

Evolutionary history—more than phenological cues—explain temporal assembly of woody plant communities

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Introduction

Climate change is altering the timing of species life history events—phenology—with average advances of 2.6-2.8 days per decade (Parmesan, 2007; Thackeray et al., 2016; Cohen et al., 2018). Phenological events and their responses to climate change, however, are highly variable. Events, such as leafout, can span a period of weeks in most communities and are shifting in response to rising temperatures at different rates (Parmesan, 2007; Fitter and Fitter, 2002; Menzel et al., 2006; Yu et al., 2010; Fridley, 2012).

Understanding and explaining this variability is an important goal that remains extremely challenging. Some degree of variability is likely due to differences in climate change itself across space—as some areas have warmed faster than others, potentially generating larger phenological shifts (Hoegh-Guldberg et al., 2018). Climate change alone, however, explains a limited amount of the total variation. In contrast, substantial variation is due to species-level differences in phenology (Vitasse et al., 2009; Wolkovich and Cleland, 2014; Zohner and Renner, 2014; Vitasse et al., 2018), but we still have a limited understanding of how these species differences compare to other potential sources of variation, including those at the population-level. Understanding the role and scale of species-level variation, however is necessary to predict future changes in phenology, and ultimately, its impacts on community dynamics and ecosystem services, like carbon cycles and pollination (Gotelli and Graves, 1996; Cleland et al., 2007; Richardson, A.D., O’Keefe, 2009).

Different species often have unique phenologies—even within the same location and climate conditions. In varying the timing of their phenological events within a community, species can limit the overlap in their resource use and the extent of competition they experience. For example, in forest communities, understory species often budburst earlier than canopy trees, when light and soil nutrients are most available. This niche partitioning allows species to differ in their resource requirements and responses to environmental conditions as they change across the growing season, ultimately filling different temporal niche (Gotelli and Graves, 1996).

While temporal niche differences allow more species to coexistence in a community, there is considerable evidence that they are also shaped by population differences. Phenology can be highly variable across populations and select for locally optimum trait phenotypes. This has been shown across many ecosystems, including for bird breeding phenology in montane meadows in Sierra Nevada, that differs

by 12 days across high and low elevation populations (Saracco et al., 2019). How much of this variability is due to local adaptation or plasticity is still unclear. Across populations, we would expect the presence of strong population-level differences in phenology to indicate that local adaptation is an important driver of variation.

While local adaptation can be inferred by comparing populations, teasing apart the effects of plasticity requires knowledge of species cue systems. Both animals and plants often have very similar cue systems, responding to variation in both temperature and photoperiod cues (Renner and Zohner, 2018; Bonamour et al., 2019). Across species distributions, we would expect to find spatial gradients in phenology in response to similar gradients in cues. Both temperatures and photoperiod vary across latitudinal gradients, potentially causing similar gradients in phenology.

To predict how communities will respond to continued climate change requires a holistic approach that accounts for the multiple drivers of phenological variability. For a given community, we must account for differences across species that shape their temporal niche. But this cannot be done in isolation of population-level variation. In conducting experiments in controlled environments, we can remove the relative effects of interannual climate variability and plasticity, allowing us to identify species primary cues. The use of recent phylogenetic methods also provides a means to account for climate variability during the long evolutionary timescales over which communities assembled (Davies et al., 2013).

Spring budburst offers an excellent system to test for species-level and spatial patterns in phenology and cue responses. Budburst of temperate woody plants is known to respond to temperature cues in both the winter and spring, referred to as chilling and forcing respectively, as well as daylength (Chuine et al., 2010; Polgar and Primack, 2011; Cooke et al., 2012; Basler and Körner, 2014; Laube et al., 2014). These three cues interact to shape the start of spring growth, with variation in the relative importance of individual cues across species. Phenotypic differences between species — such as functional groups and varying growth strategies — further promotes phenological differences and ultimately optimize species temporal niche within a community.

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. Using a phylogenetic approach allowed us to detect general trends in budburst cue responses in North American deciduous forest communities. We also explored community specific responses to 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, there were 13 shrubs and 15 trees, while our western transect included 18 shrub and 4 tree species. At all sites, we tagged 15-20 healthy, mature, individuals for each species in the summer prior to sampling. Depending on the size of the individual, we collected 1-16 cuttings from 6-20 tagged plants, using a pole pruner from the ground. We kept samples cold and immediately placed them in water upon returning from the field. We conducted the eastern study at the Arnold Arboretum, Boston, MA, USA, and the western study at the University of British Columbia, BC, Canada. We used daily weather data from local weather stations to calculate the field chilling prior to collection (see Table ??).

Growth chamber study

Drawing on decades of work identifying the primary budburst cues, we tested the effects of chilling, forcing, and photoperiod cues. 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 we moved plants 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. We collected samples in our eastern study in late January, experiencing considerable field chilling. But we collected the western samples in late October, with most chilling occurring under controlled conditions. In our eastern study, we also set the duration of forcing temperatures to correspond with the photoperiod treatments. While this is a widespread and common approach in phenology chamber studies, it leads to a confounding effect in the thermoperiodicity (Buonaiuto et al., 2023). Thus we applied forcing temperatures for 12 hours independent of the duration of the photoperiod treatments in our western study. 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 stages of budburst 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 (code 07 by Finn et al. (2007)). Our eastern study spanned 82 days, with over 19320 phenological observations, while the western study spanned 113 days and we made 47844 phenological observations in total.

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 accounts for both the evolutionary relatedness of our species, and estimates the species level cue responses and differences across sites. We obtained species phylogenetic relatedness 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). We calculated chill portions for both the chilling experienced in the field prior to sampling and during the experiment in our 4°C chilling chambers. We also converted forcing temperatures to mean daily temperatures in each treatment to account for differences in thermoperiodicity between the two studies (Buonaiuto et al., 2023). Finally, we z-scored each cue and site using two standard deviations to allow direct comparisons between results across parameters (Gelman, 2008). In addition to the overall predictors, we included all two-way interactions between cues and between cues and sites.

Our modeling approach allowed us to combine observations of budburst (i) across species (sp , to estimate both a species-level intercept (α) and slope estimates for individual cues, sites, and all possible interactions (β) to estimate the day of budburst (y) relative to the first day of forcing conditions.

$$\begin{aligned}
 y_i = & \alpha_{sp_i} + \beta_{site2} + \beta_{site3} + \beta_{site4} + \\
 & \beta_{chill_{sp_i}} + \beta_{force_{sp_i}} + \beta_{photo_{sp_i}} + \\
 & \beta_{force \times chill_{sp_i}} + \beta_{chilling \times photo_{sp_i}} + \beta_{photoperiod \times chilling_{sp_i}} + \\
 & \beta_{force \times site2_{sp_i}} + \beta_{force \times site3_{sp_i}} + \beta_{force \times site4_{sp_i}} + \\
 & \beta_{chilling \times site2_{sp_i}} + \beta_{chilling \times site3_{sp_i}} + \beta_{chilling \times site4_{sp_i}} + \\
 & \beta_{photoperiod \times site2_{sp_i}} + \beta_{photoperiod \times site3_{sp_i}} + \beta_{photoperiod \times site4_{sp_i}} + \epsilon_i
 \end{aligned}$$

$$\epsilon_i \sim \text{normal}(0, \sigma_y^2)$$

The intercept and slopes were modeled with partial pooling at the species-level:

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

We included the phylogenetic effect as a variance covariance matrix (\mathbf{V}) in the parameterization of the normal random vector:

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

$$(2)$$

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 (2024).

We used semi-informative priors for each of our model parameters, validating the model code using test data prior to analysis. Our model produced \hat{R} values close to 1, well mixed chains, and n_{eff}

values that exceeded 10% of the model iterations. Our model was 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 was 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 small effects 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 overall budburst dates did not differ, but eastern populations budburst 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). Shrubs, like *Cornus stolonifera*, made up the majority of our, with weak responses to chilling and forcing. 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 we did not find 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 relatively small differences in cues (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 across North America, the assembly of species temporal niche was partly explained by environmental cues, with little variation explained by different populations. Despite populations differing in their species assemblages, and ratio of shrub to tree species, they had similar budburst cue responses and timing. But in comparing species within communities, we found budburst to span several weeks. We also found slight gradients in environmental cue responses across each region, with the strongest responses to chilling and forcing cues. Our findings support that species phenology is largely shaped by temperature and light, but there is also strong phylogenetic structuring in budburst.

Temporal assembly across North America

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

Across latitudinal gradients, we expected to find evidence of population differences, as latitude correlates with reduced photoperiod and temperatures. Greater shifts in phenology across latitudinal gradients have been found by studies using *in situ* phenological data (Post et al., 2018; Alecrim et al.). However, this work is based on long-term observations in the field, with confounding differences in study duration and start dates, and use 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 in their responses to environmental cues, creating large potential differences in their temporal niche and ecological roles. Species ranged from early to late budburst dates and spanned a similar period as observed in natural communities (Lechowicz, 1984; Richardson, A.D., O’Keefe, 2009). This confirms that with our experiment captured a realistic breadth in temperate forest budburst phenology. Furthermore, all our focal species responded to each environmental cue, with strong responses to chilling and weak responses to photoperiod, which is consistent with previous studies. Cues, however, had complex interactions 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 budburst if warmer winters cause insufficient chilling. Despite these

strong differences in species overall cue responses, we did not find the clear, generalizable trends across species with similar growth strategies.

Shrub and tree species differ greatly in their physiology, filling different ecological niche space. But we found little overall variation in cue responses. Most of our tree species budburst later than our shrubs species, an relative order also found by previous studies (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 shrubs species to budburst at similar times as the majority of our trees. 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 and have the potential to maintain their relative temporal niche and mitigate potential effects on community composition and dynamics.

The number of shrub and tree species exhibiting later than expected budburst phenologies suggests the cues we think are important for budburst could also be important for other traits. Earlier budbursting species 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. While we associate these traits with shrubs that dominate the forest understory, it is possible that temporal niche partitioning among tree species have selected for earlier budburst in some tree species as well.

Phenology has not been well integrated with our broader understanding of how traits shape species niche and growth. But intuitively we could expect phenology to correlate with other key traits that facilitate species ability to take advantage of available resources and grow early in the spring, or infer the greater competitive abilities needed when budbursting later. Differences in species temporal niche is also likely shaped by differences in other key plant 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

Our ability to accurately forecast 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, with forest communities experiencing a breadth of environmental cues in a given year (Schwartz and Reiter, 2000; Zohner et al., 2017). It may be advantageous for species to have consistent cue responses to optimize budburst across years and space.

Population-level variation in cue responses were negligible at the species-level, but we did find important differences (Fig. 5). As climate change leads to stronger temperature cues, we are already observing advances in species budburst, but the strongest effects will occur in high latitude populations that are warming faster and to a greater extent than others (Hoegh-Guldberg et al., 2018) (Fig. 5). In future, budburst across populations will be increasingly different, as the compounding effects of warming temperatures impose varying selection across species distributions.

At a finer scale, our findings suggest the order of species budburst in a community will change with variable warming. Community dynamics are most likely to change in populations that experience greater warming. As the order in which species budburst shifts (Fig S4), species that previously exhibited distinct temporal niche will increasingly interact. This may have cascading effects on species coexistence, changing their competitive landscape, and synchrony with pollinators or herbivores. But we cannot focus solely on species cues to understand this temporal community assembly. Species phenotypes

are the result of multiple interacting and complex environmental cues that act over evolutionary time scales (Ackerly, 2009).

Our study included the three cues mostly commonly attributed to species spring phenology, but about a third of total variation was not explained by these cues (Fig 4). This suggests our model is incomplete. Contrary to our expectations, this variation was not explained by differences in geography or latitudinal gradients in cues. Our results, instead, point to a large effect of species evolutionary history on budburst.

Still missing from our understanding of budburst phenology are the unidentified latent traits that underlies the observed phylogenetic structure. Species differ in many physiological traits that also shape the temporal niche of temperate woody species. For example, we might predict shrub species to possess great photosynthetic machinery to better use the light available prior to canopy closure in early spring. By not accounting for these additional cues or traits that drive 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 also have a strong effect on their adaptive potential to future climates. Species traits are shaped over 'deep' timescales, with previous evolution influencing responses to the present climate. The conservation of ancestral phenotypes could impose physiologically constraints, preventing species from adapting to new environments. In this way, 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 to adapt to their local temperatures (Lechowicz, 1984). These phylogenetic effects could skew species assemblages, favouring species with traits and cue requirements adapted for historical climates.

Predicting budburst phenology under future climates

Our results provide new insights into the 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 could enables us to forecast trends in phylogenetically related species, for well resolved and well sampled genera (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. Combining community wide approaches with phylogenetic relationships, such as we have done, allow us to 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 their cascading effects on forest communities and ecosystem services.

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.
- Bonamour, S., L.-m. Chevin, A. Charmantier, and C. Teplitsky. 2019. Phenotypic plasticity in response to climate change : the importance of cue variation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374:1–12.
- 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., 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.
- Cohen, J. M., M. J. Lajeunesse, and J. R. Rohr. 2018. A global synthesis of animal phenological responses to climate change. *Nature Climate Change* 8:224–228.
- 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.
- Gotelli, N. J., and G. R. Graves. 1996. The temporal niche. Pages 95–112 *in* Null Models In Ecology. Smithsonian Institution Press, Washington, D. C.
- Heide, O. M. 1993. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* 88:531–540.
- Hoegh-Guldberg, O., D. Jacob, M. Taylor, M. Bindi, S. Brown, I. Camilloni, A. Diedhiou, R. Djalante, K. Ebi, F. Engelbrecht, J. Guiot, Y. Hijioka, S. Mehrotra, A. Payne, S. Seneviratne, A. Thomas, R. Warren, and G. Zhou. 2018. Impacts of 1.5°C Global Warming on Natural and Human Systems. In: *Global Warming of 1.5 °C. An IPCC Special Report on the impacts of global warming of 1.5 °C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of .* Tech. rep., Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- Lechowicz, M. J. 1984. Why Do Temperate Deciduous Trees Leaf Out at Different Times? Adaptation and Ecology of Forest Communities. *The American Naturalist* 124:821–842.
- Luedeling, E. 2020. chillR: Statistical Methods for Phenology Analysis in Temperate Fruit Trees. <https://CRAN.R-project.org/package=chillR>.
- Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aaasa, R. Ahas, K. Alm-Kübler, P. Bissolli, O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jactzak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová, H. Scheffinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Züst. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.
- Molina-Venegas, R., J. C. Moreno-Saiz, I. C. Parga, T. J. Davies, P. R. Peres-Neto, and M. Á. Rodríguez. 2018. Assessing among-lineage variability in phylogenetic imputation of functional trait datasets. *Ecography* 41:1740–1749.
- Panchen, Z. A., R. B. Primack, B. Nordt, E. R. Ellwood, A. Stevens, S. S. Renner, C. G. Willis, R. Fahey, A. Whittemore, Y. Du, and C. C. Davis. 2014. Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytologist* pages 1208–1219.
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13:1860–1872.
- Polgar, C. A., and R. B. Primack. 2011. Leaf-out phenology of temperate woody plants: From trees to ecosystems. *New Phytologist* 191:926–941.
- Post, E., B. A. Steinman, and M. E. Mann. 2018. Acceleration of phenological advance and warming with latitude over the past century. *Scientific Reports* 8:1–8.
- R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria .
- Renner, S. S., and C. M. Zohner. 2018. Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates. *Annual Review of Ecology, Evolution, and Systematics* 49:annurev-ecolsys-110617-062535.

- Richardson, A.D., O'Keefe, J. 2009. Phenological Differences Between Understory and Overstory. Pages 87–117 in A. Noormets, ed. *Phenology of Ecosystem Processes*. Springer US, New York, NY.
- Saracco, J. F., R. B. Siegel, L. Helton, S. L. Stock, and D. F. Desante. 2019. Phenology and productivity in a montane bird assemblage: Trends and responses to elevation and climate variation. *Global Change Biology* 25:985–996.
- Schwartz, M. D., and B. E. Reiter. 2000. Changes in North American spring. *International Journal of 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.
- Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, D. G. Johns, I. D. Jones, D. I. Leech, E. B. MacKay, D. Massimino, S. Atkinson, P. J. Bacon, T. M. Brereton, L. Carvalho, T. H. Clutton-Brock, C. Duck, M. Edwards, J. M. Elliott, S. J. Hall, R. Harrington, J. W. Pearce-Higgins, T. T. Høye, L. E. Kruuk, J. M. Pemberton, T. H. Sparks, P. M. Thompson, I. White, I. J. Winfield, and S. Wanless. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535:241–245.
- 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. Pontauiller, 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.
- Wolkovich, E. M., and E. E. Cleland. 2014. Phenological niches and the future of invaded ecosystems with climate change. *AoB PLANTS* 6:1–16.
- 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.

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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

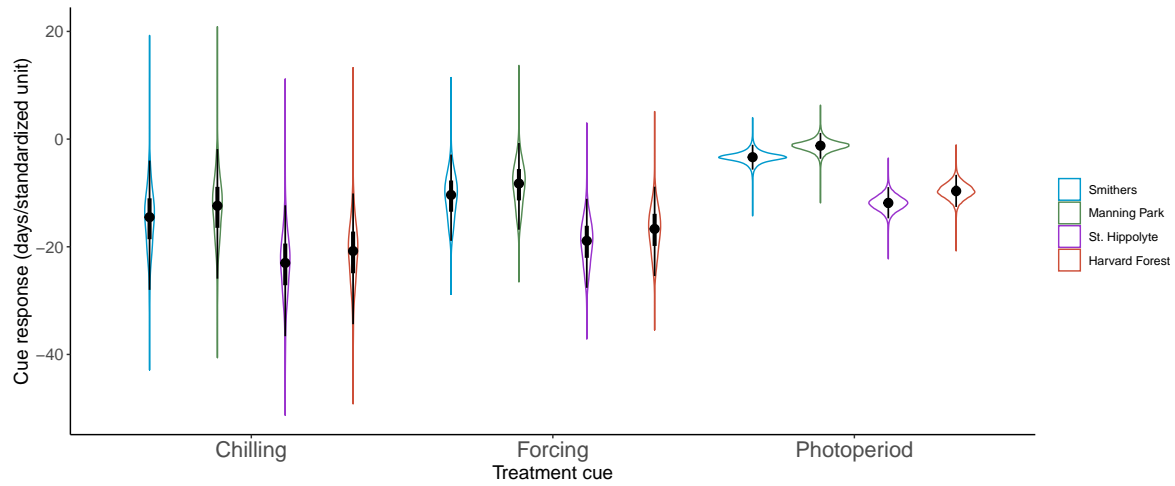


Figure 1: Posterior distributions of estimated chilling, forcing, and photoperiod responses with site level effects for individual populations. Black circles represent the median cue response, thicker black lines the 50% uncertainty interval, while the thinner black line the 90% uncertainty interval.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

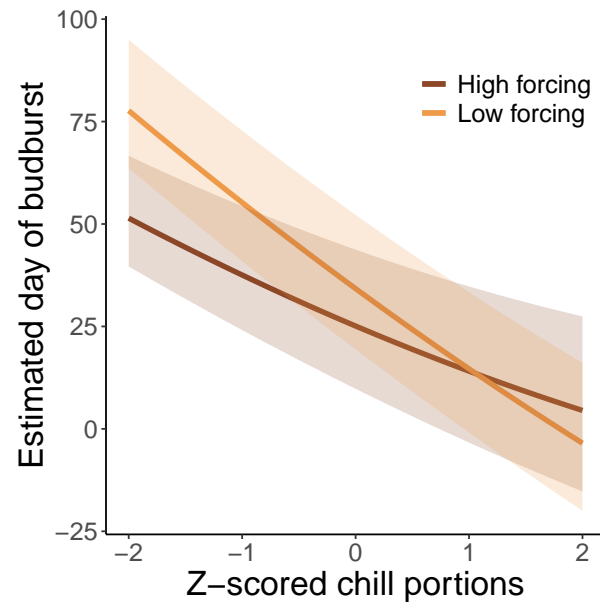


Figure 2: Estimated day of budburst of first bud in response to chill portions and forcing, estimated for our defined baseline conditions. We found a positive interaction between chilling and forcing cues, with high forcing compensating for low chilling to produce earlier budburst, while budburst occurred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

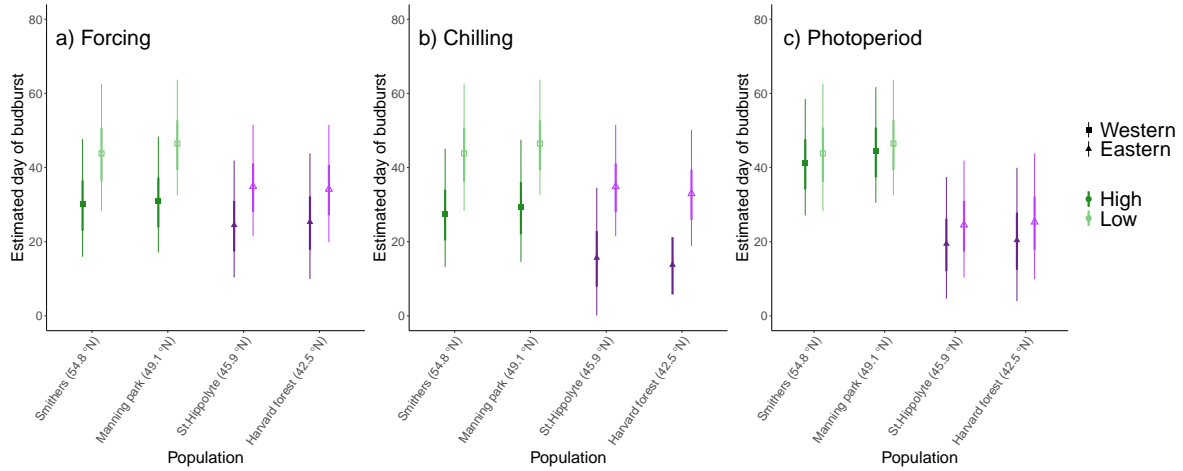


Figure 3: Estimated day of budburst of first bud in response to (a) forcing across populations under low chilling conditions and short photoperiods, (b) chilling across populations under low forcing and short photoperiods, and (c) across photoperiods under our baseline forcing and chilling conditions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

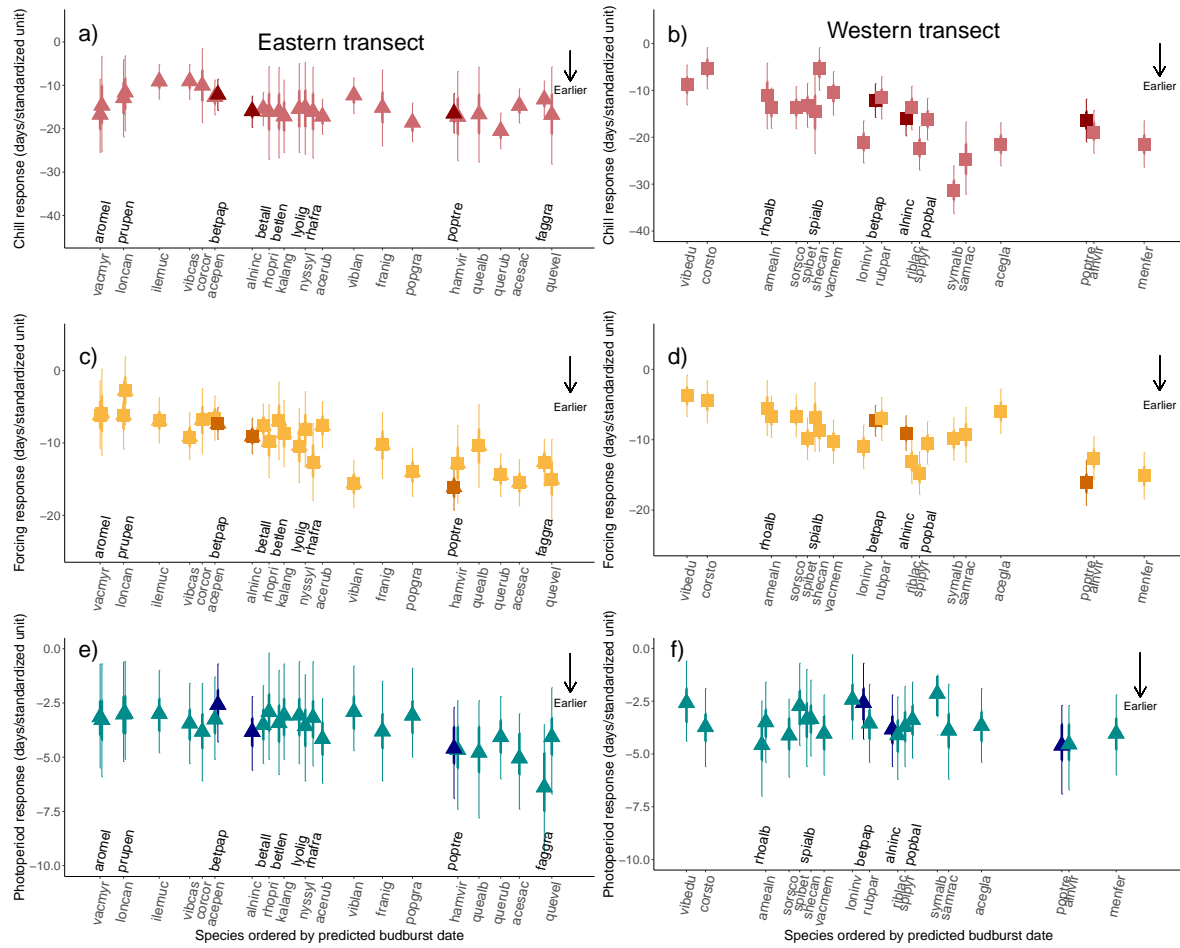


Figure 4: Estimated species chilling (a,b), forcing (c,d) and photoperiod (e,f) responses ranked by increasing estimated budburst dates for both the eastern (a, c, e) and western (b, d, f) populations. Cues are plotted on differing y-axis to better depict species differences. For each species, the thinner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

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

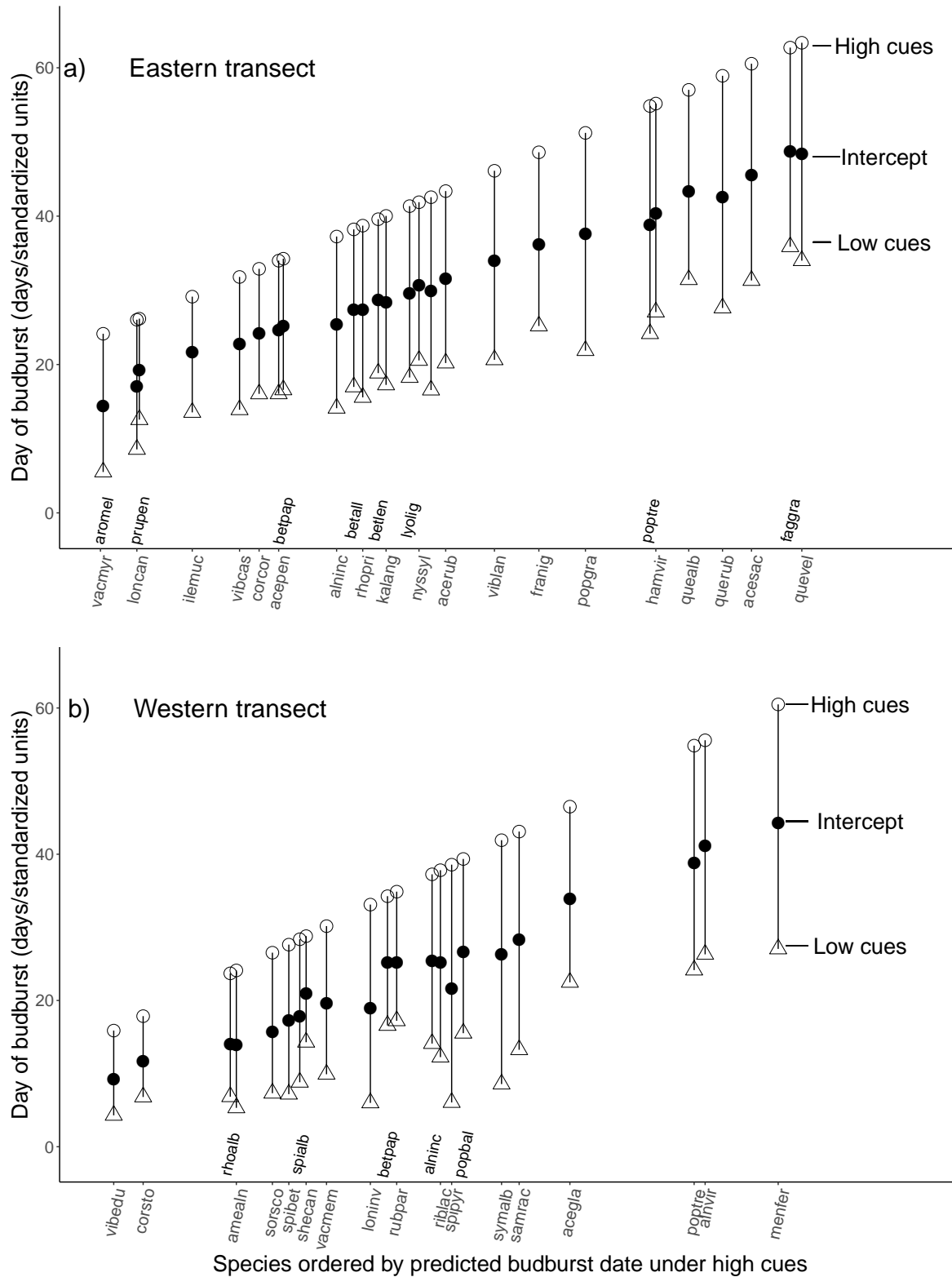


Figure 5: Comparisons of our estimated budburst based on the full model (intercept plus all cues), shown in white, versus the intercepts only (without cues), shown in black, ordered according to differences in species estimated budburst dates for both the eastern (a) and western (b) populations under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

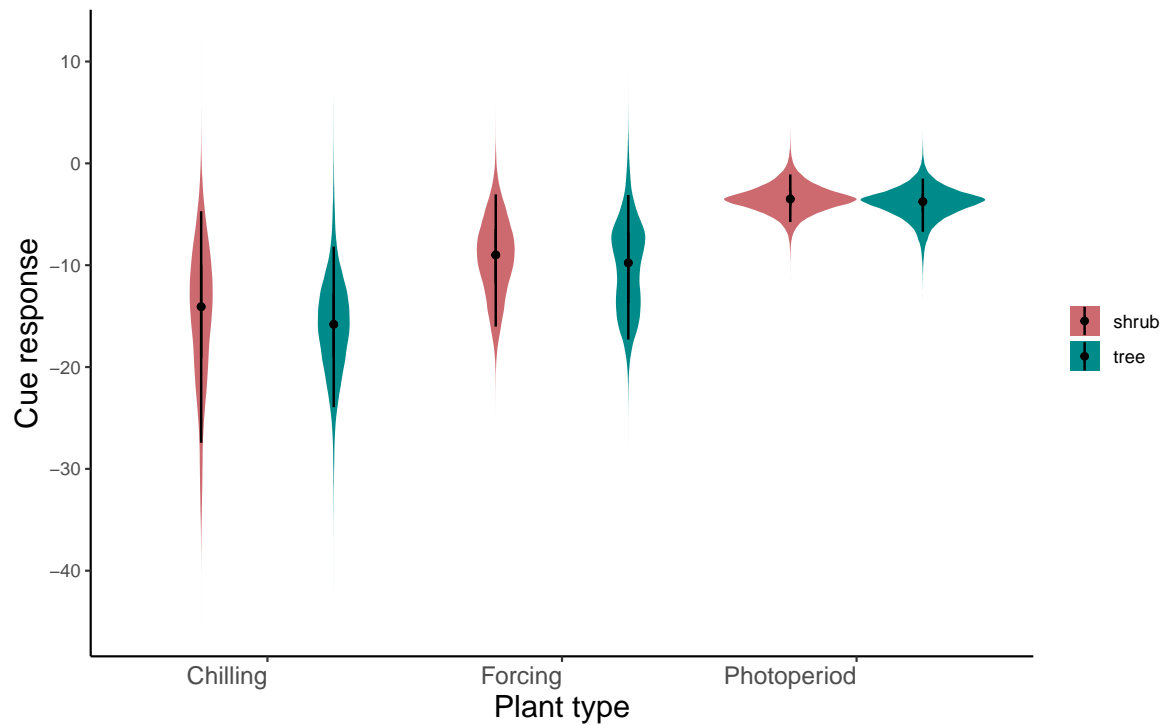


Figure 6: Comparisons of posterior distributions for cues estimates between shrub and tree species. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution is the the posterior density of the posteriors of the cue responses for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

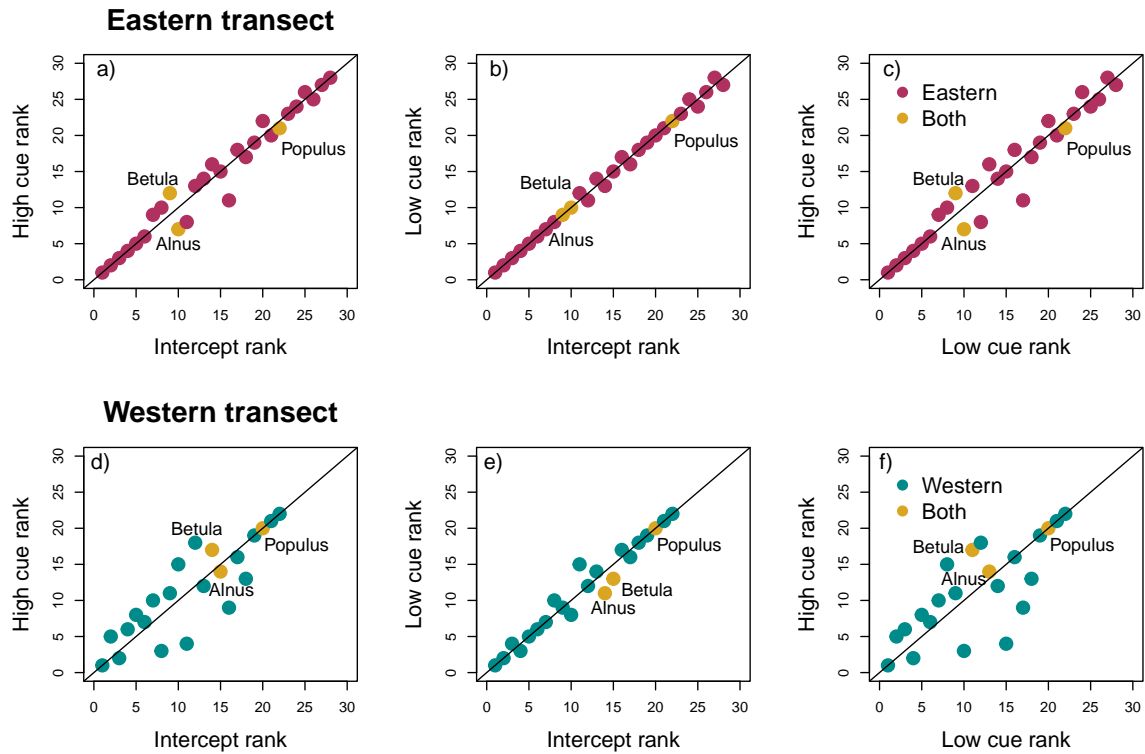


Figure 7: Estimated changes in species ranked budburst order, compared between species level effects (species intercept) and under high cue conditions (a and d), species level effects and under low cue condition (b and e), and ranked order under low and high cue conditions (c and f) for our eastern in 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.