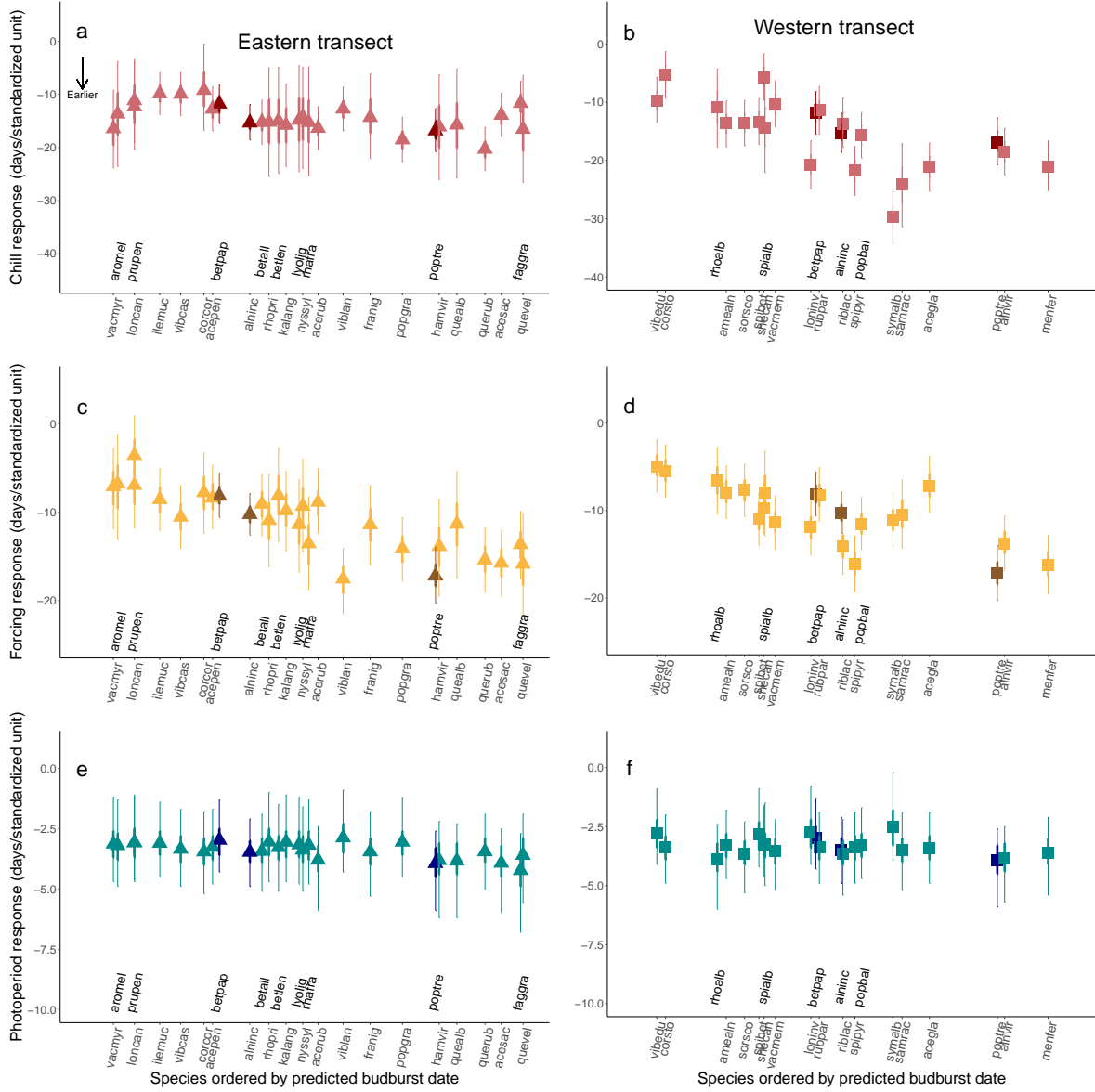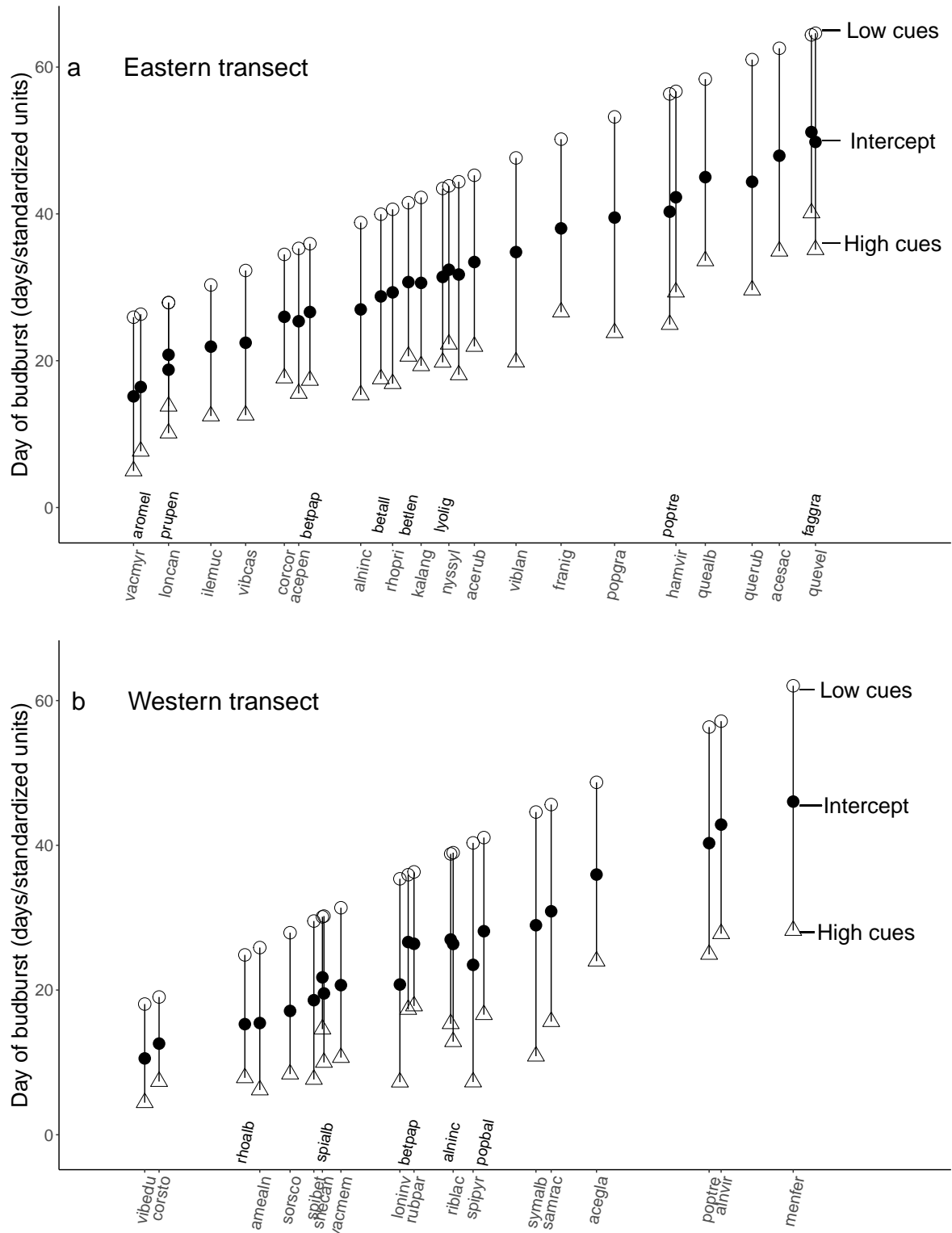
Figure 2: Estimated species **a,b**, chilling, **c,d** forcing, **e,f** and photoperiod responses ranked by increasing estimated budburst dates for both the **a,c,e**, eastern **b,d,f** and western sites. Cues are plotted on differing y-axis scales to better depict species differences across cues. For each species, the 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 3: Comparisons of estimated day of budburst based on the full model (intercept plus all cues), shown in white (open) symbols, versus the intercepts only (without effects of cues—chilling, forcing, and photoperiod), shown in 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.