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 growth chambers. 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, but these cues explained only 38.6 to 60.6% of variation, with the remaining variation 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

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et al., 2018). Climate change alone, however, explains a limited amount of the total variation. Substantial variation instead appears 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 ultimately, 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 (CITATIONS). For example, in forest communities, understory species often budburst earlier than canopy trees, when light and soil nutrients are most available (CITATIONS). 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.

Identifying if phenological differences across populations is due to local adaptation requires evidence that populations have differing underlying cue systems. 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 the 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. 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 temperature cues 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 four populations, from eastern to western North America, with pairs of populations on each coast spanning 4-6° latitude each. 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 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 (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 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. 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 2).

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.,

137 2023). Thus we applied forcing temperatures for 12 hours independent of the duration of the pho-
138 toperiod treatments in our western study, and controlled for this difference in our statistical approach
139 (see below). We had seven to ten replicates per treatment in our eastern study and eight replicates in
140 our western study, with the exception of *Sorbus scopulina*, for which we we only had six replicates per
141 treatment. Further details regarding the re-cutting of samples, water changes, and rotation through
142 chambers are presented in Flynn and Wolkovich (2018).

143

144 We assessed phenological stages of budburst using the BBCH scale, adapted for our specific species
145 (Finn et al., 2007). Every 1-3 days, we observed each sample and recorded all phenological stages up to
146 full leaf expansion (defined as code 17 by Finn et al., 2007). Here, we present the response in budburst
147 date, defined as the day of budbreak or shoot elongation (defined as code 07 by Finn et al., 2007). Our
148 eastern study spanned 82 days, with over 19320 phenological observations, while the western study
149 spanned 113 days and 47844 phenological observations.

150

Statistical Analysis

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

156

157 In our model, we included each of our three cues as continuous variables. To account for the greater
158 amounts of field chilling experienced in our eastern study, we converted our chilling treatments to chill
159 portions for each individual population using local weather station data and the chillR package (Luedel-
160 ing, 2020). We calculated chill portions for both the chilling experienced in the field prior to sampling
161 and during the experiment in our 4°C chilling chambers. We also converted forcing temperatures to
162 mean daily temperatures in each treatment to account for differences in thermoperiodicity between
163 the two studies (Buonaiuto et al., 2023). Finally, we z-scored each cue and site using two standard
164 deviations to allow direct comparisons between results across parameters (Gelman, 2008). In addition
165 to the overall predictors, we included all two-way interactions between cues and between cues and sites.

166

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

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

171

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

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

173

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

$$\dots$$

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

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

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

$$\tag{2}$$

The timing of budburst 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 fitted 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 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: 45.0, 15.2) after the start of 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 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) 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. 2 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 (Fig. 3 a-c, shown for baseline conditions) and across transects (Fig. 3, 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. 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*, 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. 6). 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 of 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 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 the western community experiencing a large change in rank with cues (Fig. 7).

In comparing the 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 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. 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 the assembly of species temporal niche was partly explained by species differences in environmental cues, with little variation explained by differences between populations. Despite our forest populations differing in their species assemblages, and ratio of shrub to tree species, they had similar phenological cues and timing. But in comparing species within communities, we found phenologies to span several weeks. For temperate woody plants, the strongest environmental responses were to temperature cues. Our findings support that species phenology is largely shaped by temperature and, to a lesser extent, light. Despite the importance of environmental cues, we also found phenology to have a strong phylogenetic structure. Species evolutionary history contributed almost equally to the phenological variation we observed. We must consider ancestral traits and conditions in addition to current environmental cues if we are 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 impose unique selective pressures, driving differences in cues responses

259 (ADDCITES). We expected differences in population latitude to cause variation in phenology, as
260 latitude correlates with reduced photoperiod and temperatures. Greater shifts in phenology across
261 latitudinal gradients have been found by studies using *in situ* phenological data (Post et al., 2018; Ale-
262 crim et al., 2023). However, this work is based on long-term observations in the field, with confounding
263 differences in study duration and start dates, and use variable methodologies and geographic extent
264 (Post et al., 2018; Alecrim et al., 2023). The lack of population-level effects that we observed suggests
265 budburst is not shaped strongly by current geography or local adaptation, at least at our continental
266 scale.

Community composition and interspecific variation in phenology

268 Our species varied in their responses to environmental cues, creating large potential differences in their
269 temporal niche and ecological roles. Species ranged from early to late budburst dates and spanned a
270 similar period as observed in natural communities (Lechowicz, 1984; Richardson, A.D., O'Keefe, 2009).
271 This suggests that our experiment captured a realistic breadth in temperate forest budburst phenol-
272 ogy. Furthermore, all our focal species responded to each environmental cue, with strong responses
273 to chilling and weak responses to photoperiod, which is consistent with previous studies. Cues, how-
274 ever, had complex interactions that appear potentially advantageous under warming climates (Heide,
275 1993; Caffarra and Donnelly, 2011; Flynn and Wolkovich, 2018). For example, the interaction between
276 chilling and forcing ensures species still budburst if warmer winters cause insufficient chilling, but will
277 require additional forcing when chilling is low. Despite these strong differences in species overall cue
278 responses, we did not find the clear, generalizable trends across species with similar growth strategies.

280 Shrub and tree species differ greatly in their physiology, filling different ecological niche space. But
281 we found little overall variation in cue responses. Most of our tree species budburst later than our
282 shrub species, a relative order also found by previous studies (Gill et al., 1998; Panchen et al., 2014).
283 About a quarter of our tree species also budburst early, with timing more similar to that of shrubs.
284 Similarly, we found a third of shrub species to budburst at similar times as the majority of our trees.
285 This deviation from our expectations for how shrub and tree species partition their budburst tim-
286 ing suggests there is more nuance to these patterns than previously found. As trees species advance
287 phenologically—resulting in earlier canopy closure and reduced light availability (Donnelly and Yu,
288 2019)—shrub species with weak cue responses may have reduced fitness. But our finding suggests
289 many shrubs will also advance phenologically and have the potential to maintain their relative tempo-
290 ral niche and mitigate potential effects on community dynamics.

292 The number of shrub and tree species exhibiting later than expected budburst phenologies suggests the
293 cues we think are important for budburst could also be important for other traits. Earlier budbursting
294 species may exhibit a suite of traits that infers a greater ability to capture light and photosynthesize
295 prior to canopy closure or improve nutrient uptake later in the season. While we associate these traits
296 with shrubs that dominate the forest understory, it is possible that temporal niche partitioning among
297 tree species have selected for earlier budburst in some tree species as well.

Community assembly in responses to cues versus evolutionary history

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

Population-level variation in cue responses was negligible at the community-level, but we did find important differences between species (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). These greater rates of warming at species more northern range limits will cause these populations to budburst earlier, altering species interactions and creating unique selective pressures across the assemblages of species within a population. This has the potential to reshape species temporal niche and conflate the effects of warming temperatures with other selective pressures acting locally 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—chilling, forcing and photoperiod—most 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 underlie the observed phylogenetic structure. These latent traits could reflect missed environmental cues or additional traits that mitigate phenological responses to cues. Species temporal niche could be similarly influenced by other physiological or structural traits. Theories of how plants vary in their growth strategies predicts phenology to 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, we might predict earlier budbursting shrub species to possess photosynthetic machinery that allows them to better use the light available prior to canopy closure in early spring. Currently, we do not understand the mechanisms that underlie these trait relationships, but incorporating phenology into a broader trait framework could provide insights into the drivers selecting for species phenotypes and forecasting abilities.

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

356 structure in budburst timing could enable us to forecast trends in phylogenetically related species for
357 well resolved and well sampled genera (Molina-Venegas et al., 2018).
358
359 Our findings have broad applications to plant communities, while our analytical approach is widely
360 applicable to forecasting species responses to climate change. To this end, future efforts should in-
361 vest in identifying latent traits contributing to the high phylogenetic structure of phenological events.
362 Combining community wide approaches with phylogenetic relationships, such as we have done, allow
363 us to combine the effects of species evolutionary history with current ecological processes. This holistic
364 approach will enable us to predict changes in spring phenology and mitigate cascading effects across
365 communities and ecosystem services.
366

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500 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
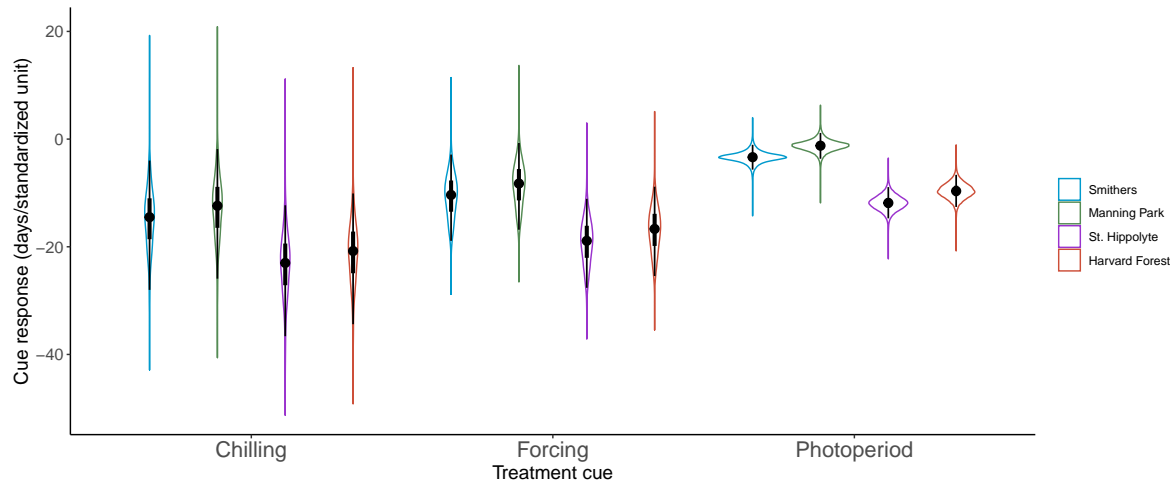
Figure 1: Posterior distributions of estimated chilling, forcing, and photoperiod responses with site level effects for individual populations. Black circles represent the median cue response, thicker black lines the 50% uncertainty interval, while the thinner black line the 90% uncertainty interval. The y-axis spans the entire range of the data. We standardized predictors (cues) via z-scores using two standard deviations, see methods for further details.
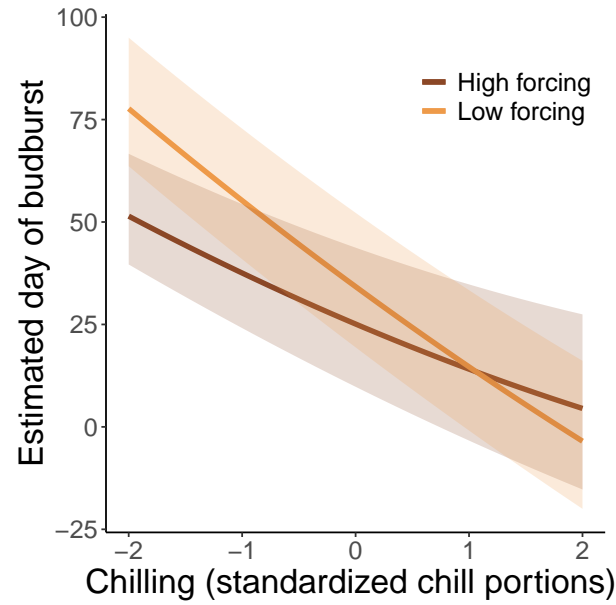
Figure 2: Estimated day of budburst of first bud in response to chill portions and forcing, estimated for our defined baseline conditions. We found a positive interaction between chilling and forcing cues, with high forcing compensating for low chilling to produce earlier budburst, while budburst occurred earlier under low forcing following high chilling. In our analysis, we standardized predictors, (here specifically chilling) via z-scores, using two standard deviations, see methods for further details.
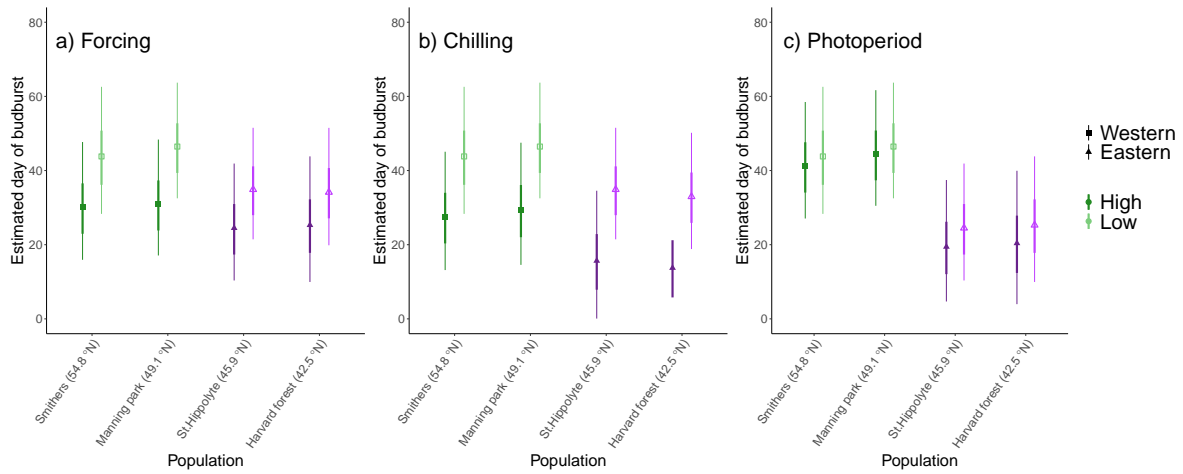
Figure 3: Estimated day of budburst of first bud in response to (a) forcing across populations under low chilling conditions and short photoperiods, (b) chilling across populations under low forcing and short photoperiods, and (c) across photoperiods under our baseline forcing and chilling conditions 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.
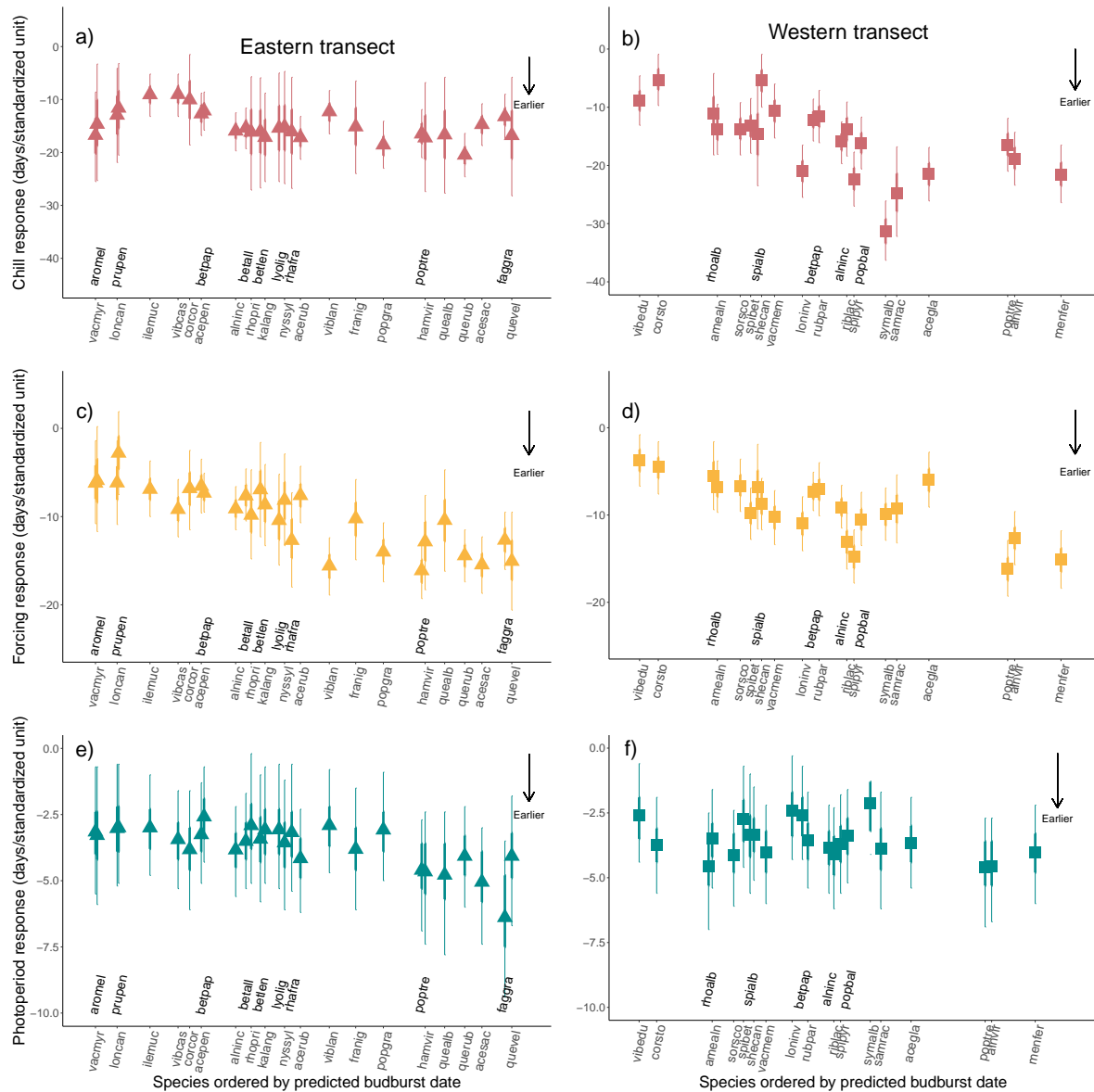
Figure 4: Estimated species chilling (a,b), forcing (c,d) and photoperiod (e,f) responses ranked by increasing estimated budburst dates for both the eastern (a, c, e) and western (b, d, f) populations. Cues are plotted on differing y-axis to better depict species differences. For each species, the thinner 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. 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.

Table 2: Approximate chill units from our two western sites, E.C. Manning Park and Smithers B.C., Canada, and our two eastern sites, Harvard Forest, USA and St. Hippolyte, Canada. Weather data was obtained from the Hope Slide weather station for our E.C. Manning Park estimates and the Smithers airport weather station for our Smithers communities. For our eastern communities, weather data was obtained from weather stations at Harvard Forest and in St. Hippolyte

| 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. Hippoltye	Field chilling	682	599.50	44.63
St. Hippoltye	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
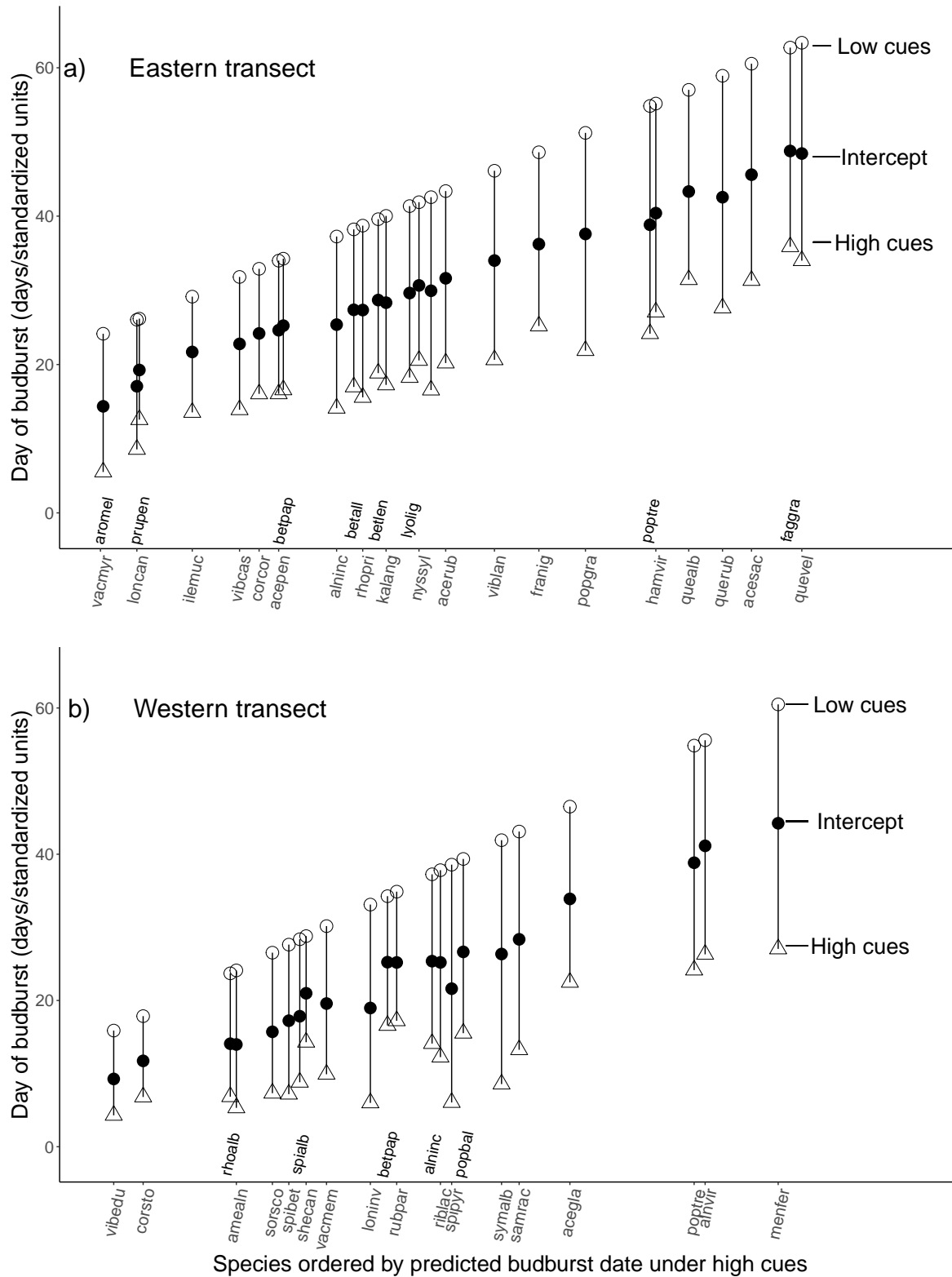
Figure 5: Comparisons of our estimated budburst based on the full model (intercept plus all cues), shown in white, versus the intercepts only (without cues), shown in black, ordered according to differences in species estimated budburst dates for both the eastern (a) and western (b) populations under high cue conditions, depicted as circles, and low cue conditions, depicted as triangles.
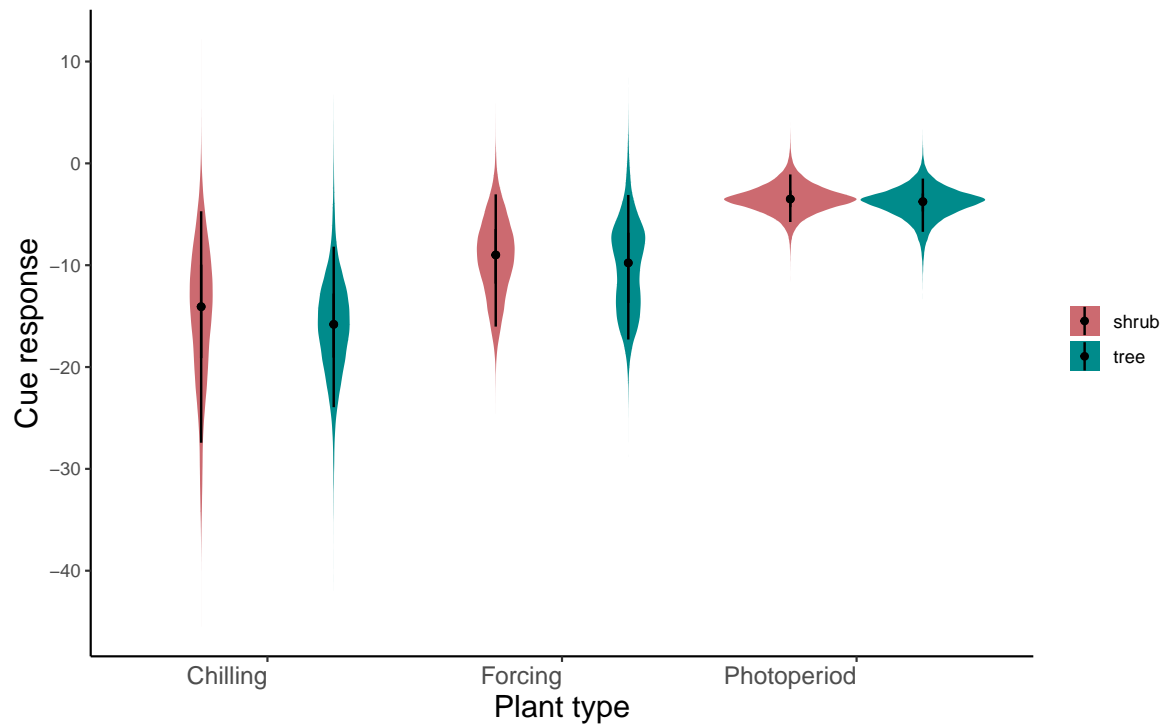
Figure 6: Comparisons of posterior distributions for cues estimates between shrub and tree species. Black circles represent the median cue response, while the thinner black line the 90% quantile interval. The coloured distribution is the the posterior density of the posteriors of the cue responses for all species within a given architectural type. The y-axis spans the entire range of the data.

Eastern transect
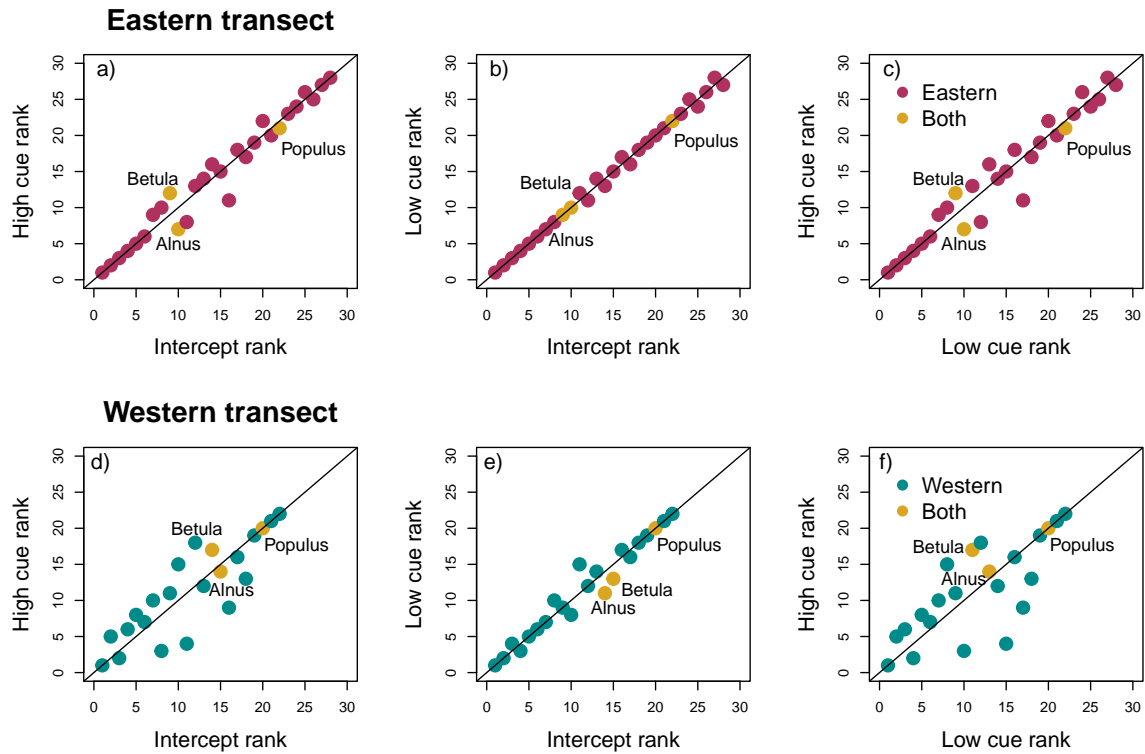
Western transect

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.