

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

Deirdre Loughnan¹ and E M Wolkovich¹

November 12, 2023

¹ Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall Vancouver, BC, Canada, V6T 1Z4.

Corresponding Author: Deirdre Loughnan, deirdre.loughnan@ubc.ca

Introduction

Climate change is altering the phenology, or the timing of life history events, of species across the tree of life. The effects however, have not been uniform, with some regions experiencing greater warming than others (Hoegh-Guldberg et al., 2018), producing high variability in phenological shifts between species and habitats (Fitter and Fitter, 2002; Menzel et al., 2006; Yu et al., 2010; Fridley, 2012).

Variation 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 phenological shifts is necessary to predict future changes, and the 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).

Across different species, phenological events can occur over several weeks, with this temporal variation allowing individual species to fill different temporal niche (Gotelli and Graves, 1996). In plant communities, understory species often budburst earlier than taller trees, and is predicted to select for differences in species growth strategies. Similar trends are occurring for animals, such as native birds in Mediterranean marsh communities that reproduce months earlier in the season than exotic invaders (Sanz-Aguilar et al., 2015). In addition to within community differences, phenological variation may also occur between populations across geographic gradients. We lack a strong understanding of the relative effects of population versus species-level variation in shaping phenology and the overall impacts on communities.

Spring budburst offers an excellent system to study spatial patterns in phenology and cue responses. Decades of work has demonstrated that despite species varying in their growth strategies, under controlled environments, budburst is consistent in its cue responses. Woody plant species, for example, respond to temperature cues, particularly winter and spring 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 cue varies in its relative importance for individual species, they can have interactive effects (Heide, 1993; Chuine, 2000; Caffarra and Donnelly, 2011; Flynn and Wolkovich, 2018). Spring temperatures, also referred to as forcing cues, can offset the delaying effects of warm winters, or low chilling conditions on spring budburst (Heide, 1993; Chuine, 2000; Caffarra and Donnelly, 2011; Flynn

and Wolkovich, 2018). Similarly, responses to daylength, also referred to as photoperiod, can offset weak forcing cues in cool springs with low forcing (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 has made it challenging to draw generalizable trends across forest communities.

Species budburst cues vary geographically and temporally, with climate change potentially driving further differences in community dynamics and species composition. Increasing winter and spring temperatures could lead to faster accumulation of chilling and forcing cues, and earlier budburst (Guy, 2014). These shifts could create novel niche space across the growing season and facilitate species invasions or alter community assemblages (Willis et al., 2010; Wolkovich et al., 2013). In addition, species with strong photoperiod cues could face reduced fitness, as constant photoperiod cues limit their ability to adapt (Way and Montgomery, 2015). Differences in cue requirements will shape species adaptive potential, altering the competitive landscape across the growing season, and reshaping species diversity and persistence.

While the impacts of climate change are recent, it is important to account for the longer timescales over which communities assembled (Davies et al., 2013). It is the historic conditions that have shaped traits, like phenology, that we observe today. Species with large distributions are more likely to have experienced different historic cues, possibly driving their variation in phenotypes and cue responses. But few studies have explored how cue use differs across spatial gradients using the same forest communities. 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 change spatially.

Here 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 respectively. Our approach allowed us to detect general trends in budburst cue responses in North American deciduous forest communities. We also explored community specific responses and detect differences between western and eastern forest communities, and across latitudes. By including diverse assemblages of species, we tested for differences between functional groups, comparing the dominant shrub and tree species that characterize our forest understories and canopy.

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, Massachusetts, 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 maximized the number of species

occurring across sites. Of the species in our eastern transect, 13 were shrubs and 15 were trees, while in 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. Samples were kept cold and we 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 differences in the timing of sample collection and the thermoperiodicity in forcing treatments. Samples eastern study were collected in late January, with samples experiencing considerable field chilling. Our western samples, however, were collected 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. 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, water changes, 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:

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

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

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

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

(2)

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 (2023).

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 (λ 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. 6). 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. 6). 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 7). 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. 7).

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 cue 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, we found species budburst to span several weeks. Across each regional community, we found slight gradients in environmental cue responses, with the strongest responses be to chilling and forcing cues. While our findings support that species phenology is largely shaped by temperature and light, there was evidence of strong phylogenetic structuring in budburst phenology.

Temporal assembly across North America

Despite differences in the species composition and local conditions of our forest communities, under controlled conditions, the populations differed only slightly in their phenology and cue responses. This contrasts our expectation of populations' local habitats imposing unique selective pressures and driving differences in cues responses. But the overall timing of budburst was only slightly earlier in our eastern populations (Fig 1). This negligible variation could be due to the earlier collection date of with our western species, and the reduced field chilling they received relative to our eastern samples.

Across latitudinal gradients, we expected to find variation in local environments, as latitude correlates with reduced photoperiod and temperatures. Studies using *in situ* phenological data have found greater shifts in phenology across latitudinal gradients and their correlation with temperature (Post et al., 2018; Alecrim et al.). This work is based on long-term observations in the field, with confounding differences in study duration and start dates, and using variable methodologies and geographic extent (Post et al., 2018; Alecrim et al.). The lack of population-level trends that we observed suggests budburst is not shaped by current geography or local adaptation, at least at our continental scale.

Community composition and interspecific variation in phenology

Our species varied considerably in the responses to our three environmental cues, which translates into large potential differences in their temporal niche and ecological roles. Species ranged from early to late budburst dates, spanning a similar period as observed in natural communities (Lechowicz, 1984; Richardson, A.D., O'Keefe, 2009), with our experiment capturing 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 our strong responses to chilling and weak photoperiod responses, consistent with previous studies. We also found complex interactions between cues that are advantageous under warming climates (Heide, 1993; Caffarra and Donnelly, 2011; Flynn and Wolkovich, 2018). For example, the interaction between chilling and forcing ensures species will budburst if warmer winters cause insufficient chilling. Despite our species differing in their cue responses, we did not find the clear, generalizable trends we expected across species with similar growth strategies.

Shrub and tree species differ greatly in their physiology, allowing them to fill different ecological niche space. But we found little variation in cue responses on a whole. Most of our tree species budburst later than our shrubs species, an order found by previous work (Gill et al., 1998; Panchen et al., 2014). But, contrary to our expectations, about a quarter of our tree species also budburst early, with timing more similar to that of a shrub. 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 suggests there is more nuance to these patterns than previously found. As trees species advance phenologically—resulting in earlier canopy closure and reduced light

availability (Donnelly and Yu, 2019)—shrub species with weak cue responses will have reduced fitness. But our finding suggests many shrubs will also advance phenologically. These species may maintain their relative temporal niche within their forests 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 could be important for other traits. Species with earlier budburst may exhibit a suite of traits that infers a greater ability to capture light and photosynthesize prior to canopy closure or improve nutrient uptake later in the season. Species differences in their temporal niche will relate to their overall fitness, and be determined by their full suite of traits. Currently, we do not understand the mechanisms that underlie these trait relationships, but incorporating phenology into a broader trait framework, will provide insights into the drivers selecting for species phenotypes.

Community assembly in responses to cues versus evolutionary history

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

Our ability to make accurate forecasts of phenology is predicated 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 breadth of environmental cues in any given year (Schwartz and Reiter, 2000; Zohner et al., 2017). It may be advantageous for North American species to have consistent responses to environmental cues across their range, optimizing their budburst across years and space.

While the effects of population-level variation on cue responses appears be negligible, individual species within community do differ (Fig. 5). We found the timing of species budburst to depend on the magnitude of the cue experienced. Our model estimated positive effects of cues on budburst under both low and high cue conditions, but with considerably earlier estimated budburst dates under stronger cues (Fig. 5). Temperatures are unlikely to change uniformly, however, with higher latitudes experiencing faster rates of temperatures change (Hoegh-Guldberg et al., 2018). This could drive future differences in population-level trends in budburst, as the compounding effects of warming temperatures impose varying selection across species distributions.

At a finer scale, our findings suggest species budburst order in a community will change with variable warming. The rank order of species differed between weak and strong cue conditions. Weak cues produced similar rank or budburst order as that estimated from species alone. But under stronger cues, particularly for our western community, the order differed (Fig S4). Populations that experience greater warming will likely have the greatest changes in species order, with cascading effects on competitive dynamics and trophic interactions. But we cannot focus solely on species cues to understand community assembly, as species phenotypes are the result of multiple interacting and complex environmental cues, acting 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. The cue responses of different species explaining about two-thirds of total 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. Since phenology is considered a highly plastic trait, we expected interannual differences in cues and in geography to drive variation in budburst. Our results, however, point to a large effect of species evolutionary history on budburst phenology. Still missing from our understanding are the unidentified latent traits—such as additional physiological traits—that cause the phylogenetic structure, and ultimately temporal niche, of temperate woody species. By not accounting for the additional cues or traits driving phenology, we have a limited ability to predict how communities will respond to future changes.

The evolutionary history and ancestral phenotype of a species will have a strong effect on their adaptive potential to future climates. Species traits are shaped over 'deep' timescales, with previous evolution influencing responses to today's climates. The conservation of ancestral phenotypes could impose physiologically constraints, preventing species from adapting to new environmental conditions. Such phylogenetic effects could skew species assemblages, favouring species with traits and cue requirements adapted for warmer climates. This favours species with low chilling and photoperiod requirements, as they can track and benefit from warmer climate conditions. But these phylogenetic trends could be an indication of limited evolutionary time to adapt. Some temperate species, like *Nyssa* and *Fagus*, have had a shorter geologic time in which to adapt to their local temperatures (Lechowicz, 1984), 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 critical to forecasting future phenologies. The consistent trends we observed across populations facilitate forecasting across similar regions with limited local phenological data but similar species assemblages. The high phylogenetic structure in budburst timing also enables us to forecast trends in phylogenetically related species. Given the high phylogenetic structure we found for our phenological trait, our results could be used to impute budburst cue responses of several genera, including *Betula* and *Quercus*. But we must be cautious in the inferences we make, as the accuracy of predictions depends on the strength of the phylogenetic signal and are strongest for recently evolved species (Molina-Venegas et al., 2018).

Our analytical approach and findings have broad applications across plant communities and in forecasting 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 more intentional sampling across under studied populations or biogeographic gradients. Combining community wide approaches with phylogenetic relationships, such as we have done, is critical to account for biases in our model estimates, reduce species-level uncertainty, and combine the effects of species evolutionary history with current ecological processes. This holistic approach will enable us to predict changes in spring phenology and mitigate the cascading effects they will have on forest communities and ecosystem services.

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

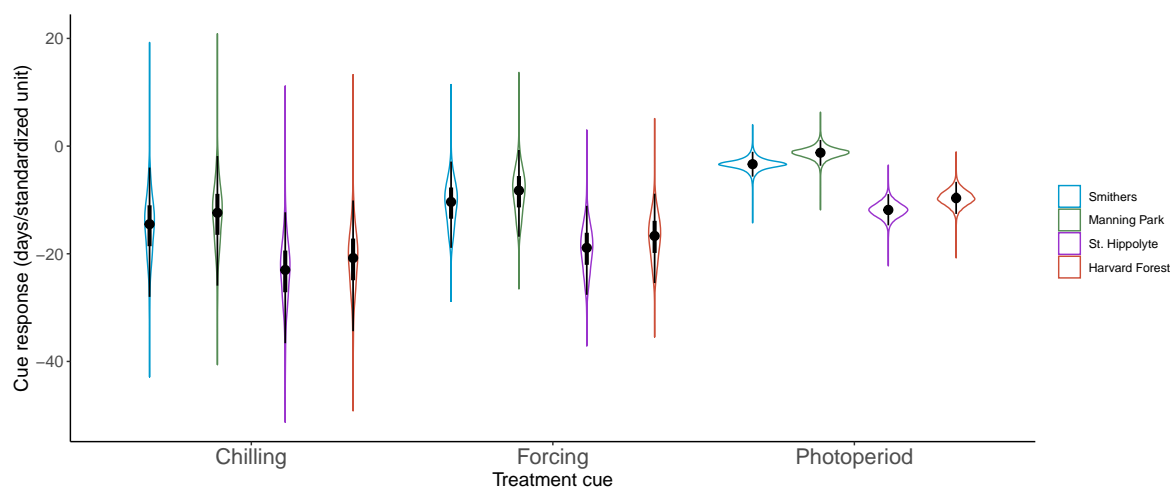


Figure 1: Posterior distributions of estimated chilling, forcing, and photoperiod responses with site level effects for individual populations. Black circles represent the median cue response, thicker black lines the 50% uncertainty interval, while the thinner black line the 90% uncertainty interval.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

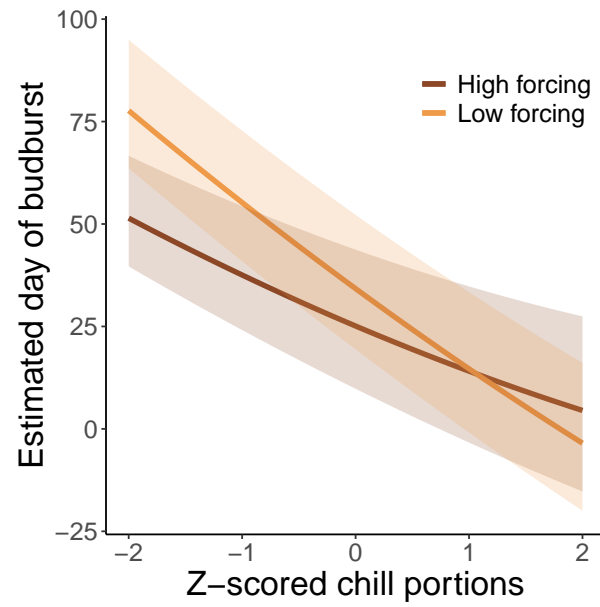


Figure 2: Estimated day of budburst of first bud in response to chill portions and forcing, estimated for our defined baseline conditions. We found a positive interaction between chilling and forcing cues, with high forcing compensating for low chilling to produce earlier budburst, while budburst occurred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

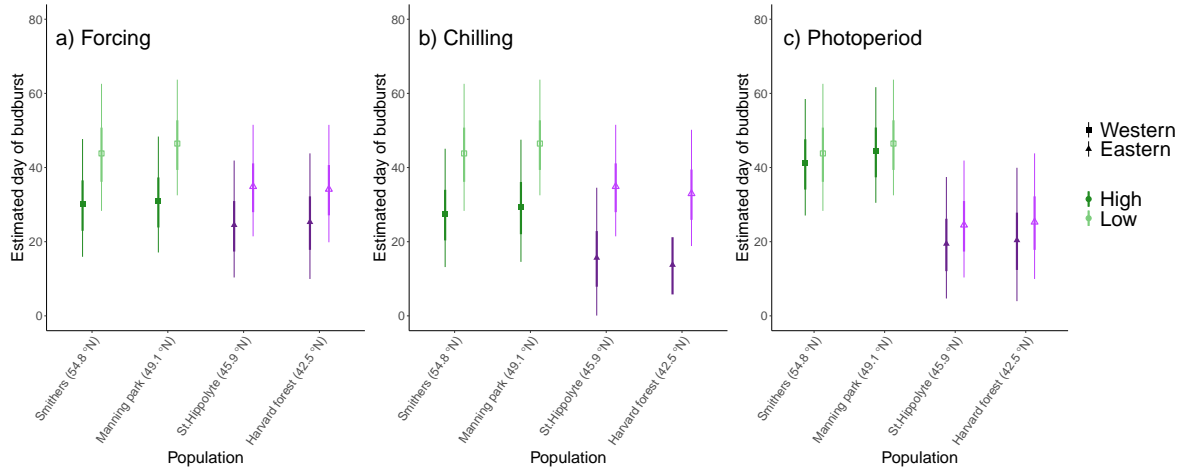


Figure 3: Estimated day of budburst of first bud in response to (a) forcing across populations under low chilling conditions and short photoperiods, (b) chilling across populations under low forcing and short photoperiods, and (c) across photoperiods under our baseline forcing and chilling conditions 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.

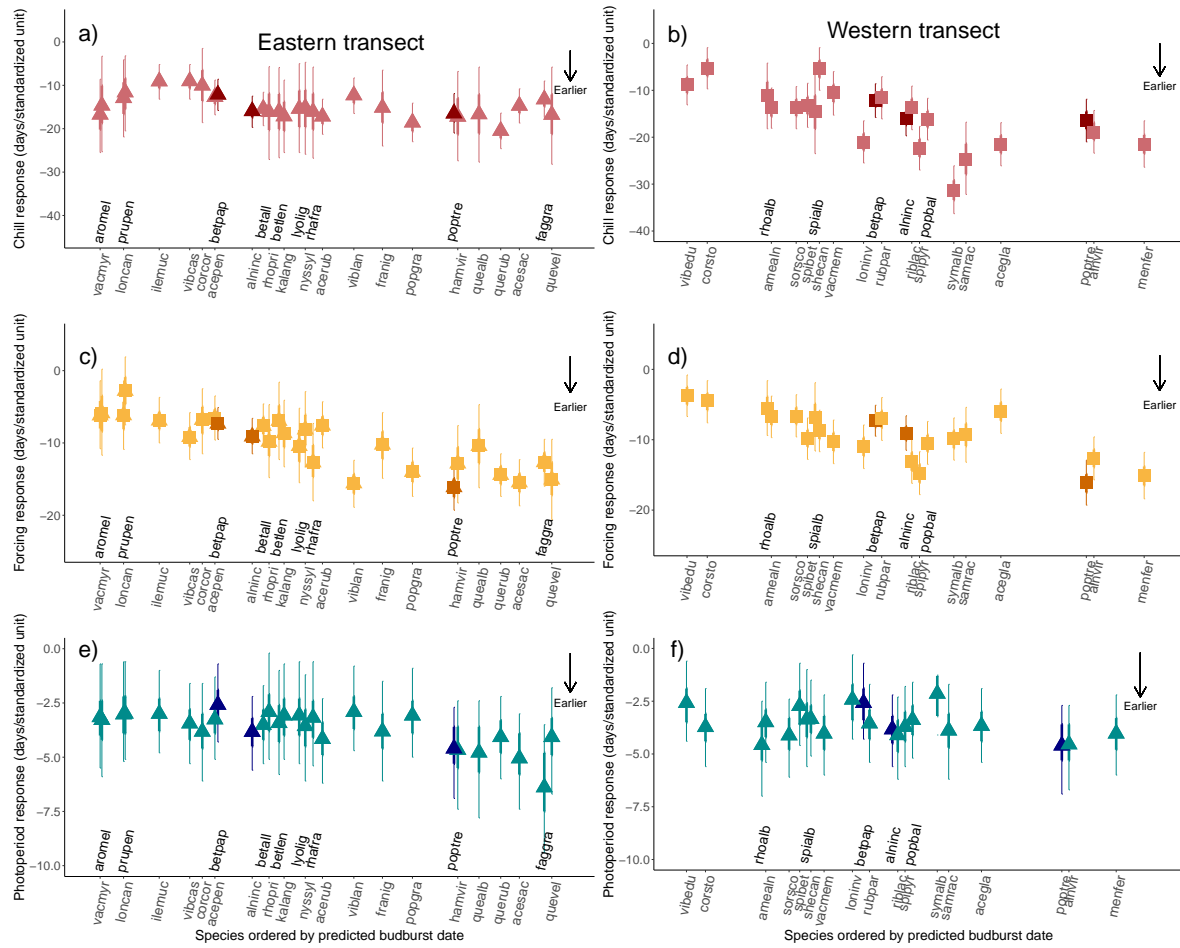


Figure 4: Estimated species chilling (a,b), forcing (c,d) and photoperiod (e,f) responses ranked by increasing estimated budburst dates for both the eastern (a, c, e) and western (b, d, f) populations. Cues are plotted on differing y-axis to better depict species differences. For each species, the thinner 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.

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

Things that will not render

Table 2: Chill units from our two western sites, E.C. Manning Park (MP) and Smithers B.C.(SM) Canada, and our two eastern sites, Harvard Forest (HF) USA and St. Hippolyte(SH) Canada.

Population	Chilling.treatment	Chilling.Hours	Utah.Model	Chill.Portions
Harvard forest	Field chilling	892	814.50	56.62
Harvard forest	Field chilling + 30 d at 4 degree C	2140	2062.50	94.06
St. Hippolyte	Field chilling	682	599.50	44.63
St. Hippolyte	Field chilling + 30 d at 4 degree C	1930	1847.50	82.06
Smithers	Field chilling + 30 d at 4 degree C	1317	1368.00	54.95
Smithers	Field chilling + 70 d at 4 degree C	1965	2016.00	74.67
Manning Park	Field chilling + 30 d at 4 degree C	1213	1377.00	55.09
Manning Park	Field chilling + 70 d at 4 degree C	1861	2025.00	75.33

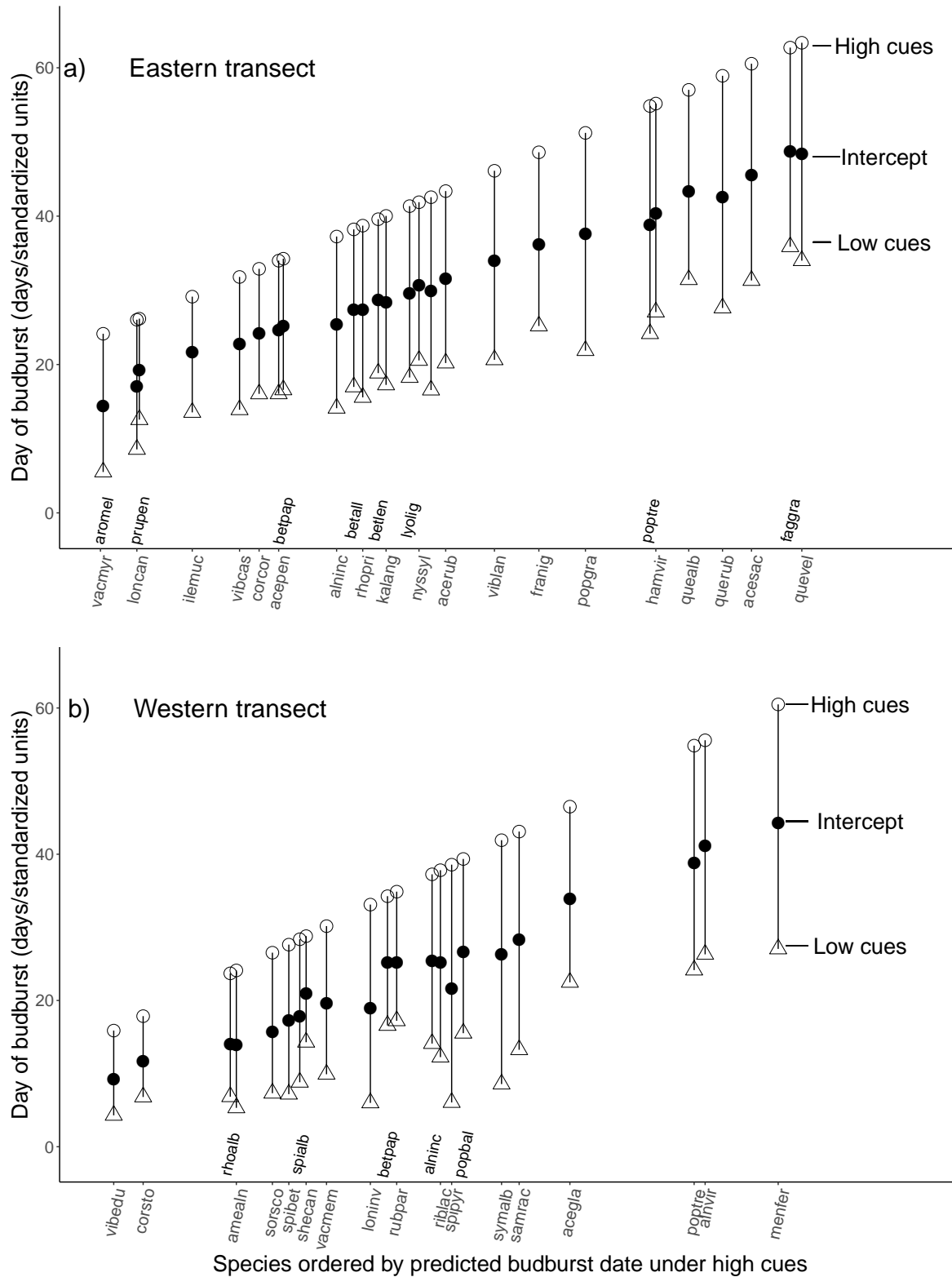


Figure 5: Comparisons of our estimated budburst based on the full model (intercept plus all cues), shown in white, versus the intercepts only (without cues), shown in black, ordered according to differences in species estimated budburst dates for both the eastern (a) and western (b) populations under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

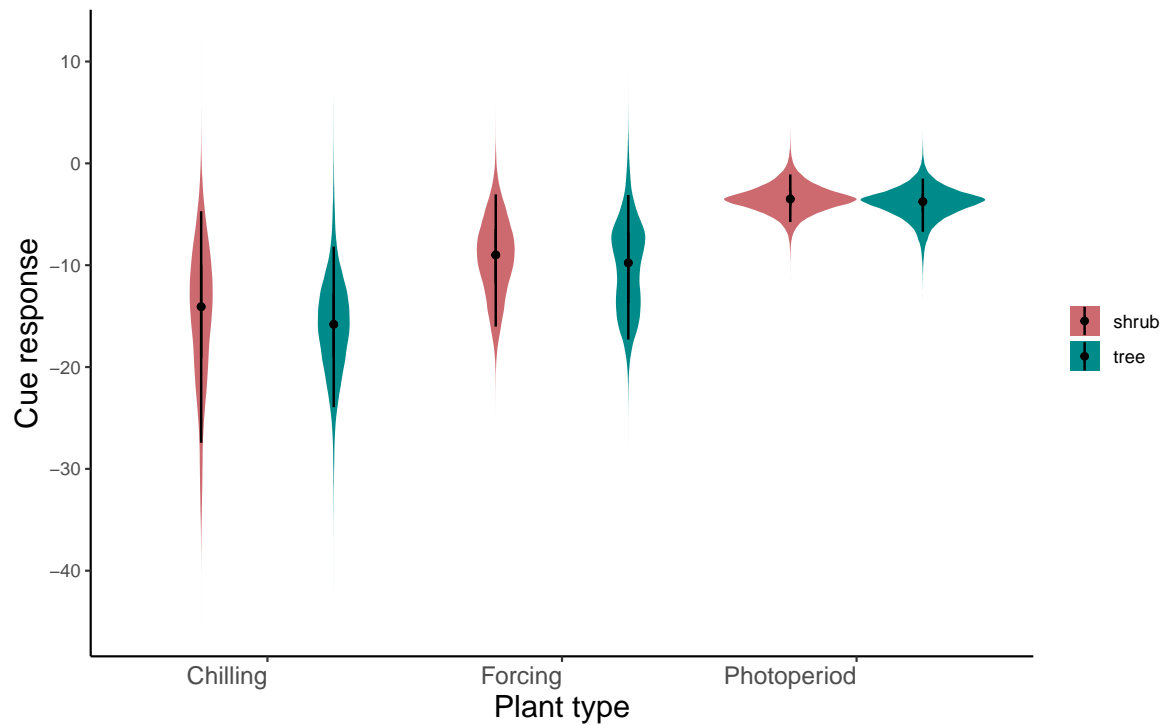


Figure 6: Comparisons of posterior distributions for cues estimates between shrub and tree species. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution is the the posterior density of the posteriors of the cue responses for all species within a given architectural type. The y-axis spans the entire range of the data.

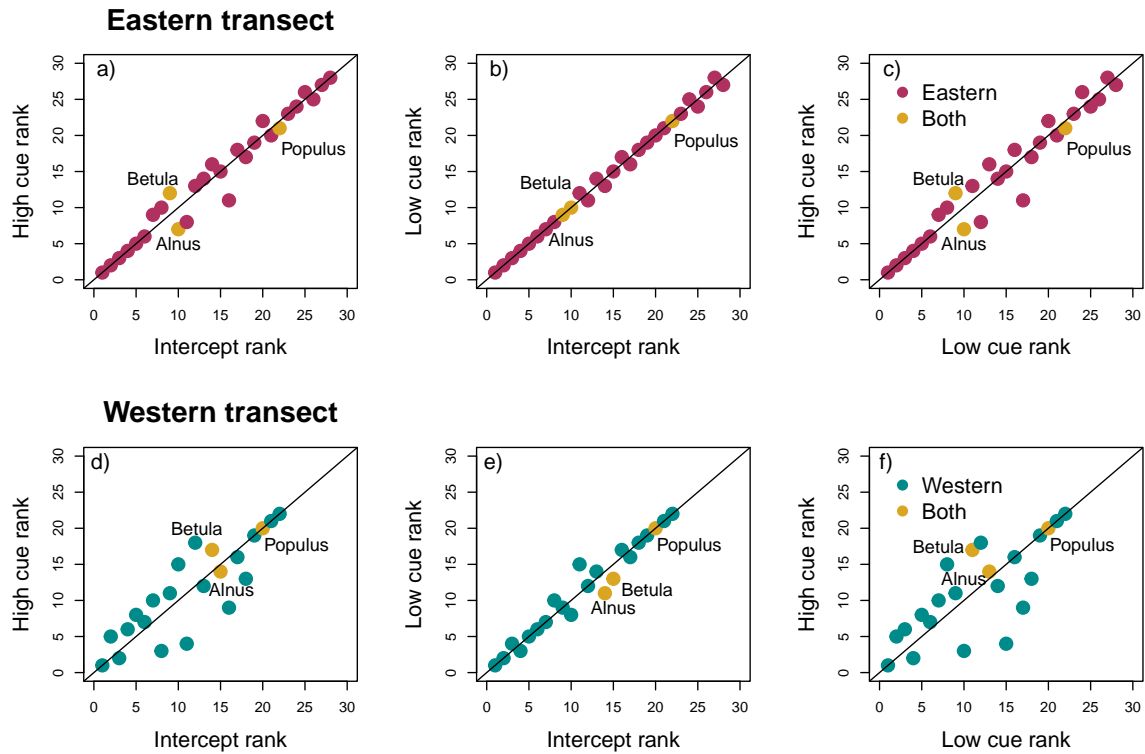


Figure 7: Estimated changes in species ranked budburst order, compared between species level effects (species intercept) and under high cue conditions (a and d), species level effects and under low cue condition (b and e), and ranked order under low and high cue conditions (c and f) for our eastern in red (a-c) and western species in blue (d-f). For the three species that occur in both transect, shown in yellow, *Alnus incana* exhibited the greatest rank change with a difference of three, while *Betula papyrifera* had a rank difference of two and *Populus tremuloides* a rank difference of one.