Current environments and evolutionary history shape forest temporal assembly

Deirdre Loughnan[1] and E M Wolkovich[1]

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[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

Abstract

With climate change the timings of many species life history events—or phenologies—are advancing. But these advances are highly variable across space and species, making it challenging to manage shifts and forecast future responses. Across space, differences in the local environment (e.g., temperature and daylength) alongside local variation in populations can produce different phenologies. But there remains considerable unexplained species-level variation within communities—where single phenological event occurs over several weeks. Such variation allows species to partition their period of growth and occupy different temporal niches, while species differences can additionally be associated with divergent evolutionary history and phylogenetic conservatism. To understand these multiple drivers of variability, we examined community-level responses to environmental cues across 47 species from eastern and western North America respectively. We focused on woody plant budburst phenology, where the underlying cues—temperature and daylength—are well known and can be manipulated in controlled environments. Using a Bayesian phylogenetic mixed effects model, we found little variation across populations, but strong variation by species. Budburst advanced in response to temperature and daylength, with these cues explaining 38.6 to 60.6% of variation, with the remaining variation mostly ascribed to intrinsic differences in species traits that were strongly phylogenetically structured ($\lambda = 0.8$). These phylogenetic effects suggest an important role of additional—and unaccounted for—traits that determine woody plant budburst, and could improve predictions of future phenological shifts and their effects on community dynamics and ecosystem services.

Introduction

Climate change has led to an advances of about 3 days per decade in the timing of species life history events—phenology (Parmesan, 2007; Thackeray et al., 2016; Cohen et al., 2018). Different types of events and the rate of their responses to climate change, however, are highly variable. Events, such as leafout, can span a period of weeks and are shift 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 warm faster than others, generating larger phenological shifts in areas with warmer temperatures (Hoegh-Guldberg et al., 2018). Climate change alone, however, explains a limited amount of the

total variation. Recent research suggests that species-level differences in phenology drive some of this variation (Vitasse et al., 2009; Wolkovich and Cleland, 2014; Zohner and Renner, 2014; Vitasse et al., 2018). How species-level differences compare to other potential sources of variation, and what predicts them, is still largely unknown. But understanding the drivers of species-level variation is necessary to predict the effects changes in phenology will have on community dynamics and ecosystem services. As a well studied phenological event, spring budburst offers an excellent system to test for species- and community-level patterns in phenology and environmental cues. Budburst of temperate woody plants is known to respond to temperatures in both the winter and spring—referred to as chilling and forcing, respectively—as well as daylength, or photoperiod (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.

Here we present results from two growth chamber studies in which we used a Bayesian phylogenetic approach to detect general trends in budburst cues in North American deciduous forest communities and estimate the contribution of species evolutionary history to current variation in budburst. We collected samples of 47 woody plant species from four communities, in eastern and western North America, with pairs of communities on each coast spanning 4-6° latitude. Our dataset includes the diverse assemblages of tree and shrubs found in eastern and western deciduous forests, allowing us to explore differences across both communities and functional groups in eastern versus western forests. We expected communities to differ in species budburst cues, given the strong differences in the dominant forest composition between populations, reflecting differences in the forest architecture and resource availability.

Materials and Methods

Field sampling

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

We selected the dominant deciduous species in each forest community and maximized the number of species occurring across sites. We observed budburst for 47 species spanning eastern and western forest communities, with 28 species at our eastern transect and 22 species at our western transect, of which 3 species occurred at both regions (Table S2). 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

87   local weather stations to calculate the field chilling prior to collection (see Table S1).

Growth chamber study

89   Drawing on decades of work identifying the primary budburst cues from cutting experiments, we
90   tested the effects of chilling, forcing, and photoperiod cues. We used growth chambers with two levels
91   of chilling—with either no additional chilling or 30 days at 4°C for our eastern study, and 30 or 70
92   days of chilling at 4°C for our western study (all dark)—after which we moved plants to one of two
93   levels of forcing—with day and night temperatures that varied to create a cool regime of 15:5°C and
94   a warm regime of 20:10°C—crossed with two photoperiods of either 8 or 12 hours—for a total of 8
95   distinct treatments in each study.

97   Our design was similar for both eastern and western species, except for differences in the timing of
98   sample collection and thermoperiodicity—alternation in day and night temperatures—in forcing treat-
99   ments. By collecting samples in our eastern study in late January, they experienced considerable field
100 chilling. But we collected the western samples in late October, with most chilling occurring under con-
101 trolled conditions. In our eastern study, we also set the duration of forcing temperatures to correspond
102 with the photoperiod treatments. While this is a widespread and common approach in phenology
103 chamber studies, it leads to a confounding effect in the thermoperiodicity (Buonaiuto et al., 2023).
104 Thus we applied forcing temperatures for 12 hours independent of the duration of the photoperiod
105 treatments in our western study, and controlled for this difference in our statistical approach (see
106 below). We had seven to ten replicates per treatment in our eastern study and eight replicates in our
107 western study, with the exception of *Sorbus scopulina*, for which we we only had six replicates per
108 treatment. Further details regarding the re-cutting of samples, water changes, and rotation through
109 chambers are presented in Flynn and Wolkovich (2018). We controlled for differences in the number of
110 replicates across species in our statistical approach using partial pooling (see section on our statistical
111 analysis).

113 We assessed phenological stages of budburst using the BBCH scale, adapted for our specific species
114 (Finn et al., 2007). We also created photographic guides to help define each stage of the BBCH scale
115 for our specific species (?Loughnan and Wolkovich, 2024). Every 1-3 days, we observed each sample
116 and recorded all phenological stages up to full leaf expansion (defined as code 17 by Finn et al., 2007).
117 Here, we present the response in budburst date, defined as the day of budbreak or shoot elongation
118 (defined as code 07 by Finn et al., 2007). Our eastern study spanned 82 days, with over 19320 phe-
119 nological observations, while the western study spanned 113 days and 47844 phenological observations.

Statistical Analysis

122 We tested for differences in budburst cues across species and communities using a phylogenetic mixed
123 effects model with partial pooling ('shrinking') across species. This approach accounts for both the
124 evolutionary relatedness of our species, and estimates the species-level cues and differences across sites.
125 We obtained species phylogenetic relatedness by pruning the Smith and Brown (2018) megatree of an-
126 giosperms (Fig. S5).

128 In our model, we included each of our three cues as continuous variables. To account for the greater
129 amounts of field chilling experienced in our eastern study, we converted our chilling treatments to chill
130 portions for each individual community using local weather station data and the chillR package (Luedel-
131 ing, 2020). We calculated chill portions for both the chilling experienced in the field prior to sampling
132 and during the experiment in our 4°C chilling chambers. We also converted forcing temperatures to
133 mean daily temperatures in each treatment to account for differences in thermoperiodicity between
134 the two studies (Buonaiuto et al., 2023). Finally, we z-scored each cue and site using two standard

deviations to allow direct comparisons between results across parameters (Gelman, 2008). In addition to the overall predictors, we included all two-way interactions between cues and between cues and sites.

Our modelling approach allowed us to combine observations of budburst (y_i) across species (sp), to estimate both a species-level intercept (α_{sp_i}) and slope estimates for individual cues, sites, and all possible interactions between cues and between cues and sites (β) to estimate the day of budburst ($\hat{y}$) relative to the first day of forcing conditions.

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

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

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

$$
\beta_{force_{sp}} \sim \text{normal}(\mu_{force_{sp}}, \sigma_{force}^2)
$$
$$
\ldots
$$
$$
\beta_{photoperiod \times site4_{sp}} \sim \text{normal}(\mu_{photoperiod \times site4_{sp}}, \sigma_{photoperiod \times site4_{sp}}^2)
$$

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

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

$$\tag{2}$$

The timing of budburst ancestrally (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. (In review).

We used semi-informative priors for each of our model parameters, validating the model code using test data prior to analysis. Our model produced $\hat{R}$ values close to 1, well mixed chains, and n_{eff} values that exceeded 10% of the model iterations. Our model was fit using the Stan language (Stan Development Team, 2018) using the rstan package in R (R Development Core Team, 2017), version 3.3.6).

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

Results

On average, we observed species budburst 28.1 days (uncertainty interval: 45.0, 15.2, 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) after the start of forcing and photoperiod treatments. 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 the timing of the earliest and latest species spanned a period of 38.5 and 30.7 days for the eastern and western species respectively. Overall we found species budburst was strongly phylogenetically structured (λ of 0.8, UI: 0.9, 0.6, estimated on the intercept) 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 a subadditive effect where low chilling is offset by high forcing conditions, and vice versa (Fig. S1 and see Table 1 for model output).

Overall we found small population-level effects compared to differences between cues. Across all species, there was considerable overlap in the responses of the 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 and across transects (Fig. S1 a-c, shown for baseline conditions, see Table 1 for model output). Overall budburst dates did not differ between populations, though eastern populations budburst marginally earlier (34.1, UI: 40.7, 27.1) compared to the western populations (46.5, UI: 52.7, 39.4, see also Table 1 for model output). This could be due to the earlier collection date of our western species, which reduced the field chilling they received relative to our eastern samples.

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. 2). Despite our expectations that species responses should differ across the canopy layer, with shrubs being less sensitive to cues than trees, we did not find strong differences across these two functional groups (Fig. S2). Shrubs, like *Cornus stolonifera*, showed weak responses to chilling and forcing. But 36.7% of the shrubs, including *Menziesia ferruginea* and *Symphoricarpos alba*, exhibited the opposite response and budburst relatively late (Fig. S2). Similarly for trees, some matched our predictions for their cues, but 23.5% budburst earlier than expected. Specific tree species, such as *Quercus velutina*, did have stronger chilling and photoperiod responses as predicted, and *Fagus grandifolia* produced the strongest photoperiod response. But overall we did not find clear differences between the cues of trees and shrubs across the four forest communities.

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

In comparing the earliest and latest budbursting species, we found relatively small differences in cues (Fig. 2). This is contrary to our prediction of stronger cue requirements—especially chilling cues—for later budbursting species. For example, an early budbursting shrub, *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 trees, *Quercus alba*. Yet the 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 cues (intercept values, see Fig. 3). 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—which was strongly phylogenetically structured—explaining the rest (Fig. 3).

Discussion

In our study, species temporal niches were partly explained by differences in environmental cues, but varied very little across communities or functional groups. While the timing of budburst generally advanced in response to each cue, the greatest responses were to chilling and forcing respectively. We found no evidence of community-level differences in budburst cues, as responses were similar across our communities despite their inherent differences in environments and photoperiod. There was, however, considerable variation in the importance of cues across species, driven by their evolutionary history. Budburst phenology had a strong phylogenetic structure, with both species evolutionary history and cues contributing almost equally to the phenological variation we observed. These findings highlight the need to account for evolutionary history in addition to current environmental cues to accurately forecast phenological responses under continued warming.

Despite differences in the composition of our communities and local environments, under controlled conditions, communities differed only slightly in their phenological cues. This contrasts our the hypothesis that local habitats—due in part to latitudinal trends in photoperiod and temperature—impose unique selective pressures, and thus may drive community-level differences in responses to cues (Keller et al., 2011). Latitudinal gradients in spring phenological shifts have been found by studies using *in situ* phenological data (Post et al., 2018; Alecrim et al., 2023). But, this work is based on long-term observations in the field, with confounding differences in study duration and start dates, variable methodologies, and geographic extent (Post et al., 2018; Alecrim et al., 2023). The lack of community-level effects that we observed suggests budburst is not shaped strongly by local adaptation, at least at our study scale.

0.1   Community composition and interspecific variation in phenology

Our species varied in their responses to environmental cues, creating large potential differences in their temporal niches 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 suggests 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 comparatively weak responses to photoperiod, trends consistent with previous studies. Cues, however, had complex interactions that appear potentially advantageous under warming climates (Heide, 1993; Caffarra and Donnelly, 2011; Flynn and Wolkovich, 2018). The interaction between chilling and forcing ensures species can budburst if warmer winters cause insufficient chilling, but will require additional forcing. Despite differences in species responses to cues, we did not find the clear, generalizable trends across functional groups.

Shrubs and trees differ greatly in their physiology, filling different ecological niche space. Most of our trees budburst later than the shrubs, a relative order also found by previous studies (Gill et al., 1998; Panchen et al., 2014). About a quarter of the trees also budburst early, with timing more similar to that of shrubs. Similarly, we found a third of shrubs to budburst at similar times as the majority of our trees. These deviations from our expectations for how shrubs and trees partition their budburst timing suggests there is more nuance to these patterns than previously found. As trees species ad-

vance phenologically—resulting in earlier canopy closure and reduced light availability (Donnelly and Yu, 2019)—shrubs with weak cues may have reduced fitness. But as 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 dynamics.

The number of shrubs and trees 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 trees have selected for earlier budburst as well.

0.2   Community assembly in responses to cues versus evolutionary history

Our ability to accurately forecast phenology is predicated on our understanding of environmental cues at the population, species, and community levels. In North America, spring is associated with high inter-annual variability, with forest communities experiencing a breadth of environmental conditions in a given year (Schwartz and Reiter, 2000; Zohner et al., 2017). It may, thus, be advantageous for species to have consistent cues to optimize budburst across years and space.

Variation in cues was negligible at the community-level, but we did find important differences between species (Fig. 3). 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 communities that are warming fastest and to a greater extent (Hoegh-Guldberg et al., 2018). Our results suggest that these greater rates of warming at species northern range limits will cause these communities to budburst earlier (Fig. 3), altering species interactions and creating unique selective pressures across the assemblages of species within a population. This may reshape species temporal niches and conflate the effects of warming temperatures with other selective pressures acting locally across species distributions.

Our findings also suggest the order of species budburst in a community will change with variable warming. Community dynamics are most likely to change in communities that experience greater warming. As species budburst order changes (Fig. S3), species that previously exhibited distinct temporal niches will increasingly interact. This may have cascading effects on species, changing their competitive landscape, and synchrony with pollinators or herbivores. But we cannot focus solely on cues to understand this temporal community assembly. Species phenotypes are the result of multiple interacting and complex environmental cues that act over evolutionary timescales (Ackerly, 2009).

Our study included the three cues—chilling, forcing and photoperiod—commonly thought to determine budburst timing, but about a third of total variation was not explained by these cues (Fig. 2), suggesting our model may be incomplete. Contrary to our expectations, this variation was not explained by differences in geography or population differences in cues. Our results, instead, point to a large effect of species evolutionary history on budburst timing.

The observed phylogenetic structure in budburst timing suggests unidentified latent traits are still missing from our understanding of budburst phenology (Webb et al., 2002; Davies et al., 2019). These latent traits could reflect missing environmental cues or additional traits that mitigate phenological cues. Species temporal niches could be similarly influenced by other physiological or structural traits. Theories of how plants vary in their growth strategies predict phenology could correlate with other key traits, including those that facilitate greater resource use and earlier spring growth, or the greater competitive abilities needed when budbursting later (Grime, 1977). Early successional species are

predicted to budburst early in the season and possess traits associated with faster growth rates and resource acquisition, like high specific leaf areas or low wood density (Wright et al., 2004; Chave et al., 2009). Incorporating phenology into a broader trait framework could thus provide insights into traits that correlate with budburst timing, and—ultimately—the drivers selecting for species phenotypes.

The evolutionary history and ancestral phenotypes 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 physiological 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 respond to their local temperatures (Lechowicz, 1984). These phylogenetic effects could skew species assemblages, favouring species with traits and cue requirements adapted for historical climates.

0.3 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 communities facilitate forecasting across similar regions with limited local phenological data but similar species assemblages. The high phylogenetic structure in budburst timing could enable us to forecast trends in phylogenetically related species for well resolved and well sampled genera (Molina-Venegas et al., 2018).

While our findings have broad applications to plant communities, our analytical approach is widely applicable to forecasting species responses to climate change. To this end, future efforts should invest in identifying latent traits contributing to the high phylogenetic structure of phenological events. Combining more species rich and 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, possibly helping to mitigate cascading effects across 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. 2023. 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.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366.

Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. Science 329:277–278.

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., J. Regetz, E. M. Wolkovich, and B. J. McGill. 2019. Phylogenetically weighted regression: A method for modelling non-stationarity on evolutionary trees. Global Ecology and Biogeography 28:275–285.

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.

Grime, J. P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. The American Naturalist 111:1169–1194.

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.

Keller, S. R., R. Y. Soolanayakanahally, R. D. Guy, S. N. Silim, M. S. Olson, and P. Tiffin. 2011. Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). American Journal of Botany 98:99–108.

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.

Loughnan, D., and E. M. Wolkovich. 2024. A photopgraphic guide to spring phenology for woody plants in Western North America. Knowledge Network for Biocomplexity (KNB) .

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. Jatczak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová, H. Scheifinger, M. Striz, A. Susnik, A. J. Van Vliet, F. E. Wielgolaski, S. Zach, and A. Zust. 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.

Morales-Castilla, I., T. J. Davies, G. Legault, D. M. Buonaiuto, C. J. Chamberlain, A. K. Ettinger, M. Garner, F. A. M. Jones, D. Loughnan, W. D. Pearse, D. S. Sodhi, and E. M. Wolkovich. In review. Phylogenetic estimates of species-level phenology improve ecological forecasting. Nature Climate Change .

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 203:1208–1219.

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.

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.

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. Pontailler, 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.

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.

Wolkovich, E. M., and E. E. Cleland. 2014. Phenological niches and the future of invaded ecosystems with climate change. AoB PLANTS 6:1–16.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, Ü. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

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.

₄₆₃ # 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%	n_eff	Rhat
Intercept	12.51	3.14	7.40	17.60	3183.32	1.00
Phylogenetic effect	0.79	0.12	0.60	0.90	2156.20	1.00
Forcing	-9.55	0.74	-10.70	-8.30	1391.78	1.00
Photoperiod	-3.62	0.41	-4.30	-3.00	3089.29	1.00
Chilling	-15.21	1.25	-17.30	-13.20	2142.42	1.00
Manning Park	2.09	0.36	1.50	2.70	4061.13	1.00
Harvard Forest	-6.04	1.03	-7.80	-4.40	486.95	1.01
St. Hippolyte	-8.71	0.97	-10.30	-7.10	485.37	1.01
Forcing x photoperiod	0.23	0.71	-1.00	1.40	3698.87	1.00
Forcing x chilling	9.06	0.90	7.60	10.50	3005.09	1.00
Photoperiod x chilling	-0.67	0.90	-2.20	0.80	2690.36	1.00
Forcing x Manning Park	-1.76	0.77	-3.00	-0.50	3836.43	1.00
Photoperiod x Manning Park	0.58	0.79	-0.70	1.90	3375.92	1.00
Chilling x Manning Park	-0.36	1.60	-3.00	2.20	1714.08	1.00
Forcing x Harvard Forest	3.81	1.22	1.80	5.80	1752.75	1.00
Photoperiod x Harvard Forest	-1.96	0.86	-3.30	-0.60	2877.96	1.00
Chilling x Harvard Forest	9.97	2.03	6.60	13.40	911.46	1.01
Forcing x St. Hippolyte	5.25	1.19	3.20	7.20	1659.45	1.00
Photoperiod x St. Hippolyte	-2.13	0.84	-3.50	-0.70	2606.20	1.00
Chilling x St. Hippolyte	8.65	1.70	5.90	11.50	1021.36	1.01
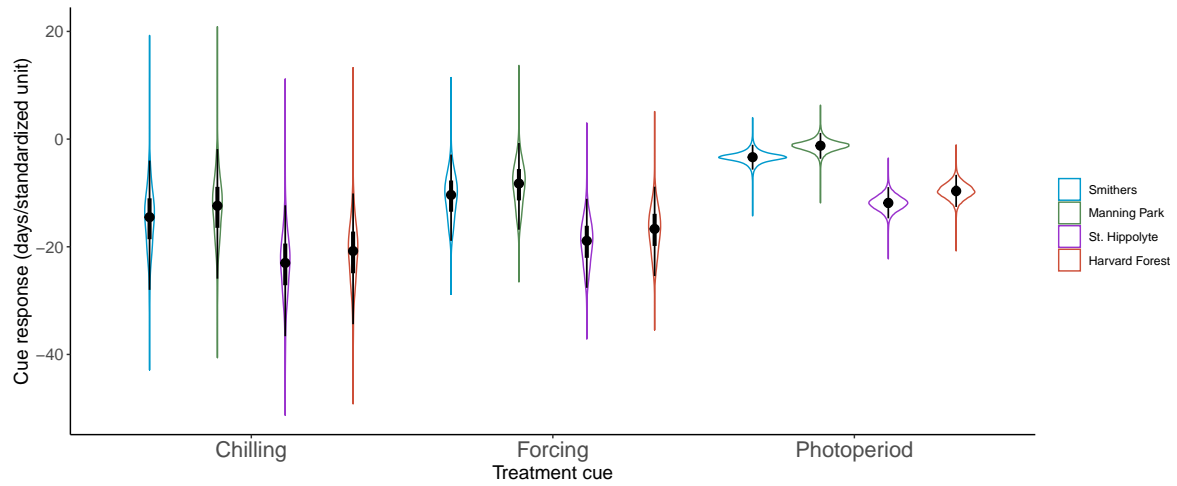
Figure 1: Posterior distributions of estimated chilling, forcing, and photoperiod responses with site level effects for individual communities. Black circles represent the median cue, thicker black lines the 50% uncertainty interval, while the thinner black line the 90% uncertainty interval. The y-axis spans the entire range of the data. We standardized predictors (cues) via z-scores using two standard deviations, see methods for further details.
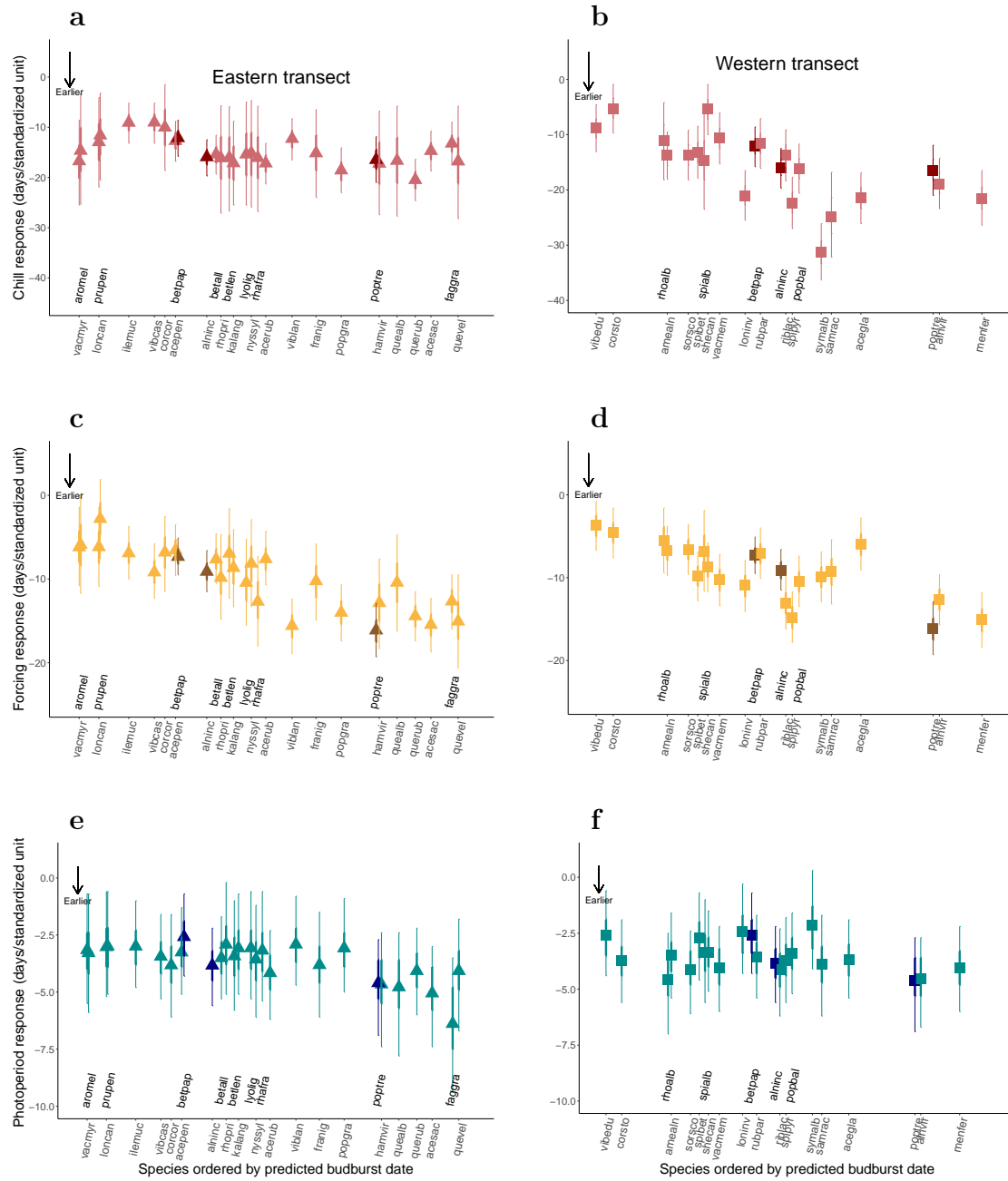
Figure 2: Estimated species **a,b**, chilling, **c,d** forcing, **e,f** and photoperiod responses ranked by increasing estimated budburst dates for both the **a,c,e**, eastern **b,d,f** and western populations. Cues are plotted on differing y-axis to better depict species differences. For each species, 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. To make the results across cues directly comparable, we standardized predictors (here, cues) via z-scores using two standard deviations, see methods for further details.
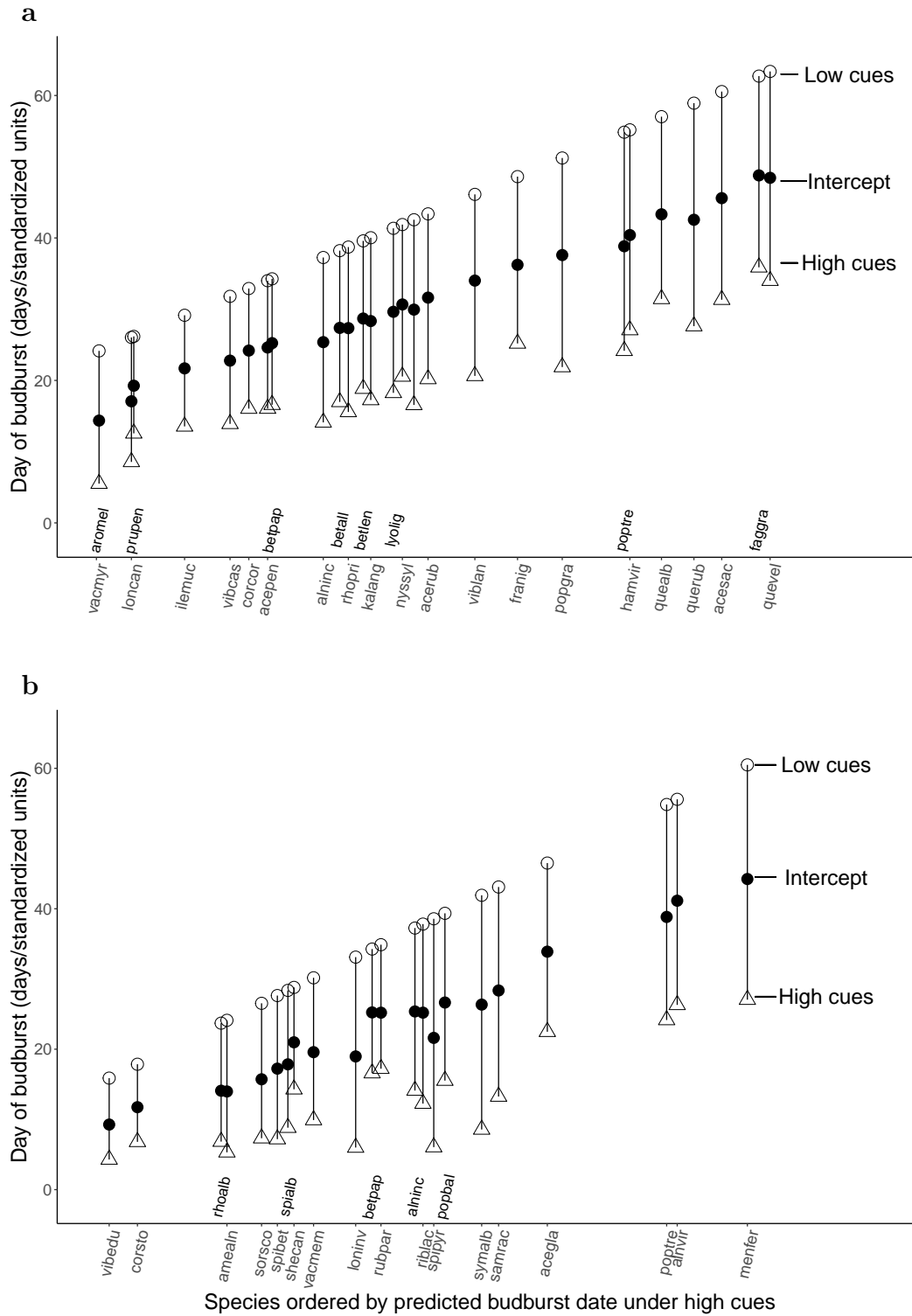
Figure 3: Comparisons of our estimated budburst based on the full model (intercept plus all cues), shown in white, versus the intercepts only (without cues), shown in black, ordered according to differences in species estimated budburst dates for both the **a**, eastern **b**, and western populations under low cue conditions, depicted as circles, and high cue conditions, depicted as triangles.