

# Evolutionary history as important as phenological cues in the temporal assembly of woody plant communities

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## Introduction

Climate changes is altering phenology, or the timing of life history events, for species across the tree of life. These effects of climate change, however, have not been uniform, given that some regions are experiencing greater warming than others (Hoegh-Guldberg et al., 2018). This has produced high variability in phenological shifts, with unique responses observed for different species and across habitats (Fitter and Fitter, 2002; Menzel et al., 2006; Yu et al., 2010; Fridley, 2012).

Species differences in phenological responses can be attributed to species-level differences and geographic variability in environmental cues (Vitasse et al., 2009; Wolkovich and Cleland, 2014; Zohner and Renner, 2014; Vitasse et al., 2018). Identifying the relative importance of different drivers of key life event is necessary to understand and predict future changes in phenology, and their ultimate impacts on community dynamics and ecosystem services, including growing season length, carbon cycles, and species interactions (Gotelli and Graves, 1996; Cleland et al., 2007; Richardson, A.D., O’Keefe, 2009).

In a community, the timing of individual phenological events can vary over weeks or months (Lechowicz, 1984). This breadth in the period of when individual species’ events occur allows species’ to fill different temporal niche (Gotelli and Graves, 1996). In plant communities, understory species often budburst earlier than taller canopy species, a niche difference predicted to infer overarching differences in species growth strategies. Similarly, in Mediterranean marsh communities, native bird species have a distinct temporal niche from exotic species, reproducing earlier in the season (Sanz-Aguilar et al., 2015). In addition to these within community differences, variation in phenological responses is likely to also exist between different populations across species’ ranges (cite). At present, however, we lack a strong understanding of the relative effects of population versus species-level variation in shaping budburst of individual species and forest communities overall.

Decades of research has been done to understand the mechanisms shaping budburst phenology in woody plants, making them a good system to study spatial patterns in phenological cues. Woody plants vary in their growth strategies, but under controlled environments have consistent cue responses. Temperate woody plants show strong responses to temperature, particularly winter and temperatures, and daylength (Chuine et al., 2010; Polgar and Primack, 2011; Cooke et al., 2012; Basler and Körner, 2014; Laube et al., 2014). While each of these three cues vary in their relative importance for a given species,

they can also interact (Heide, 1993; Chuine, 2000; Caffarra and Donnelly, 2011; Flynn and Wolkovich, 2018). Previous work has shown that spring temperatures, also referred to as forcing cues, can offset the effects of warm winter temperatures, or chilling (Heide, 1993; Chuine, 2000; Caffarra and Donnelly, 2011; Flynn and Wolkovich, 2018). Photoperiod responses also offsets weak forcing cues in cool springs conditions (Heide, 1993; Chuine, 2000; Caffarra and Donnelly, 2011; Flynn and Wolkovich, 2018). The highly variable nature of both species cue requirements and the magnitude of their responses, however, has made it challenging to draw generalizable trends across species with large distributions.

The environmental cues that shape species budburst can vary geographically and temporally. Under future climates this could create differences in community dynamics and species composition. Increasing winter and spring temperatures will lead to the faster accumulation of chilling and forcing cues (Guy, 2014), which is associated with earlier budburst in many temperate plant species. Changes in temperature cues with climate change could therefore create novel niche space early in growing season and facilitate species invasions or alter community assemblages (Willis et al., 2010; Wolkovich et al., 2013). Species with strong photoperiod cues may experience a reduction in their fitness, as their ability to adapt will be constrained by constant daylengths (Way and Montgomery, 2015). Differences in species cue requirements will therefore shape species adaptive potential to future change, altering the competitive landscape experienced across the growing season, and reshaping the diversity and persistence of species across forest communities.

While climate change has caused temperatures to change over recent decades, it is also important to account for the longer timescales over which forest communities have assembled (Davies et al., 2013). It is local, historic conditions that have shaped traits like phenology, the results of which we observe today. Across a species' spatial distribution we expect local cues to have differed, driving differences in their budburst phenotype and cue responses. Species with large latitudinal distributions, for example, experience differences in their photoperiod cues across their spatial range and may differ in their responsiveness to photoperiods across populations. But to date, few studies have explored how cue use differs across spatial gradients using the same forest communities, testing the relative role of local environments and biotic communities in shaping budburst. To better predict how forest communities will respond and assemble under continued climate change we need to identify the cues that drive budburst in our dominant forest species and functional groups, and how these responses can change across populations.

In this study we combined results from two growth chamber studies of woody species budburst cues. We used data from four populations, from eastern to western North America, with pairs of populations on each coast spanning 4-6° latitude. Our approach allowed us to detect general trends in how budburst of North American deciduous forest communities respond to forcing, chilling, and photoperiod cues. We were also able to explore community specific responses and detect differences between western and eastern forest communities, and across different latitudes. By including diverse assemblages of species, we also tested for trends across different functional groups, exploring differences between the dominant shrubs and tree species that characterize the understory and canopy of our forest communities.

## Materials and Methods

### Field sampling

We combined data from two growth chamber studies using branch clippings of North American deciduous woody plants. Such cutting experiments are a commonly used and powerful approach to understanding the responses of adult trees to known environmental conditions (Vitasse et al., 2014). Our first study used samples taken from two eastern populations—Harvard Forest, Mas-

sachusetts, USA (42.55°N, 72.20°W) and St. Hippolyte, Quebec, Canada (45.98°N, 74.01°W), which we sampled from the 20-28 January, 2015. The second growth chamber study spanned two western populations—Smithers (54.78°N, 127.17°W) and E.C. Manning Park (49.06°N, 120.78°W), British Columbia, Canada, respectively, sampled from the 19-28 of October, 2019.

We observed budburst for 47 species spanning our two transects, with 28 species at our eastern transect and 22 species at our western transect, 3 of which occur at both transects. We selected the dominant deciduous species in the forest communities at each population and to maximize the number of species occurring across sites. Of the species we sampled in our eastern transect, 13 were shrubs and 15 were trees, while in our western forest community we sampled 18 shrub and 4 tree species. At all sites, we tagged 15-20 healthy, mature, individuals for each species in the summer prior to the growth chamber study. Depending on the size of the individual, we collected 1-16 cuttings from 6-20 tagged plants, with samples being taken using a pole pruner from the ground. We kept samples cold during sampling and immediately placed them in water upon returning from the field. Our eastern study was conducted 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 ??).

## Growth chamber study

To estimate the effects of chilling, forcing and photoperiod, 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 days or 70 days of chilling at 4°C for our western study (all dark)—after which plants were moved to one of two levels of forcing—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, except for the thermoperiodicity in forcing treatments. In our eastern study, we 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. 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. Further details regarding the re-cutting of samples, changing water in containers, and rotation through chambers are presented in Flynn and Wolkovich (2018).

We assessed phenological observations of budburst were assessed using the BBCH scale, adapted for our specific species (Finn et al., 2007). 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)). In total, our eastern study spanned 82 days, with over 19320 phenological observations. The western study in turn spanned 113 and we made 47844 phenological observations across all samples.

## Statistical Analysis

To test for differences in cue responses across species and populations, we used a phylogenetic mixed effect model with partial pooling across species. This approach allowed us to account for both the evolutionary relatedness of our species, and estimate the species level cue responses and differences across sites. Species phylogenetic relatedness was obtained by pruning the Smith and Brown (2018) megatree of angiosperms.

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 population using local weather station data and the chillR package (Luedeling, 2020). Chill portions were calculated 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 results across parameters to be directly compared (Gelman, 2008). In addition to the overall predictors, we included all two-way interactions between cues and between cues and sites:

$$\begin{aligned} \hat{y}_i \sim & \text{normal}(\alpha_{sp_i} + \beta_{site2} + \beta_{site3} + \beta_{site4} + \\ & \beta_{chill_{sp_i}} + \beta_{force_{sp_i}} + \beta_{photo_{sp_i}} + \\ & \beta_{force \times chilling_{sp_i}} + \beta_{chilling \times photo_{sp_i}} + \beta_{photoperiod \times chilling_{sp_i}} + \\ & \beta_{force \times site2_{sp_i}} + \beta_{force \times site3_{sp_i}} + \beta_{force \times site4_{sp_i}} + \\ & \beta_{chilling \times site2_{sp_i}} + \beta_{chilling \times site3_{sp_i}} + \beta_{chilling \times site4_{sp_i}} + \\ & \beta_{photoperiod \times site2_{sp_i}} + \beta_{photoperiod \times site3_{sp_i}} + \beta_{photoperiod \times site4_{sp_i}}) \end{aligned}$$

$$\begin{aligned} \beta_{force_{sp}} & \sim \text{normal}(\mu_{force_{sp}}, \sigma_{force}^2) \\ \dots & \\ \beta_{photoperiod \times site4} & \sim \text{normal}(\mu_{photoperiod \times site4}, \sigma_{photoperiod \times site4}^2) \end{aligned}$$

We included the phylogenetic effect as a variance covariance matrix in the parameterization of the normal random vector:

$$\begin{aligned} \boldsymbol{\alpha} = [\alpha_1, \dots, \alpha_n]^T \text{ such that } \boldsymbol{\alpha} & \sim \text{multi-normal}(\mu_{\boldsymbol{\alpha}}, \mathbf{V}), \\ & (1) \\ & (2) \end{aligned}$$

The timing of budburst prior to evolution is represented as root values of the means of the multivariate normal distributions. For more detail on this method of phylogenetic modeling, see Morales-Castilla et al (XXXX).

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 fitted using the Stan language (Stan Development Team, 2018) using the rstan package in R (R Development Core Team, 2017) (version).

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

## Results

On average, we observed species budburst 28.1 days (uncertainty interval: 45, 15.2) after the start of our forcing and photoperiod treatments (all estimates are given as mean  $\pm$  90 uncertainty intervals, henceforth ‘UI,’ and budburst dates given as relative to baseline conditions, see methods for more details). Some species, such as *Aronia melanocarpa*, budburst as early as day 13.6, and as late as day 52.1 for *Quercus velutina*. The difference in timing of our earliest and latest species spanned a period of 38.5 and 30.7 days for our eastern and western species respectively. Overall we found species budburst to be strongly phylogenetically structured ( $\lambda$  of 0.8, UI: 0.9, 0.6) and that all cues led to an advance in budburst date. Of the three cues, chilling had the strongest effect (-15.2, UI: -17.3, -13.2) and photoperiod the weakest (-3.6, UI: -4.3, -3.0, Fig. 1). But we found a strong, positive interaction between forcing and chilling (9.1, UI: 7.6, 10.5). This results in subadditive effects between chilling and forcing cues, with low chilling being offset by high forcing conditions (Fig. 2 and see Table 1 for model output).

Overall we found population effects were small compared to differences between cues. Across all species, there was considerable overlap in the responses of our four populations 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 populations (Fig. 3 a-c, shown for baseline conditions) and across transects (Fig. 3, see Table 1 for model output). Populations were similar in their overall budburst dates, but eastern populations were marginally earlier (34.1, UI: 40.7, 27.1) compared to our western populations (46.5, UI: 52.7, 39.4, see also Table 1 for model output).

Budburst of individual species showed distinct differences in their timing and the relative importance of cues. Both chilling and forcing responses varied with budburst, with later budbursting species having slightly stronger responses to each cue respectively (Fig. 4). Despite our expectations that species responses should differ across the canopy layer, with shrubs being less sensitive to cues than tree species, we did not find strong differences across these two functional groups (Fig. ??). Many of our earliest species were shrubs with weaker responses to chilling and forcing, like *Cornus stolonifera*. But 36.7% of our shrubs species, including *Menziesia ferruginea* and *Symphoricarpos alba*, exhibited the opposite response and budburst relatively late (Fig. ??). Similarly for tree species, some matched our predictions for their cue responses, but 23.5% budburst earlier than expected. Specific tree species, such as *Quercus velutina*, did have stronger chilling and photoperiod responses as predicted, and of all our focal species, such as *Fagus grandifolia* produced the strongest photoperiod response. But overall there were no clear differences between the cue responses of trees and shrubs across our 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 of the magnitude of the cue, and small compared to overall species differences. The rank order of species estimated budburst changed more under high cue conditions than under low cues (Fig ??). The budburst ranking for the three species that occurred in both transects remained relatively consistent across the two communities (Fig. 4), with only *Alnus incana* in our western community experiencing a large change in rank with cues (Fig. ??).

In comparing our earliest and latest budbursting species, we found the differences in the cue responses were relatively small (Fig. 4). This is contrary to our prediction of stronger cue requirements—especially chilling cues—for later budbursting species. For example, an early (shrub) species *Lyonia ligustrina* had chilling and forcing cues of -15.4 and -10.4 respectively, which are comparable to the estimates of -16.6 and -10.4 for the much later tree species, *Quercus alba*. Yet our model predicts these species to have a 15.9 day difference in day of budburst. This highlights how the timing of budburst across species was mostly attributed to species level differences outside of cue responses (Fig. 5). Across the range of cue values, cues explained only between 38.6 and 67.0% of variation for eastern

species and between 48.3 and 60.6% for western species, with the intercept explaining the rest (Fig. 5).

## Discussion

In our study of woody plant budburst phenology across North America, the assembly of species' temporal niche was partly explained by environmental cues, with little variation explained by different populations. Despite differing in their species assemblages, and in the ratio of shrub to tree species, populations had very similar cue responses and overall timing in budburst. But in comparing species within our eastern and western communities respectively, individual species differed in the timing of their budburst. Across each assemblage of species, we found slight gradients in species responses to environmental cues, with the strongest gradients being for chilling and forcing cues. While our findings support that species phenology is largely shaped by temperature and light cues, we also found evidence of strong phylogenetic structuring to species budburst phenology.

## Temporal assembly across North America

Our western and eastern forest communities differ in both their species composition and local environments, but under a controlled environment, budburst phenology and cue responses only differed slightly across populations. This contrasts our expectation of local habitats selection, as we would expect different selective pressures across populations to lead to differences in cues responses. Overall, the timing of budburst was only slightly earlier in our eastern populations when compared to western populations (Fig 1). These negligible differences could be due to the difference in the timing of sample collection, with our eastern species being collected later in the season and therefore receiving greater field chilling than species in our western growth chamber study.

Across latitudinal gradients, we expect to find variation in local environments, as photoperiod and temperatures can differ with increasing latitude. Studies using *in situ* phenological data from diverse species have found greater shifts in phenology with increasing in latitude, and associated gradients in temperature (Post et al., 2018; Alecrim et al.). This work is based on long-term observations in the field, however, and confounded by differences in study duration and start dates for high versus lower latitude time-series (Post et al., 2018), or varying in their methodologies, geographic extent. The lack of population-level trends in budburst that we observed, suggests the drivers determining budburst timing are not shaped by current geography or local adaptation, at least at our continental scale.

## Community composition and interspecific variation in phenology

Species varied considerably in the responses to our three environmental cues, which translates into large potential differences in species temporal niche and ecological role within the communities we sampled. The timing of budburst differed by species, with timing from early to late budbursting species 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 phenology within temperate forest communities. In general, all of our focal species showed some degree of a response to each of the environmental cues, with responses that were consistent with previous studies. Of our three cues, chilling had the strongest effect, while photoperiod had the weakest. But collectively, we found complex interactions between cues that are advantageous under warming climates (Heide, 1993; Caffarra and Donnelly, 2011; Flynn and Wolkovich, 2018). With climate change, some forests may experience winter temperatures above their chilling threshold. The interactive effects we found between chilling and forcing would ensure species still budburst if future temperatures result in insufficient winter chilling. While species differed in their cue responses, we did not find the clear, generalizable

trends we expected across species with similar growth strategies.

Despite shrub and tree species differing greatly in their physiology, filling different ecological niche space, we found little variation in their cue responses on a whole. Most of our tree species budburst later than the shrubs species, an order which is in line with previous work (Gill et al., 1998; Panchen et al., 2014). But, in contrast to our expectations, we found about a quarter of tree species also budburst early, with timing more similar to that of shrub species. Similarly, we found a third of our shrubs species to budburst at similar times as the majority of our tree species. This deviation from our expectations for how shrub and tree species partition their budburst timing suggesting there is more nuance to these patterns than previously found. As trees species advance phenologically—which is predicted to result in earlier canopy closure and reduced light availability (Donnelly and Yu, 2019)—shrubs species that are less responsive to changing conditions will experience reduced fitness. But our finding suggests many shrub species have similar cue responses and are likely to also advance with warming. These species have the potential to maintain their relative temporal niche space within a community and mitigate potential effects on community composition and dynamics.

The number of shrub and tree species exhibiting later than expected budburst phenologies indicates that the cues we think are important for budburst may also be important for other functional traits. Species with earlier budburst may exhibit a suite of traits that allow shrubs to have greater abilities to capture light and photosynthesize prior to canopy closure or improve nutrient uptake in later budbursting trees. How species differ in their temporal niche will relate to their overall fitness, and will also be in part determined by their full suite of traits. But currently do not understand the mechanisms that underlie these trait relationships. We can gain greater insights into the considerable phenotypic variation observed within species functional groups by incorporating phenology into a broader trait framework.

## Community assembly in responses to cues versus evolutionary history

Within our forest communities, species varied in their timing of budburst by several weeks, but whether these temporal differences across species will persist depends on future phenological responses across different spatial scales. The similarities in spring phenology we found across populations suggests there is little change in the community level response to local habitats. This may indicate strong niche conservatism within species, with the persistence of ancestral traits reducing the potential variability of ecological traits (Westoby et al., 1995; Webb et al., 2002).

To accurately forecast shifts in spring phenology will depend on our understanding of cue responses at the population, species and community levels. In North America, springs conditions show high inter-annual variability, meaning forest communities can experience a greater breadth of environmental cues in any given year (Schwartz and Reiter, 2000; Zohner et al., 2017). It may be advantageous for species to have consistent response to environmental cues, allowing them to optimize their budburst across years and large spatial scales.

While the effects of population-level variation on cue responses appears be negligible, individual species within community do differ in their responses to cue (Fig. 5). We found species budburst responses were dependent on the magnitude of cues experienced. Our model estimated positive effects of cues on budburst under both low and high cue conditions, but with earlier estimated budburst dates under stronger cue conditions (Fig. 5). Temperatures are not change uniformly, however, with higher latitudes experiencing faster rates of temperatures change (citation). This could drive future changes in population-level trends in budburst, as confounding effects of warming temperatures impose varying selection across species distributions.

At a finer scale, our findings also suggest the order with which species budburst in a community will change with future climate change. We found the rank order of species within our communities differed between weak and strong cue conditions, with low cues producing similar rank order to the species-level rank than estimated under high cues, particularly for our western community (Fig S4). This suggests that populations that experience greater warming will experience the greatest changes in species rank order, which will have cascading effects on competitive dynamics and possibly trophic interactions. But we cannot simply focus solely on species cues to understand community assembly, as species phenotypes are the result of multiple interacting and complex environmental cues that have shaped species over evolutionary time scales (Ackerly, 2009).

The high degree of phylogenetic relatedness among species suggests that those with shared ancestry, and presumably more similar phenotypes and growth strategies, exhibit similar timing in budburst. We found species-level effects to explain a high proportion of variation in budburst, with the cue responses of different species explaining about two-thirds of variation (Fig 4). While our study includes the three cues mostly commonly attributed to species spring phenology, this finding suggests our model of what drives spring phenology is incomplete.

Given that phenology is thought of as a highly plastic trait, we expected differences in cues across years and geography to drive variation in budburst timing. Our results, however, suggest that species evolutionary history has a large effect on budburst phenology. Still missing from our understanding of budburst phenology are the unidentified latent traits—such as additional physiological traits—that contribute to the phylogenetic structuring, and ultimately temporal niche, of temperate forest communities. By not accounting for the additional cues or traits driving spring phenology, we have a limited ability to predict how communities will respond to continued changes in climate.

The evolutionary history and ancestral phenotype of a species has the potential to effect their ability to adapt to future climates. Species' traits are shaped over 'deep' timescales, with the potential for this previous evolution to influencing species' responses to recent climate change today. There is the potential for the previous evolution of a species' traits shaped over 'deep' timescales to influencing species' responses to recent climate change today. This could limit species from adapting to new environmental conditions, if they are physiologically constrained by their ancestral phenotype. Such phylogenetic constraints could skew species assemblages, favouring species with traits and cue requirements adapted for warmer climates. Species with low chilling and photoperiod requirements would be better able to track and benefit from future climate conditions. But the phylogenetic trends we observed could also indicate our focal species have had limited evolutionary time to adapt. Some temperate species, like *Nyssa* and *Fagus* (Lechowicz, 1984), have had a shorter geologic time in which to adapt to their local temperatures, especially in populations at northern range limits such as the ones we sampled.

## Predicting budburst phenology under future climates

Our results provide new insights into the key factors and ecological processes that are critical to forecasting future phenologies under climate change. We found strong evidence that changes in budburst cues will produce consistent trends across populations. This allows us to forecast across populations for which we have limited local phenological data but similar species assemblages. The high phylogenetic structure in budburst timing could also allow us to use our existing knowledge of species phenological cue responses to forecasts trends in phylogenetically related species. But we must also be cautious in the inferences we can make, as the accuracy of these predictions is dependent on the strength of the phylogenetic signal and whether closely related species evolved recently with more even branch lengths (Molina-Venegas et al., 2018). Given the high phylogenetic structure we found for our phenological trait, our results could be used to impute the budburst responses of several genera, including *Betula* and *Quercus*, for which branch lengths are relatively even.



Our study approach and findings can be more broadly applied across temperate plant communities to better forecast species responses to climate change. To this end, future efforts should invest in identifying latent traits contributing to the high phylogenetic structure of budburst, and require less sampling across populations or biogeographic gradients. Combining community wide approaches with phylogenetic relationships, such as we have done, are critical to account for biases in our model estimates, reduce species-level, and combine the effects of species evolutionary history with current biological responses. This holistic approach is needed to predict changes in spring phenology and mitigate the cascading effects they will have on forest communities and ecosystem services.

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# 1 Tables and figures

Table 1: Summary output from a phylogenetic Bayesian model in which species are partially pooled and phylogeny is included on the intercept. The model includes photoperiod and site as dummy variables, while the forcing and chilling effect is included as continuous. Parameter estimates were used to estimate day of budburst for sites under low cue conditions and for Smithers only when relevant.

	mean	sd	5%	95%
Intercept	12.51	3.14	7.40	17.60
Phylogenetic effect	0.79	0.12	0.60	0.90
Forcing	-9.55	0.74	-10.70	-8.30
Photoperiod	-3.62	0.41	-4.30	-3.00
Chilling	-15.21	1.25	-17.30	-13.20
Manning Park	2.09	0.36	1.50	2.70
Harvard Forest	-6.04	1.03	-7.80	-4.40
St. Hippolyte	-8.71	0.97	-10.30	-7.10
Forcing x photoperiod	0.23	0.71	-1.00	1.40
Forcing x chilling	9.06	0.90	7.60	10.50
Photoperiod x chilling	-0.67	0.90	-2.20	0.80
Forcing x Manning Park	-1.76	0.77	-3.00	-0.50
Photoperiod x Manning Park	0.58	0.79	-0.70	1.90
Chilling x Manning Park	-0.36	1.60	-3.00	2.20
Forcing x Harvard Forest	3.81	1.22	1.80	5.80
Photoperiod x Harvard Forest	-1.96	0.86	-3.30	-0.60
Chilling x Harvard Forest	9.97	2.03	6.60	13.40
Forcing x St. Hippolyte	5.25	1.19	3.20	7.20
Photoperiod x St. Hippolyte	-2.13	0.84	-3.50	-0.70
Chilling x St. Hippolyte	8.65	1.70	5.90	11.50

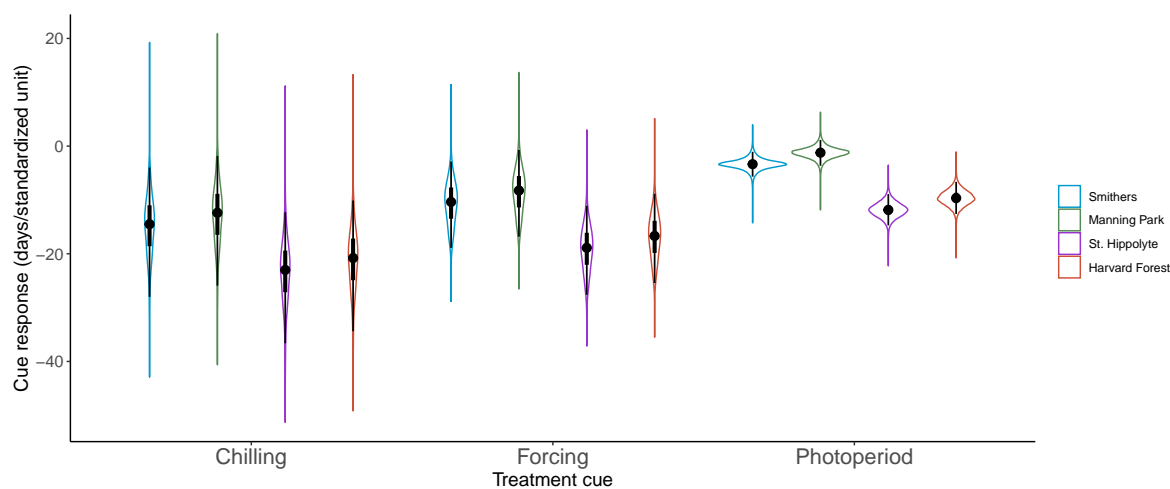


Figure 1: Posterior distributions of estimated chilling, forcing, and photoperiod responses with site level effects for individual populations. Black circles represent the median cue response, thicker black lines the 50% uncertainty interval, while the thinner black line the 90% uncertainty interval. The y-axis spans the entire range of the data. Cues were z-scored using two standard deviations, see methods.

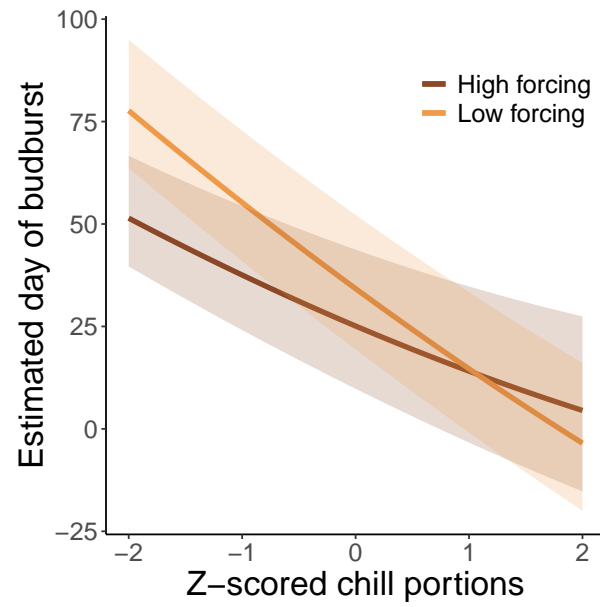


Figure 2: Estimated day of budburst of first bud in response to chill portions and forcing, estimated for our defined baseline conditions. We found a positive interaction between chilling and forcing cues, with high forcing compensating for low chilling to produce earlier budburst, while budburst occurred earlier under low forcing following high chilling.

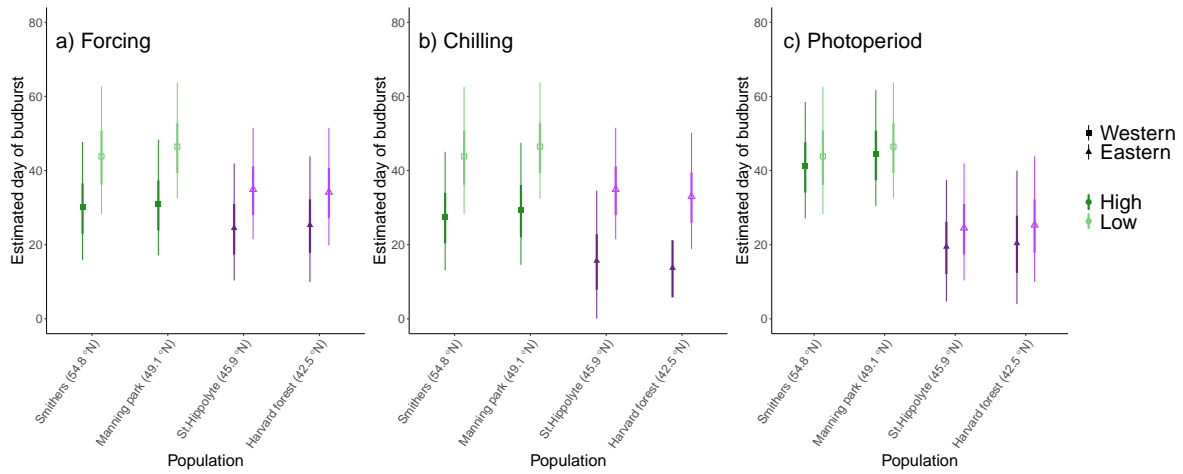


Figure 3: Estimated day of budburst of first bud in response to (a) forcing across populations under low chilling conditions and short photoperiods, (b) chilling across populations under low forcing and short photoperiods, and (c) across photoperiods under our baseline forcing and chilling conditions for species sampled from our four populations. The thin error bars represent the 90% uncertainty interval, while the thicker error bars represent the 50% uncertainty interval.

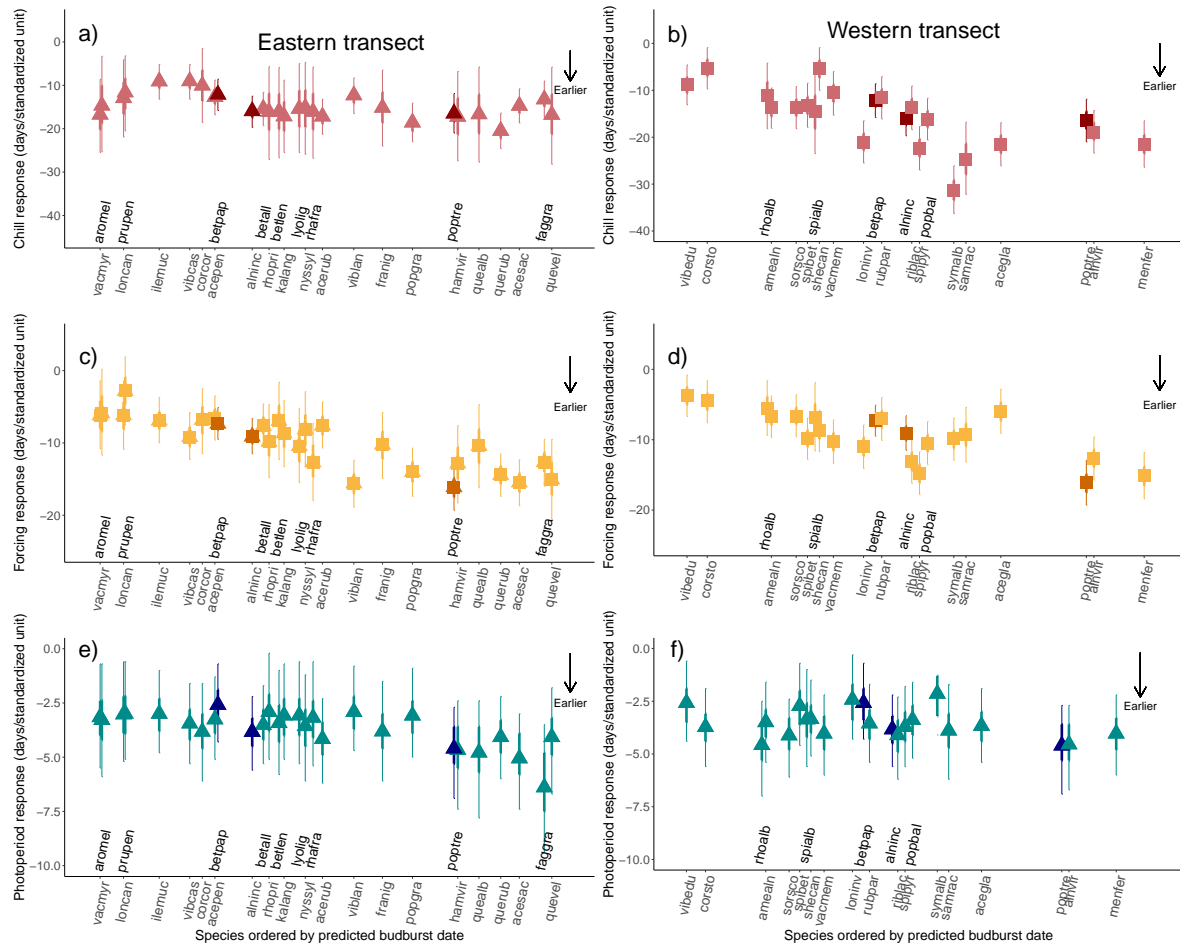


Figure 4: Estimated species' chilling (a,b), forcing (c,d) and photoperiod (e,f) responses ranked by increasing estimated budburst dates for both the eastern (a, c, e) and western (b, d, f) populations. Cues are plotted on differing y-axis to better depict species differences. For each species, the thinner error bars represent the 90% uncertainty interval, and thicker bars represent the 50% uncertainty interval. Species that occur in both the eastern and western transects are depicted using darker colours. Each cue was z-scored, using two standard deviations, to make the results across cues directly comparable, see methods.

## References

- Ackerly, D. 2009. Conservatism and diversification of plant functional traits: Evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences of the United States of America* 106:19699–19706.
- Alecrim, E. F., R. D. Sargent, and J. R. K. Forrest. 2000. Higher-latitude spring-flowering herbs advance their phenology more than trees with warming temperatures. *Journal of Ecology* 111:156–169.
- Basler, D., and C. Körner. 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiology* 34:377–388.
- Buonaiuto, D. M., E. M. Wolkovich, and M. J. Donahue. 2023. Experimental designs for testing the interactive effects of temperature and light in ecology : The problem of periodicity. *Functional Ecology* 37:1747–1756.
- Caffarra, A., and A. Donnelly. 2011. The ecological significance of phenology in four different tree species: Effects of light and temperature on bud burst. *International Journal of Biometeorology* 55:711–721.
- Chuine, I. 2000. A unified model for budburst of trees. *Journal of Theoretical Biology* 207:337–347.
- Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. *Science* 329:277–278.
- Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* 22:357–365.
- Cooke, J. E., M. E. Eriksson, and O. Junttila. 2012. The dynamic nature of bud dormancy in trees: Environmental control and molecular mechanisms. *Plant, Cell and Environment* 35:1707–1728.
- Davies, T. J., E. M. Wolkovich, N. J. Kraft, N. Salamin, J. M. Allen, T. R. Ault, J. L. Betancourt, K. Bolmgren, E. E. Cleland, B. I. Cook, T. M. Crimmins, S. J. Mazer, G. J. McCabe, S. Pau, J. Regetz, M. D. Schwartz, and S. E. Travers. 2013. Phylogenetic conservatism in plant phenology.
- Donnelly, A., and R. Yu. 2019. Temperate deciduous shrub phenology : the overlooked forest layer. *International Journal of Biometeorology* 65:343–355.
- Finn, G. A., A. E. Straszewski, and V. Peterson. 2007. A general growth stage key for describing trees and woody plants. *Annals of Applied Biology* 151:127–131.
- Fitter, A. H., and R. S. Fitter. 2002. Rapid changes in flowering time in British plants. *Science* 296:1689–1691.
- Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* 219:1353–1362.
- Fridley, J. D. 2012. Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature* 485:359–362.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27:2865–2873.
- Gill, D. S., J. S. Amthor, and F. H. Bormann. 1998. Leaf phenology , photosynthesis , and the persistence of saplings and shrubs in a mature northern hardwood forest. *Tree Physiology* 18:281–289.

- 410 Gotelli, N. J., and G. R. Graves. 1996. The temporal niche. Pages 95–112 in *Null Models In Ecology*.  
411 Smithsonian Institution Press, Washington, D. C.
- 412 Guy, R. D. 2014. The early bud gets to warm. *New Phytologist* 202:7–9.
- 413 Heide, O. M. 1993. Daylength and thermal time responses of budburst during dormancy release in  
414 some northern deciduous trees. *Physiologia Plantarum* 88:531–540.
- 415 Hoegh-Guldberg, O., D. Jacob, M. Taylor, M. Bindi, S. Brown, I. Camilloni, A. Diedhiou, R. Djalante,  
416 K. Ebi, F. Engelbrecht, J. Guiot, Y. Hijioka, S. Mehrotra, A. Payne, S. Seneviratne, A. Thomas,  
417 R. Warren, and G. Zhou. 2018. Impacts of 1.5°C Global Warming on Natural and Human Systems.  
418 In: *Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C*  
419 *above pre-industrial levels and related global greenhouse gas emission pathways, in the context of* .  
420 *Tech. rep.*, Cambridge University Press, Cambridge, UK and New York, NY, USA.
- 421 Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs  
422 photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- 423 Lechowicz, M. J. 1984. Why Do Temperate Deciduous Trees Leaf Out at Different Times? *Adaptation*  
424 *and Ecology of Forest Communities*. *The American Naturalist* 124:821–842.
- 425 Luedeling, E. 2020. *chillR: Statistical Methods for Phenology Analysis in Temperate Fruit Trees*.  
426 <https://CRAN.R-project.org/package=chillR>.
- 427 Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aaasa, R. Ahas, K. Alm-Kübler, P. Bissolli,  
428 O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Don-  
429 nelly, Y. Filella, K. Jatzak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová,  
430 H. Scheffinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Zust. 2006.  
431 European phenological response to climate change matches the warming pattern. *Global Change*  
432 *Biology* 12:1969–1976.
- 433 Molina-Venegas, R., J. C. Moreno-Saiz, I. C. Parga, T. J. Davies, P. R. Peres-Neto, and M. Á. Ro-  
434 dríguez. 2018. Assessing among-lineage variability in phylogenetic imputation of functional trait  
435 datasets. *Ecography* 41:1740–1749.
- 436 Panchen, Z. A., R. B. Primack, B. Nordt, E. R. Ellwood, A. Stevens, S. S. Renner, C. G. Willis,  
437 R. Fahey, A. Whittemore, Y. Du, and C. C. Davis. 2014. Leaf out times of temperate woody plants  
438 are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytologist* pages  
439 1208–1219.
- 440 Polgar, C. A., and R. B. Primack. 2011. Leaf-out phenology of temperate woody plants: From trees  
441 to ecosystems. *New Phytologist* 191:926–941.
- 442 Post, E., B. A. Steinman, and M. E. Mann. 2018. Acceleration of phenological advance and warming  
443 with latitude over the past century. *Scientific Reports* 8:1–8.
- 444 R Development Core Team. 2017. *R: A language and environment for statistical computing*. R  
445 Foundation for Statistical Computing, Vienna, Austria .
- 446 Richardson, A.D., O’Keefe, J. 2009. Phenological Differences Between Understory and Overstory.  
447 Pages 87–117 in A. Noormets, ed. *Phenology of Ecosystem Processes*. Springer US, New York, NY.
- 448 Sanz-Aguilar, A., M. Carrete, P. Edelaar, J. Potti, and J. L. Tella. 2015. The empty temporal niche:  
449 breeding phenology differs between coexisting native and invasive birds. *Biological Invasions* 17:3275–  
450 3288.
- 451 Schwartz, M. D., and B. E. Reiter. 2000. Changes in North American spring. *International Journal of*  
452 *Climatology* 20:929–932.



- Smith, S. A., and J. W. Brown. 2018. Constructing a broadly inclusive seed plant phylogeny. *American journal of botany* 105:302–314.
- Stan Development Team. 2018. RStan: the R interface to Stan. R package version 2.17.3.
- Vitasse, Y., D. Basler, and D. Way. 2014. Is the use of cuttings a good proxy to explore phenological responses of temperate forests in warming and photoperiod experiments? *Tree Physiology* 34:174–183.
- Vitasse, Y., S. Delzon, E. Dufrene, J.-Y. Pontailleur, J.-M. Louvet, A. Kremer, and R. Michalet. 2009. Leaf phenology sensitivity to temperature in European trees : Do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology* 149:735–744.
- Vitasse, Y., C. Signarbieux, and Y. H. Fu. 2018. Global warming leads to more uniform spring phenology across elevations. *PNAS* 115:1004–1008.
- Way, D. A., and R. A. Montgomery. 2015. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell and Environment* 38:1725–1736.
- Webb, C. O., D. D. Ackerly, M. A. Mcpeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology Evolution and Systematics* 33:475–505.
- Westoby, M., M. R. Leishman, and J. M. Lord. 1995. On Misinterpreting the ‘phylogenetic Correction’. *Journal of Ecology* 83:531–534.
- Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable Climate Change Response Explains Non-Native Species’ Success in Thoreau’s Woods. *PLoS ONE* 5:1–5.
- Wolkovich, E. M., and E. E. Cleland. 2014. Phenological niches and the future of invaded ecosystems with climate change. *AoB PLANTS* 6:1–16.
- Wolkovich, E. M., T. J. Davies, H. Schaefer, E. E. Cleland, B. I. Cook, S. E. Travers, C. G. Willis, and C. C. Davis. 2013. Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany* 100:1407–1421.
- Yu, H., E. Luedeling, and J. Xu. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America* 107:22151–22156.
- Zohner, C. M., B. M. Benito, J. D. Fridley, J.-C. Svenning, and S. S. Renner. 2017. Spring predictability explains different leaf-out strategies in the woody floras of North America, Europe and East Asia. *Ecology Letters* 20:452–460.
- Zohner, C. M., and S. S. Renner. 2014. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. *Ecology Letters* 17:1016–1025.

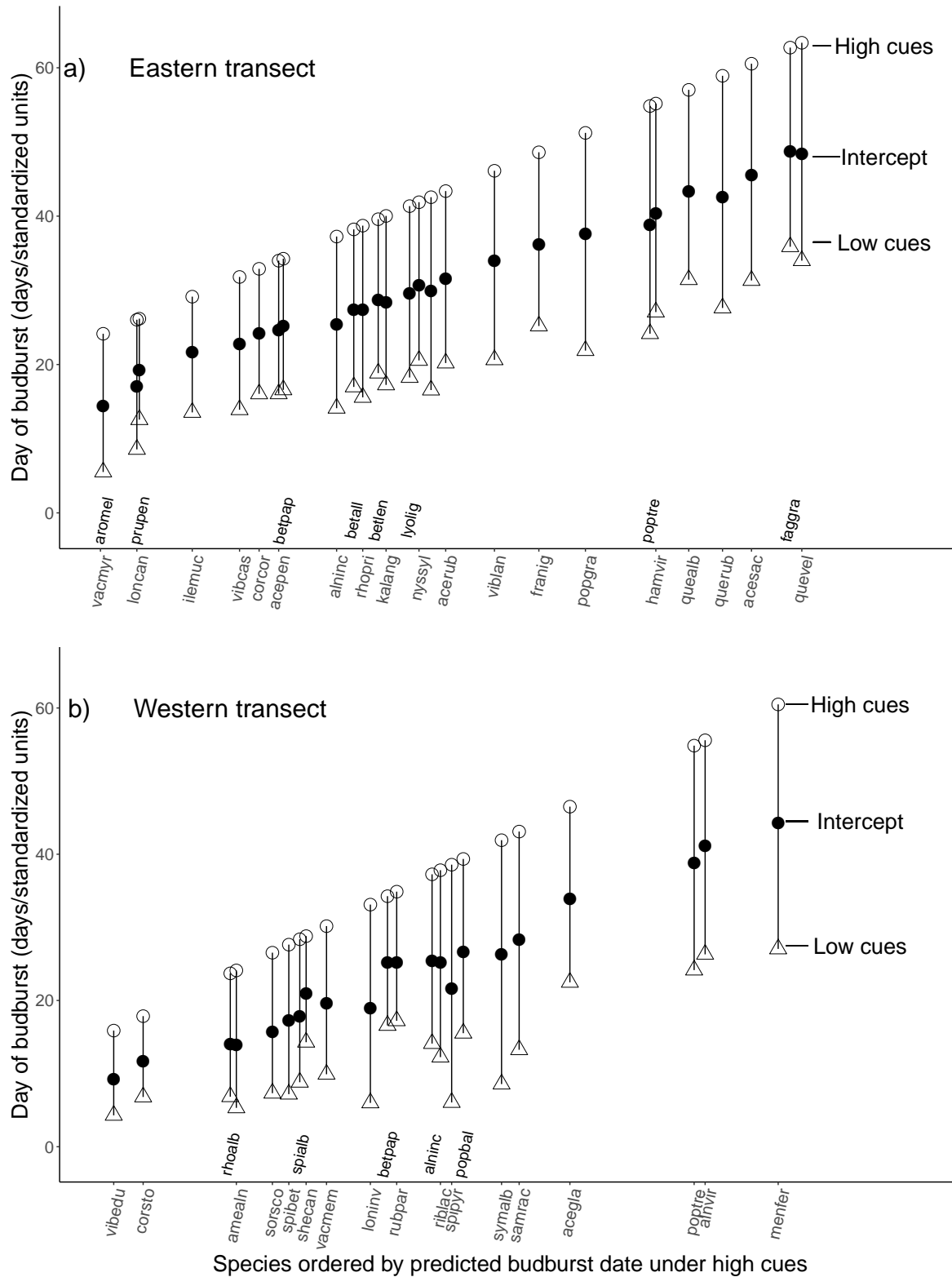


Figure 5: Comparisons of our estimated budburst based on the full model (intercept plus all cues), shown in white, versus the intercepts only (without cues), shown in black, ordered according to differences in species estimated budburst dates for both the eastern (a) and western (b) populations under high cue conditions, depicted as circles, and low cue conditions, depicted as triangles.