Temperature and photoperiod drive spring phenology across all species in a temperate forest community

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Abstract

Accurate predictions of spring plant phenology with climate change are critical for robust projections of growing seasons, plant communities and a number of ecosystem services, including carbon storage. Progress towards prediction, however, has been slow because the major cues known to drive phenology—temperature (including intensity of winter chilling and spring forcing) and photoperiod—generally covary in nature and may interact, making accurate predictions of plant responses to climate change complex and non-linear. Alternatively, recent work suggests many species may be dominated by one cue, making predictions much simpler. Here, using results from manipulating all three cues across 28 woody species from two North American forests—we find that all species responded to all cues. Chilling exerting a strong effect, and responses to photoperiod and forcing temperature were correlated. Cues varied across species, leading to staggered leafout within each community and supporting the idea that phenology may be a critical aspect of species' temporal niches. Our results suggest that predicting the spring phenology of communities will be difficult, as all species we studied could have complex, non-linear responses to future warming.

Plant phenology—the timing of recurring life history events, such as leafout and flowering—is critical to the structure and function of ecosystems (Cleland et al., 2007). Spring plant phenology in particular drives local ecosystem properties, from the length of the growing season to energy balance between land and atmosphere, and scales up to impact global carbon cycles (Richardson et al., 2009).

Phenology is also one of the major biological indicators of climate change, with plant phenology shifting earlier across the globe 4-6 days/°C with warming (IPCC, 2014). While this average response is strikingly consistent when considered across diverse datasets (Wolkovich et al., 2012), it masks tremendous variation. Variation is extreme when examined across species (Wolkovich et al., 2014), but additional variation can be seen within species over space (Kramer et al., 2017; Vitasse et al., 2013) and time (Fu et al., 2015; Yu et al., 2010). Understanding this variation has been the goal of much recent work (Donnelly et al., 2017; Laube et al., 2015; Rutishauser et al., 2008; Zohner et al., 2017), with research focusing on two major linked aims: (1) identifying and quantifying the environmental cues that drive spring phenology (i.e., leafout and budburst), and (2) identifying what drives variation in cues between different species.

Decades of study on wild species spring phenology—mainly focused on temperate woody species—show that three major cues underlie budburst and leafout: warm spring temperatures (forcing), increasing daylength (photoperiod), and length and intensity of winter temperature (chilling). Across studies increasing temperatures in the spring appear to be a dominant factor that controls spring phenology, yet many of these studies have been observational—making it nearly impossible to tease out the co-varying effects of longer days and reduced cold temperatures, which generally reduce chilling (Chuine, 2000; Cook et al., 2012). In contrast, studies from controlled environments (e.g., growth chambers or greenhouses) have highlighted the additional importance of photoperiod and chilling (Caffarra et al., 2011; Falusi and Calamassi, 1996; Foley et al., 2009; Ghelardini et al., 2010; Heide, 1993), with longer days and increased chilling leading to more rapid leafout (Caffarra and Donnelly, 2011). Many of these cues are known to interact: photoperiod and chilling can together determine spring phenology through their complex impacts on dormancy release (Chuine, 2000), insufficient chilling may be offset by additional forcing, and photoperiod and chilling often interact, as a long photoperiod enhances cell growth, compensating for a lack of chilling during plants' winter dormancy (Caffarra et al., 2011; Heide, 1993; Myking and Heide, 1995).

Yet, while such complexities have been identified in some species, a growing body of hypotheses and experimental studies has suggested many species are dominated by one cue and may lack any response to other cues (Körner and Basler, 2010). If true, this would have critical implications for predicting responses to climate change, as a species dominated by a forcing cue could march forever earlier in the timing of leafout with continued warming, while species with strong photoperiod cues could stop advancing at some threshold point (Körner and Basler, 2010). Alternatively, if all three cues—forcing, photoperiod, and chilling—are present and interact then predictions would be far more complex (Chuine and Cour, 1999). A species experiencing a mild winter with insufficient chilling (as predicted with climate change) could still break bud, but it would require longer photoperiods and/or more warm temperatures (Heide, 1993) than it has in the historical record—a trend increasingly seen in long-term observational records (e.g, Carter et al., 2017; Fu et al., 2015).

Research to date shows cues clearly vary across species, and recent efforts have focused on understanding and predicting this variation. Studies have focused on attributes of species: native/exotic (Willis et al., 2010), the successional stage (i.e., pioneer or climax communities) to which species traditionally belong (Basler and Körner, 2012; Laube et al., 2014), and a variety of possibly related traits (Lechowicz, 1984; Polgar et al., 2014).

Most of these studies hinge on an often implicit assumption that phenology—by helping define the temporal niche of a species—is a critical axis along which plant species assemble within communities (Gotelli and Graves, 1996; Loreau and de Mazancourt, 2008). Support for this hypothesis comes from work showing that phenology is often staggered within communities, and from the special case of plant invasions, where research suggests that climate change has provided open temporal niche space for new species to occupy (Willis et al., 2010; Wolkovich et al., 2013).

Improved understanding and predictions of phenology with climate change would benefit from a fuller understanding of the interacting environmental cues that drive phenology within (and eventually across) communities. To this aim we studied how forcing, photoperiod and chilling cues vary in their impact on spring phenology across a community of 28 woody plant species from two temperate forest locations (Table S1), separated by 4° latitude. We used clipped dormant branches, which have been shown to approximate whole plant responses (Vitasse and Basler, 2014), and forced them in controlled environments that varied forcing temperatures, photoperiod and chilling. We predicted that: (1) Cues would vary across species, driving staggered leafout across the spring, and (2) within-species cues would trade off, such that some species would be dominated by one or another cue, while others would show a mix of cues. To our knowledge this is the first multi-species study to assess all three cues in one experiment through a controlled environment approach; while several studies have done this for one species (Skuterud et al., 1994; Søgaard et al., 2008; Sønsteby and Heide, 2014; Worrall and Mergen, 1967), other studies of all three cues have used separate experiments (e.g., Caffarra and Donnelly, 2011) or relied on field sampling to asses one or more cues (e.g, Basler and Körner, 2012; Laube et al., 2014; Zohner et al., 2016).

In total we monitored 2,136 clippings and took over 19,320 observations of phenology (budburst and leafout as assessed by the BBCH scale) in an experiment comprising 12 unique treatments that ran 82 days. We analyzed our data using Bayesian hierarchical models because they allowed us to best-estimate responses to our full experimental design at both the species and across-species levels (see Methods for more detail). Higher forcing temperatures, longer photoperiod (12 vs. 8 h), and more chilling all caused large advances in budburst and leafout (Fig. 1, Tables S2-S3).

Forcing temperatures (20°C / 10°C warm vs. 15°C / 5°C cool) and chilling (no additional chilling, additional 33 d at 4°C, or 33 d at 1.5°C) caused the largest advances in budburst and leafout, and these two effects offset one another, as shown by their interactive delayed response (Fig. 1). The interactive effects of forcing and chilling has been noted repeatedly before (e.g., Caffarra et al., 2011; Heide, 1993) and highlights that insufficient chilling can be overcome by additional forcing—a hypothesis suggested by recent studies that have found shifting temperature sensitivities in observational data over time (Fu et al., 2015; Yu et al., 2010). We found similar effects of chilling across two different base temperatures, with only minor differences: responses to the colder (1.5°C) chilling treatment were similar or more muted compared to responses to the warmer (4°C) chilling treatment (Fig. 1, S5-S6, Tables S2-S3). This could indicate that either plants cannot assess chilling temperatures below some threshold (Coville, 1920; Guy, 2014; Harrington et al., 2010).

The two forest sites showed similar responses, with only a very minor possible delay in overall timing for the northern site, and a more pronounced effect of site through its interaction with chilling (Fig. 1, Tables S2-S3). The full effect of chilling depended on site, with a larger impact of site on the lower chilling temperature (1.5°C). This could indicate that chilling requirements vary across populations due to local adaptation, or it could be due to the field chilling experienced before we took cuttings for our experiments (see Table S4). Effects of forcing temperatures and photoperiod were not clearly impacted by site.

At the community level we found that all species were responsive to all cues (forcing temperatures, photoperiod and chilling, Fig. S2-3), with each species having slightly different cues such that each species would budburst and leafout at a distinct time compared to other species (Fig. S4). This provides support for the idea that spring phenology is an important component of the temporal niche (Gotelli and Graves, 1996; Loreau and de Mazancourt, 2008).

These results also suggest that simple classification of some species as 'sensitive' or 'insensitive' to any cue would be artificial, as species did not form distinct clusters (Fig. 2). Previous studies have classified some of our studied species as non- or low-responsive to photoperiod (i.e., *Alnus incana, Aronia melanocarpa,* Zohner et al., 2016), but we found these species were responsive to photoperiod and that any one species cues were only slightly different from several other species, yielding no clear way to define such a binary classification. This is despite the fact that our species spanned a diversity of genera, including canopy and understory species. We did find that shrubs tended to show smaller budburst responses to photoperiod (Fig. 2a) than many trees, but this was not seen for leafout (Fig. 2c).

In contrast to our expectations that within a species cues would trade off (i.e., a species could be dominated by one cue over all others), we found that species tended to show correlated cues, especially between forcing and photoperiod (Fig. 2a,c). Thus, a species with a strong response to forcing temperature generally also had a strong response to photoperiod, and similarly a species with a comparatively weak response to forcing also had a weaker response to photoperiod. This was also seen somewhat with chilling (Fig. 2b,d), though we have fewer species with which to assess the relationship (see Methods).

Our finding that all species responded strongly to all three cues is at odds with some recently published work (Basler and Körner, 2012; Laube et al., 2014; Zohner et al., 2016), but is coherent with many other studies (e.g., Heide, 1993; Worrall and Mergen, 1967), with related process-based models of woody plant phenology (Chuine et al., 2016, 2000) and with recent trends in long-term data (e.g, Carter et al., 2017; Fu et al., 2015). The contrasting results may be due to varying methodologies. Our study used samples collected from the field in January—when species in these locations had likely not fully met requirements for any cue—then used controlled environments (growth chambers) to manipulate all three cues. In contrast, many other studies have used multiple field sampling dates (i.e., sampling once each month from January to March in the northern hemisphere) to assess the effect of one cue, most often chilling (Laube et al., 2014; Weinberger, 1950; Zohner et al., 2017). This is done based on the assumption that chilling increases across a winter season, yet forcing temperatures and photoperiod generally increase as well—meaning it may be hard to fully assess any one cue using this method. Studies using this method may thus underestimate the full suite of cues used to control spring phenology. They may, however, have the advantage of providing more realistic environmental conditions by capturing realistic shifts in all three cues across the winter-spring season (Basler and Körner, 2012), and thus play an important role in predicting near-term impacts of climate change. In contrast, our study used a more extreme photoperiod difference between the two treatments (4 hours, which is equivalent to a difference of 10-12 weeks in the spring at our two sites, see Supplemental Materials), which may better detect photoperiod responses and may be important for longer-term predictions of phenological responses with climate change.

Responses to cues were qualitatively similar across both budburst and leafout, but quantitatively varied greatly between the two phenophases (Fig. 1-2), with responses generally greater for leafout (Fig. 1). This change was dramatic for the response to forcing and photoperiod where the advance in days more than doubled from budburst to leafout (Fig. 1, Table S2-S3). Species cues varied depending on the phenophase considered, meaning species' responses also shuffled between the two stages (Fig. 2). This fundamentally means that the species that bursts bud first will not necessarily leaf out first.

These quantitatively diverging findings for each phenophase suggest complex dynamics in the early season within a community of woody plant species. Increasing evidence suggests the period between budburst and leafout is when plants are at greatest risk of tissue loss from frost (Lenz et al., 2013), and these new insights have come at the same time that research suggests risk of frost damage may increase with climate change (Augspurger, 2009; Dai et al., 2013). For early season species in particular, this period may be critical to their current and future performance. Our results suggest that the cues for each stage are not identical and supports other work suggesting cues on bud swelling and budburst may be distinct from the cues governing the development afterwards (Basler and Körner, 2014). Understanding budburst is particularly difficult as it is the first observable event after a series of unobservable (but see Rinne et al., 2011), yet important physiological events required for budburst (Caffarra et al., 2011; Vitasse et al., 2014) and our results echo calls for increased research in this topic (Chuine et al., 2016), which spans both molecular, cellular and whole plant areas of study (Morin et al., 2009; Rinne et al., 2011; Singh et al., 2017).

Conclusions

Across the two communities we studied, our results suggest species within a community have staggered budburst and leafout due to a mix of all three major environmental cues: forcing temperatures, photoperiod and chilling. In contrast to our hypothesis (and others', e.g., Körner and Basler, 2010), we found no evidence of any species being dominated by one or another cue; instead, species tended to show correlated cues, especially between forcing and photoperiod cues. Thus, accurately predicting the phenology of any one of our studied species under diverse environmental conditions would require considering how all three cues will change in concert. Shifting climate has already clearly altered forcing and potentially chilling across the globe (IPCC, 2014; Stocker et al., 2013) with trends expected to only continue and possibly accelerate; in contrast, photoperiod has not, and will not, shift. These trends combined with our results mean that all 28 species we studied could potentially show complex, non-linear responses in the future, with cascading community and ecosystem consequences.

Methods

Field sampling

Woody plant cuttings were made in January 2015 for 28 species which occurred in both Harvard Forest (HF, 42.5°N, 72.2°W) and the Station de Biologie des Laurentides in St-Hippolyte, Québec (SH, 45.9°N, 74.0°W). The typical late January temperatures are -3.4 and -22°C, respectively. Weather station data from each field site was obtained for calculations of chilling units (see

Table S4).

Species were chosen based on the dominant forest vegetation at each site, aiming to maximize the number of shared species between the two sites. Of the 28 species, at least 19 occurred at both sites. Comparing only shared species, the mean days to budburst and leafout across all treatments for Harvard Forest and St. Hippolyte was 25.6/36.8 and 24.8/36.1 days, respectively (Table S1). For each species, up to 15 representative healthy, mature individuals with branches accessible by pole pruners from the ground were tagged in late summer and fall 2014. In winter 2015, six individuals were located and 4-16 cuttings taken from each individual, depending on size of the individual and number of treatments to be applied. Cuttings were kept cold and transported back to the Arnold Arboretum in Boston, MA.

Growth Chamber Study

Cuttings were placed in growth chambers at the Arnold Arboretum in Erlenmeyer flasks with distilled water; water was changed every 7-10 days. The base of cuttings was re-cut at each water change under water to prevent callusing. For 11 of the 28 species, sufficient cuttings were obtained from each individual tree to apply the full set of 12 experimental treatments: 2 temperature (20°C / 10°C warm vs. 15°C / 5°C cool) x 2 photoperiod (12 vs. 8 h) x 3 chilling (no additional chilling, additional 33 d at 4°C, or 33 d at 1.5°C) treatments. For the remaining 17 species, only sufficient cuttings were obtained to apply the temperature and photoperiod treatments, without the additional chilling levels. The total number of cuttings for a given species thus ranged from 24 to 144, depending on presence at each site and application of the chilling treatment (Fig. S1). Lighting was a combination of halogen incandescent bulbs and T5HO fluorescent lamps with the lamploft adjusted to provide roughly 400 $\mu moles/m^2/s$ as measured by Apogee QSO-A5E quantum PAR light sensors in each chamber (sensor set to the height of the cuttings). Treatments were rotated across chambers every two weeks, as was flask position within chamber, to remove any possible bias of chamber or flask position.

Phenology of the cuttings was assessed using a modified BBCH scale (Finn et al., 2007), with observations on each of the 2,136 cuttings made every 2-3 days for the course of the 82-day experiment, a total of 48 observation days. The phenological stages assessed in the present study are budburst, defined as beginning of sprouting or bud breaking or shoot emergence (Code 07 in Finn et al., 2007) and leafout, defined as first leaves unfolded (Code 11 in Finn et al., 2007).

Additional stages up to flowering and stem elongation were also recorded and we provide a photographic guide to help visualize stages across species (Savas et al., 2017). In total, we made 19,318 phenological observations at the cutting level.

Statistical analysis

For the two phenological responses measured, budburst and leafout, we fit Bayesian mixed-effects hierarchical models using site, warming, photoperiod, and chilling treatments, and all two-way interactions as predictors (fixed effects) and species as modeled groups (random effects). This approach allowed us to calculate the posterior probabilities of the effects for each of the abiotic drivers individually and interactively across all species sampled. The models were fit using the programming languages `Stan` (Carpenter et al., 2016)(`www.mc-stan.org`), accessed via the *rstan* package (version 2.15.1) in R (R Development Core Team, 2017), version 3.3.3. Stan provides efficient MCMC sampling via a No-U-Turn Hamiltonian Monte Carlo approach (more details can be found in Carpenter et al. (2016); Gelman et al. (2014)).

The model was fit as follows:

$$
\begin{aligned}
y_i \sim N(\alpha_{sp[i]} + &\beta_{site_{sp[i]}} + \beta_{forcing_{sp[i]}} + \beta_{photoperiod_{sp[i]}} + \beta_{chilling1_{sp[i]}} + \beta_{chilling2_{sp[i]}} \\
&+ \beta_{forcing \times photoperiod_{sp[i]}} + \beta_{forcing \times site_{sp[i]}} + \beta_{photoperiod \times site_{sp[i]}} \\
&+ \beta_{forcing \times chilling1_{sp[i]}} + \beta_{forcing \times chilling2_{sp[i]}} \\
&+ \beta_{photoperiod \times chilling1_{sp[i]}} + \beta_{photoperiod \times chilling2_{sp[i]}} \\
&+ \beta_{site \times chilling1_{sp[i]}} + \beta_{site \times chilling2_{sp[i]}})
\end{aligned}
$$

The α and each of the 14 β coefficients were modeled at the species level, as follows:

1. $\beta_{site_{sp}} \sim N(\mu_{site}, {\sigma^2}_{site})$

   ...

14. $\beta_{site \times chilling2_{sp}} \sim N(\mu_{site \times chilling2}, {\sigma^2}_{site \times chilling2})$

For the μ and σ parameters, weakly informative priors were chosen (increasing the priors three-fold did not change the model results). We validated our model code could return valid parameter values using test data.

We ran four chains simultaneously, with 4 000 warm-up iterations followed by 3 997 sampling iterations, resulting in 15 998 posterior samples for each parameter. We used a non-centered parameterization on all interactions terms and assessed good model performance through $\hat{R}$ close to 1 and high n_{eff} (15 998 for most parameters, but as low as 2440 for several parameters) as well as visual consideration of chain convergence and posteriors (Gelman et al., 2014).

In our figures we show means ± 50% credible intervals from this model. We used 50% intervals because of our focus here is on the most likely value for each parameter (e.g., estimated response to forcing) and because they are computationally stable (Carpenter et al., 2016; Gelman et al., 2014). For those interested in a more traditional significance-testing approach, we provide 95% credible intervals in Table S2-S3.

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Data, Code & Model Output:

`Stan` model code and output is provided as Supplemental Materials. Raw data will be available via the Harvard Forest Data Archive upon publication and are available to all reviewers upon request.

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Figures

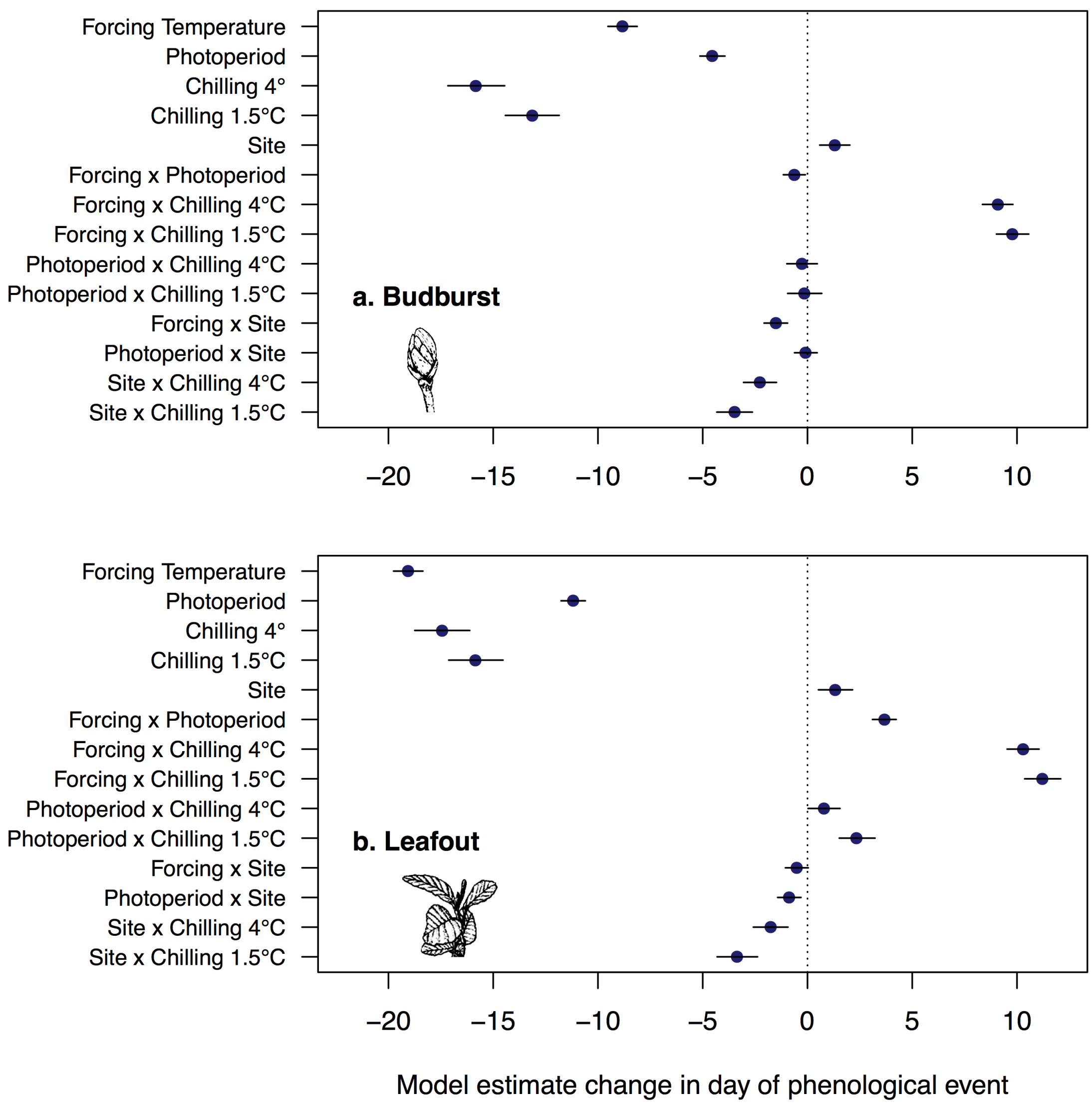

Figure 1: Effects of forcing temperature, photoperiod, chilling and site on budburst (a) and leafout (b) days across 28 species. Dots and bars show mean and 50% credible intervals from a Bayesian hierarchical model that also incorporated species-level variations (see Tables S2-S3; Figs. 1, S2-S3). Advances in phenology are shown by negative numbers; delays are shown as positive. Forcing temperatures and photoperiods were two levels each (see Methods), and chilling treatments were applied for 33 days. Budburst and leafout images from Finn et al. (2007).

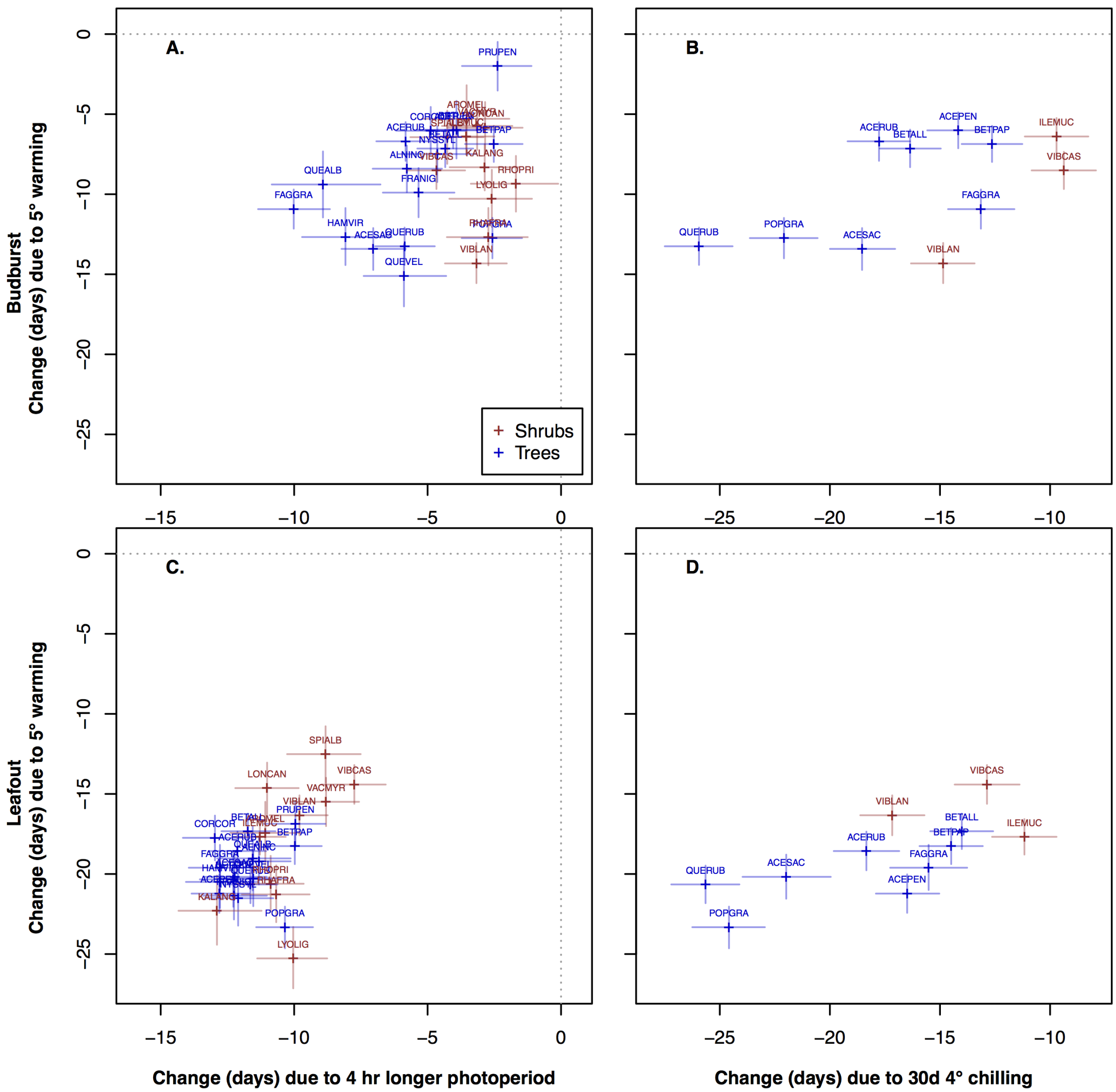

Figure 2: Effects of photoperiod, temperature and chilling across species: Crosses and bars show mean and 50% credible intervals from a Bayesian hierarchical model (see Tables S2-S3; Figs. 1, S2-S3). For visualization purposes, species names are represented by the first three letters of the genus and first three letters of the species epithet (see Table S1 for full species names and Fig. S5-S6 for additional versions of figure).