Temporal assembly of woody plant communities shaped equally by evolutionary history as by current environments

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Abstract

With climate change the timings of many 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-adaptation by populations can produce different phenologies. This however, does not explain the considerable species-level variation observed within communities—where the same phenological event often occurs over several weeks or more. Such variation suggests species may partition their period of growth to occupy different temporal niches, but species differences can additionally be caused by their evolutionary history (phylogeny). To understand these multiple drivers of variability, we examined community-level responses to environmental cues across 47 species from four populations across eastern and western North America. We focused on budburst phenology of woody plants, 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 only 38.6 to 60.6% of variation, with the remaining variation mostly ascribed to intrinsic differences in species 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 is altering the timing of species life history events—phenology—with average advances of about 3 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 warm 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. Substantial variation appears to be related to species-level differences in phenology (Vitasse et al., 2009; Wolkovich and Cleland, 2014; Zohner and Renner, 2014; Vitasse et al., 2018), but how their relative effects compare to other potential sources of variation, like population-level variation, is still largely unknown. Understanding the role and scale of species-level variation, however, is necessary to predict future changes in phenology, and its effects on community dynamics and ecosystem services, including 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 thus, the competition they experience (Chesson and Huntly, 1997; Albrecht and Gotelli, 2001). For example, in forest communities, understory species often budburst earlier than canopy trees, when light and soil nutrients are most available (Mahall and Bormann, 1978; Muller, 1978). This niche partitioning allows species to differ in their temporal resource use as environmental conditions change across the growing season, ultimately filling different temporal niches (Gotelli and Graves, 1996).

While in theory temporal niche differences should allow more species to coexist in a community, there is considerable evidence that species phenologies further depend on population differences. Phenology can be highly variable across populations to select for locally optimum trait phenotypes (De Villemereuil et al., 2020). This has been shown across many ecosystems, including for bird breeding phenology in montane meadows in Sierra Nevada, which differs by 12 days across high and low elevation populations (Saracco et al., 2019). How much of this phenological variability is due to local adaptation or plasticity combined with interannual variation in climate, however, is unclear.

Populations differences in underlying cue systems are often used as evidence that phenological differences are shaped by local adaptation. Both animals and plants often respond to variation in temperature and photoperiod (Renner and Zohner, 2018; Bonamour et al., 2019), with expectations that responses may shift with latitude. Since both temperature and photoperiod vary across latitudinal gradients, populations may use different temperature thresholds and photoperiods, driving observed latitudinal gradients in phenology (Post et al., 2018; Alecrim et al., 2023).

To predict how communities will respond to continued climate change requires a holistic approach that accounts for these many drivers of phenological variability. For a given community, we must account for differences in temperature and photoperiod across species that shape their temporal niches. Species differences, however, may not be predicted perfectly by current temporal niches. Past climate variability over the long evolutionary timescales over which communities assembled could effect species-level variation today (Davies et al., 2013)—a potential effect that recent phylogenetic methods can help test. But this cannot be done in isolation of variation in populations due to plasticity, local adaptation, or both their effects. Conducting experiments in controlled environments can help remove the relative effects of interannual climate variability that drives plastic variation in phenology, allowing us to identify species primary cues and test for evidence that populations vary in these cues.

Spring budburst offers an excellent system to test for species- and population-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. Phenotypic differences between species—such as functional groups that represent varying growth and resource-use strategies—may further promote phenological differences and ultimately optimize species temporal niches within a community.

Here we present results from two growth chamber studies of woody species budburst cues. We used data from a total of four populations, from eastern to western North America, with pairs of populations on each coast spanning 4-6° latitude. We explored the differences in cues between western and eastern forest communities, and across populations. Sampling 47 woody plant species, our dataset includes a diverse assemblage of tree and shrubs. Given known differences in architecture and resource use between canopy and understory species, we expected shrubs to budburst earlier, with weaker overall cues. Finally, using a Bayesian phylogenetic approach allowed us to detect general trends in budburst cues in North American deciduous forest communities, while at once estimating the contribution of species evolutionary history to current variation in budburst.

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 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 (previously reported in Flynn and Wolkovich, 2018). 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 (not previously published).

We selected the dominant deciduous species in the forest communities at each population and maximized the number of species occurring across sites. We observed budburst for 47 species spanning our two transects, with 28 species at our eastern transect and 22 species at our western transect, with 3 species occurring at both transects. 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 S1).

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 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, and controlled for this difference in our statistical approach (see below). We had seven to ten replicates per treatment in our eastern study and eight replicates in our western study, with the exception of *Sorbus scopulina*, for which we we only had six replicates per treatment. Further details regarding the re-cutting of samples, water changes, and rotation through chambers are presented in Flynn and Wolkovich (2018). Our statistical approach uses partial pooling that controls for differences in the number of replicates across species.

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 (defined as code 07 by Finn et al., 2007). Our eastern study spanned 82 days, with over 19320 phenological observations, while the western study spanned 113 days and 47844 phenological observations.

Statistical Analysis

To test for differences in budburst cues across species and populations, we used a phylogenetic mixed effects model with partial pooling across species. This approach accounts for both the evolutionary relatedness of our species, and estimates the species level cues and differences across sites. We obtained species phylogenetic relatedness by pruning the Smith and Brown (2018) megatree of angiosperms (Fig S6).

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 between cues and between cues and sites (β) to estimate the day of budburst (y) relative to the first day of forcing conditions.

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

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

175 The intercept and slopes were modeled with partial pooling at the species-level:
176

$$\beta_{force_{sp}} \sim \text{normal}(\mu_{force_{sp}}, \sigma^2_{force})$$

$$\dots$$

$$\beta_{photoperiod \times site4} \sim \text{normal}(\mu_{photoperiod \times site4}, \sigma^2_{photoperiod \times site4})$$

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

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

$$\tag{2}$$

179 The timing of budburst prior to evolution is represented as root values of the means of the multivariate
180 normal distributions. For more detail on this method of phylogenetic modeling, see Morales-Castilla
181 et al. (In review).
182

183 We used semi-informative priors for each of our model parameters, validating the model code using
184 test data prior to analysis. Our model produced $\hat{R}$ values close to 1, well mixed chains, and n_{eff}
185 values that exceeded 10% of the model iterations. Our model was fit using the Stan language (Stan
186 Development Team, 2018) using the rstan package in R (R Development Core Team, 2017) (version
187 3.3.6).
188

189 We present model estimates, relative to baseline conditions of low chilling, low forcing, and short pho-
190 toperiod treatments, and—when relevant—for the Smithers population. We present results as means
191 and 90% posterior uncertainty intervals from our Bayesian phylogenetic models.
192

Results

194 On average, we observed species budburst 28.1 days (uncertainty interval: 45.0, 15.2) after the start
195 of forcing and photoperiod treatments (all estimates are given as mean ± 90% uncertainty intervals,
196 henceforth 'UI,' and budburst dates given as relative to baseline conditions, see methods for more
197 details). Some species, such as *Aronia melanocarpa*, budburst as early as day 13.6, and as late as day
198 52.1 for *Quercus velutina*. The difference in the timing of the earliest and latest species spanned a
199 period of 38.5 and 30.7 days for the eastern and western species respectively. Overall we found species
200 budburst was strongly phylogenetically structured (λ of 0.8, UI: 0.9, 0.6, estimated on the intercept)
201 and that all cues led to an advance in budburst date. Of the three cues, chilling had the strongest
202 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
203 strong, positive interaction between forcing and chilling (9.1, UI: 7.6, 10.5); this results in a subadditive
204 effect where low chilling is offset by high forcing conditions, and vice versa (Fig. S1 and see Table 1
205 for model output).
206

207 Overall we found small population-level effects compared to differences between cues. Across all species,
208 there was considerable overlap in the responses of the four populations to each cue (Fig. 1). As such,
209 low forcing, chilling, and shorter photoperiods all produced later estimated budburst dates compared
210 to higher temperature and longer photoperiod treatments across all populations and across transects

(Fig. S2a-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 tree species, we did not find strong differences across these two functional groups (Fig. S3). Shrubs, like *Cornus stolonifera*, showed weak responses to chilling and forcing. But 36.7% of the shrub species, including *Menziesia ferruginea* and *Symphoricarpos alba*, exhibited the opposite response and budburst relatively late (Fig. S3). Similarly for tree species, 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 small compared to 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 S4). 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. S4).

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 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 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 populations or functional groups. While the timing of budburst generally advanced in response to each cue, we found the greatest responses to chilling and forcing respectively. There was no evidence, however, of local adaptation in budburst cues, as we found similar responses across our populations despite their inherent differences in environments and photoperiod. There was, however, considerable variation in the importance of cues across species, not driven by functional differences, but rather their evolutionary history. We found budburst phenology to have a strong phylogenetic structure, with species evolutionary history 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 populations 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 population-level differences in responses to cues (Keller et al., 2011). Greater shifts in phenology across latitudinal gradients have been found by studies using *in situ* phenological data (Post et al., 2018; Alecrim et al., 2023). However, 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 population-level effects that we observed suggests budburst is not shaped strongly by local adaptation, at least at our study scale.

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 that 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, which is 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). For example, the interaction between chilling and forcing ensures species can budburst if warmer winters cause insufficient chilling, but will require additional forcing. Despite these strong differences in species responses to chilling, forcing, and photoperiod, 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 consistent variation in budburst phenology. Most of our tree species budburst later than our shrub species, a relative order also found by previous studies (Gill et al., 1998; Panchen et al., 2014). About a quarter of our tree species also budburst early, with timing more similar to that of shrubs. Similarly, we found a third of shrub species to budburst at similar times as the majority of our trees. These deviations 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 cues may 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 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.

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 conditions show 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.

Population-level 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 populations that are warming faster and to a greater extent than others (Hoegh-Guldberg et al., 2018). Our results suggest that these greater rates of warming at species northern range limits will cause these populations 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 niche 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 populations that experience greater warming. As species budburst order changes (Fig S4), 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 to 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 we observed 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). For example, 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 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.

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 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.

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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%	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
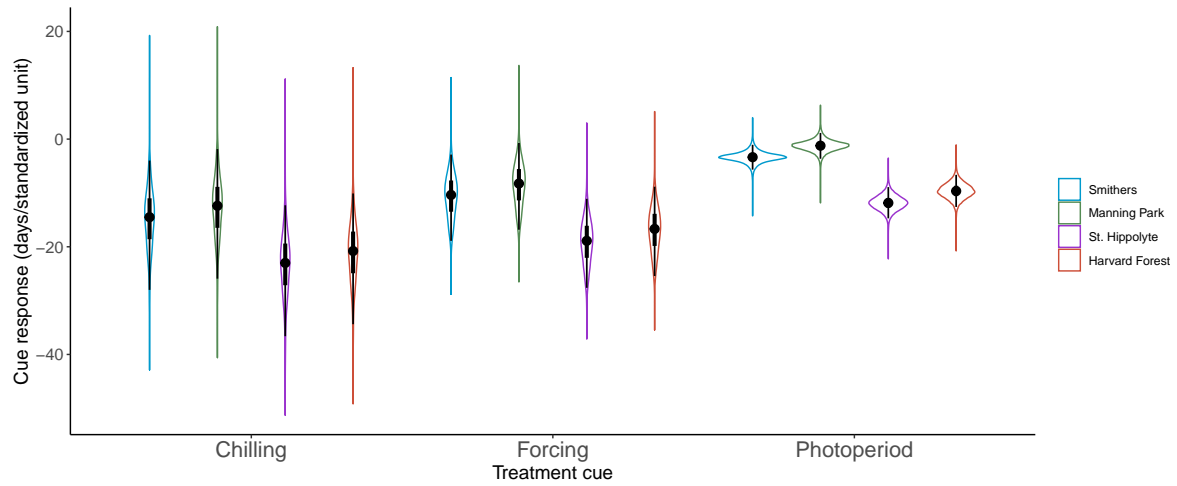
Figure 1: Posterior distributions of estimated chilling, forcing, and photoperiod responses with site level effects for individual populations. Black circles represent the median cue, thicker black lines the 50% uncertainty interval, while the thinner black line the 90% uncertainty interval. The y-axis spans the entire range of the data. We standardized predictors (cues) via z-scores using two standard deviations, see methods for further details.
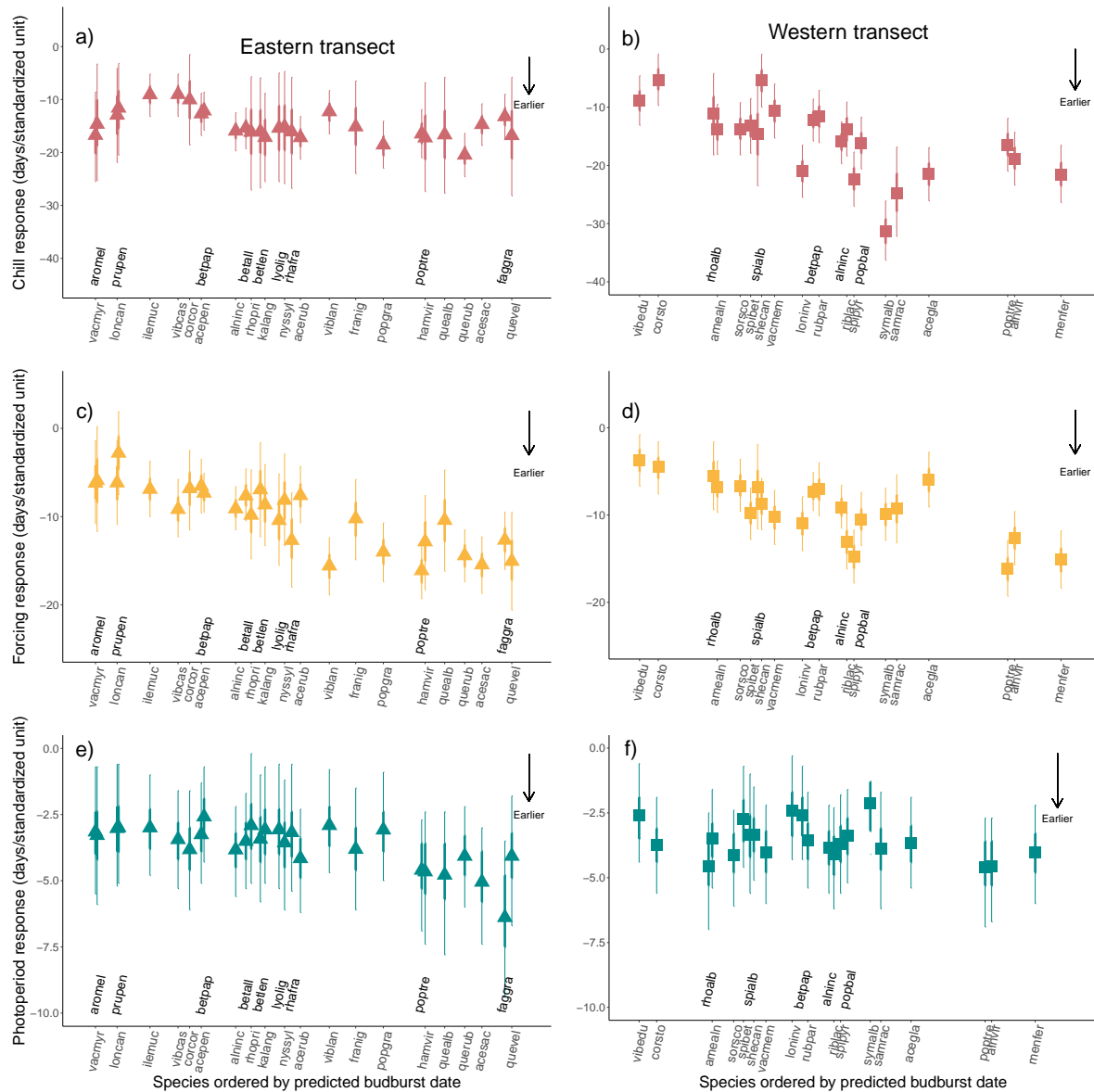
Figure 2: Estimated species chilling (a,b), forcing (c,d) and photoperiod (e,f) responses ranked by increasing estimated budburst dates for both the eastern (a, c, e) and western (b, d, f) populations. Cues are plotted on differing y-axis to better depict species differences. For each species, the thinner 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. 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.
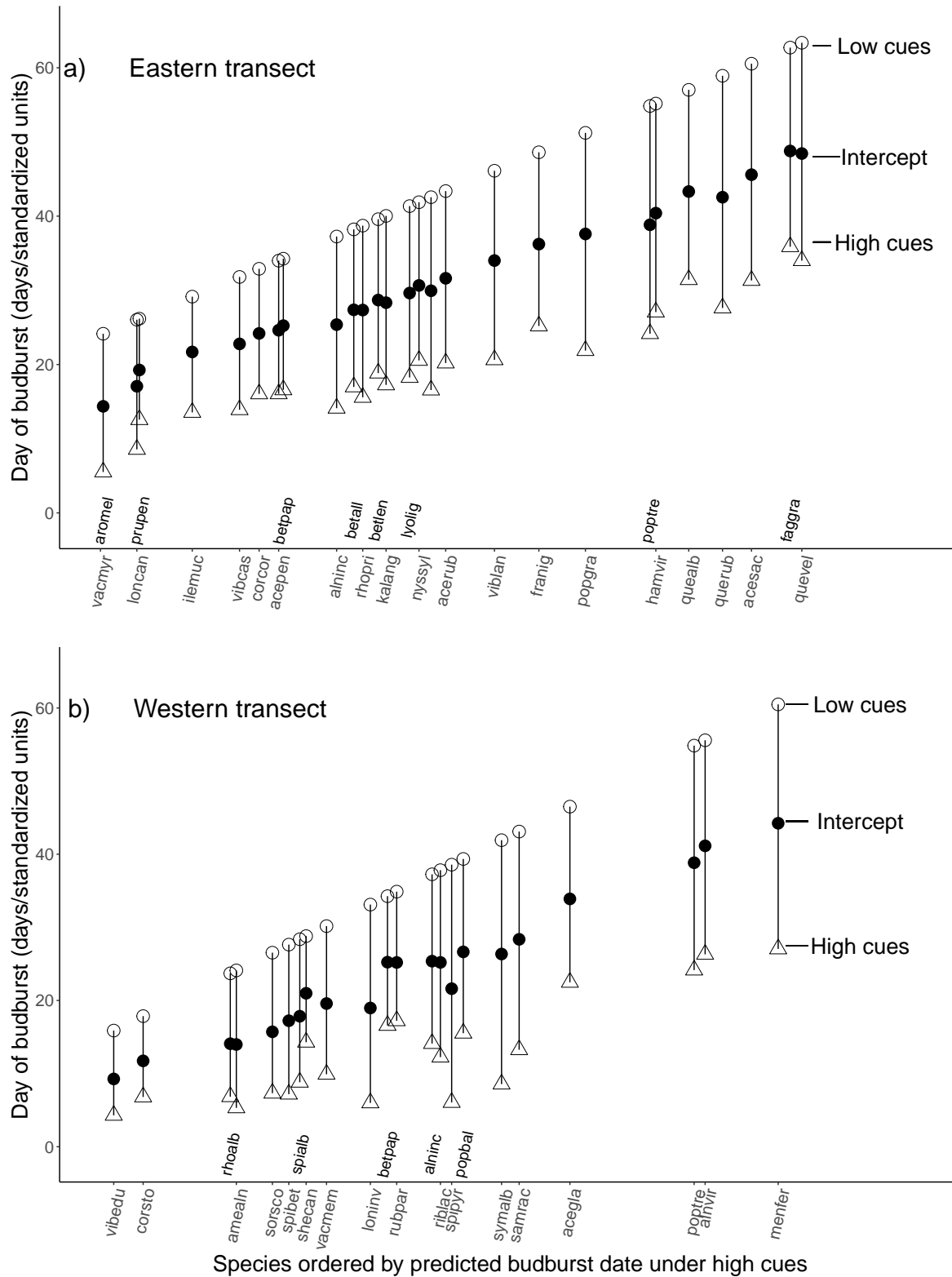
Figure 3: Comparisons of our estimated budburst based on the full model (intercept plus all cues), shown in white, versus the intercepts only (without cues), shown in black, ordered according to differences in species estimated budburst dates for both the eastern (a) and western (b) populations under high cue conditions, depicted as circles, and low cue conditions, depicted as triangles.