Chilling outweighs photoperiod and forcing cues for temperate trees in experiments, but not in natural systems

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Abstract

Decades of fundamental research on woody plant species highlight how three major cues shape spring phenological events: forcing, daylength, and chilling (e.g., Campbell and Sugano, 1975; Heide, 2008; Flynn and Wolkovich, 2018). Increasing research on the phenological impacts of climate change has led to debate over whether forcing cues may dominate for some species, while fewer respond to chilling and/or daylength (Heide, 2011; Koerner and Basler, 2010b; Zohner et al., 2016). The debate has wide-reaching consequences for the future of spring phenology, as the presence of strong chilling or daylength cues could slow, stall, or even reverse current trends towards ever-earlier spring phenology with warming (Fu et al., 2015; Koerner and Basler, 2010a). Here we use a global meta-analysis of all published controlled environment studies to test for the relative effects of these three major cues across 203 species. We find almost all species show strong responses to all three cues, with chilling being the strongest cue (-2.86), followed by forcing (-0.79) and daylength (-0.53). Simple forecasts from our findings, however, suggest that the impact of chilling and daylength cues is highly location-specific—dependent largely on whether chilling increases or decreases with warming—and has major effects on projections only above a warming of 4°C or more, at least in the well-studied areas included in our database (e.g., Central Europe). Our results unify both sides of the debate over phenological cues: while all species may respond to all cues strongly in experimental conditions, in current environmental conditions the dominant impact of climate change is—and may remain—from increased forcing.

Text so far...

For decades, plant phenology has been one of the most reported and consistent biological imprints of climate change (IPCC, 2014), with many temperate plants leafing and flowering days to weeks earlier with rising temperatures (Miller-Rushing and Primack, 2008; Menzel et al., 2006). Understanding such shifts is important as phenology shapes a suite of ecosystem services, including pollination and carbon sequestration, and scales up to impact projections of climate change itself Richardson et al. (2013).

As research interest in phenology has progressed, critical discrepancies and uncertainties in our understanding have emerged. Though responses to warming are consistent on average, they show high unexplained variation across species and sites (Wolkovich et al., 2012). Furthermore, long-term observational studies provide increasing evidence that sensitivities of phenology to temperature are weakening in recent decades Rutishauser et al. (2008); Yu et al. (2010), especially in Europe, where researchers suggest that responses to environmental cues beyond forcing underlie declining temperature sensitivities Fu et al. (2015).

Fundamental research in phenology outlines how three major cues, chilling (cool temperatures, generally occurring in the fall and late winter), forcing (warm temperatures, generally occurring in the late winter and early spring), and daylength, provide multiple routes to budburst each spring, depending on the environment

(Chuine, 2000). For example, in some species a cool winter resulting in high chilling will lower the amount of forcing required to trigger budburst, compared to a warmer winter (Harrington and Gould, 2015). Additionally, daylength may trigger budburst, given low chilling and/or forcing (Basler and Körner, 2014; Caffarra et al., 2011b; Zohner et al., 2016). Research suggests that all three cues may underlie spring phenology for many temperate woody species (Flynn and Wolkovich, 2018; Basler and Körner, 2014; Caffarra et al., 2011a), which could have critical forecasting implications—predicting delays in spring phenology as further global warming reduces chilling in many areas (Fraga et al., 2019) or where earlier budburst shortens the experienced photoperiod. However, there is strong debate, with some research suggesting some cues—such as photoperiod—may be effectively absent in some species, but dominate in others (Zohner et al., 2016; Koerner and Basler, 2010a).

Resolving this debate requires overcoming major hurdles to estimate responses to each cue. Studies attempting to estimate cues using long-term observational data (e.g., Vitasse and Basler, 2013; Zohner et al., 2016) generally fail to overcome the fundamental challenge that all three cues are strongly correlated in nature (e.g., during the transition from winter to spring at temperate latitudes, forcing and daylength usually increase in step). In contrast to observational studies, controlled environment experiments can breakdown correlations between chilling, forcing. These experiments—most often conducted in growth chambers or similar systems to control temperature and light—have been conducted for decades, but have produced often contrasting results (Zohner et al., 2016; Laube et al., 2014; Basler and Körner, 2012; Caffarra et al., 2011b; Caffarra and Donnelly, 2011).

Here, we leverage nearly 40 years of controlled environment studies to understand how chilling, forcing, and photoperiod contribute to budburst timing in woody species. Using a meta-analytic approach we reviewed XX papers from controlled environment studies, then extracted data from any papers that reported budburst responses, yielding data from 49 studies across 39 years and 203 species (reference map of studies). This database includes only studies for which we could identify forcing, photoperiod, and chilling treatments quantitatively. As field chilling was rarely reported, we estimated chilling (when possible) using local climate data (see Supplemental Materials). We used a Bayesian hierarchical model to estimate the effects of chilling, forcing, and photoperiod. This model estimates both species-level responses (generally yielding more accurate estimates for well-studied species, such as *Fagus sylvatica* and *Betula penndula*), and the distribution from which they are drawn, yielding a higher-level estimate of the overall response across species (see Supplemental Materials- mention).

Across studies, all cues—chilling, forcing, and photoperiod—advance budburst phenology (Fig. 1). Chilling was the strongest cue (-2.86 days/standard unit or -8.87 days per 240 Utah units, which is typically about 10 days of chilling, Fig. 2), followed by forcing (-0.79 days/standard unit or -4.37 days per °C of warming, Fig. 2), and photoperiod (-0.53 days/standard unit or -3.13 days per hour of daylength). (See Supplemental Materials for full comparison of models using standardized versus unstandardized predictors). While photoperiod had the smallest effect among the three cues, our results contrast with the extensive literature suggesting photoperiod is a weak or non-existent cue for many species (Zohner et al., 2016; Koerner and Basler, 2010a)—instead we found it was surprisingly large and consistent across species, even in models accounting for its interaction with latitude (see Supplemental Materials for details, especially Fig. 7S). Only *Fagus sylvatica*, a species well-known for having a large response to photoperiod deviated far from the overall estimate (Fig. 1). Species also showed fairly consistent responses to chilling (sigma = 2.06 days per 240 Utah units, Fig. 1. Responses to forcing, in contrast, were the most variable across species (sigma = 0.91 days per °C of warming).

As temperature is fundamentally altered by climate change, our finding that different ends of the temperature spectrum—chilling and forcing—have the strongest effects on budburst suggests that understanding these cues will be critical for forecasting phenology with climate change. Many previous studies attribute advances in budburst to increased forcing (Basler and Körner, 2014; Bradley et al., 1999; Menzel et al., 2006; Harrington and Gould, 2015), and forcing sensitivity in our model (-4.37 days per degree of warming) is consistent with what previous experiments and observational studies have reported (Wolkovich et al., 2012; Menzel et al.,

2006). Our results, however, suggest chilling has a greater effect on budburst than forcing (Fig. 1). This has not been widely suggested previously, perhaps because little work has directly manipulated chilling, and the few studies that have were designed to compare chilling versus photoperiod effects (e.g., Basler and Körner, 2014; Caffarra et al., 2011a; Laube et al., 2014; Zohner et al., 2016), not forcing versus chilling effects.

A simple interpretation of our model supports the hypotheses that chilling and photoperiod cues may underlie declining sensitivities to warming in long-term European data (Rutishauser et al., 2008; Yu et al., 2010; Fu et al., 2015). Under these hypotheses, warming increases forcing and thus advances budburst, but such advances become muted if warming also causes declines in chilling and shorter photoperiods experienced near the timing of budburst (cite our photoperiod paper?)(Koerner and Basler, 2010a). Our model also predicts that increased forcing advances budburst, whereas reduced chilling and shorter photoperiods both delay budburst (Fig. 3). This basic agreement, however, integrates across experimental conditions—a more robust test of the model's implications requires examining predictions under conditions closer to those found in nature.

Reinterpreting our model using the climate and phenology data that has led to observations of declining temperature sensitivities across Europe suggests that chilling and photoperiod cues are unlikely to cause the observed declines in sensitivity. Our model predicts such declines occur only at extreme warming, for most sites (Supplemental Materials for details). In contrast to the common hypothesis that chilling declines with warming we found that for many sites chilling increased with warming (Fig. 3 A,D), though this varied with local climate prior to warming (supp heat map fig). Portions of Europe have experienced more dramatic warming in winter versus summer Balling Jr et al. (1998), but even if warming *only* occurs in the winter, our results suggest that delays due to decreased chilling will occur at warming levels of 4°C or more, for most sites (Fig. 3). At high warming, predicted declines in sensitivity were due to declines in chilling—photoperiod had little effect on budburst day of year, even for the photosensitive species *F. sylvatica* (Fig. 6S).

Our predictions leave open the question of what underlies declining sensitivities across Europe, but simple analyses suggest it could be a statistical artifact of how temperature sensitivities are calculated (Vitasse et al., 2018; Güsewell et al., 2017). Physiologically, budburst is triggered by the accumulation of forcing temperatures during one year's spring (Hänninen, 1995; Chuine et al., 2016). Yet, researchers today often estimate temperature sensitivities from long-term observational data using a linear regression of annual budburst date versus mean or other aggregated metrics of spring temperature (e.g., Wolkovich et al., 2012). This approach has the benefit of yielding an easily interpretable metric—days change per °C—but will systematically estimate lower sensitivities given warmer daily temperatures, even with no change in the underlying cues (Fig. S8). We found the declining sensitivities observed in European data are of the same magnitude as those predicted from a statistical artifact (sensitivity declines of 0.9±0.3 days/°C in European data versus 0.9±0.5 days/°C in simulations), and the data also show a related decline in leafout variance that would not be immediately predicted from shifting cues (see *Understanding declines in temperature sensitivity in European long-term data* in the Supplemental Materials for further details). This statistical artifact is likely not confined to phenological studies; it should apply to any research using a similar days/°C metric to estimate an underlying thermal accumulation model where the thermal time per day is non-stationary, as is the case with climate change.

A consistent result of our findings—across both the experimental and *in situ* environmental conditions—is the importance of chilling. Yet chilling and its related physiological stage, endodormancy, are not well understood (Chuine et al., 2016). Models of how species accumulate chilling are poorly developed for forest trees, with few relevant tests evaluating the particular temperatures at which species do or do not accumulate chilling. Instead, researchers generally rely on models developed for perennial fruit trees (i.e., Utah (Richardson, 1974) and chill portions (Fishman et al., 1987) which were developed for peach species). These models are themselves *hypotheses* for how chilling may accumulate and produce dormancy release, but are likely to be inaccurate for many species (Dennis, 2003). Progress on developing models for wild species is especially slow, as only a few studies manipulate chilling directly. Instead many studies (J out of Y; the remaining XX studies did not manipulate chilling in any way) estimate chilling effects through sequential removal of tissue from

the field followed by exposure to 'forcing' conditions (Weinberger et al., 1950), with the assumption that tissues collected later experience more chilling. The challenge with this method is multifold: first, chilling duration may not always co-vary with the magnitude of total accumulated chilling (Dennis, 2003), and, second, photoperiod and other factors also change over time. Indeed, we found estimates varied in XX way when derived from direct manipulations of chilling versus the sequential 'Weinberger' method (Weinberger et al., 1950; Polgar et al., 2013) (ref table or figure), suggesting estimates from this method may be inaccurate.

An improved understanding of chilling could in turn alter our understanding of forcing. Although researchers often define 'chilling' and 'forcing' treatments based on a temperatures, physiologically plants appear to accumulate forcing mainly after chilling requirements have been met (Chuine et al., 2016). Our results show that these two temperature-derived cues strongly affect budburst, thus identifying the physiological processes plants undergo when accumulating chilling versus forcing will be critical for accurate forecasts. With progress in this fundamental area, research may begin to address how these cues interact (see Supplemental Materials)—since climate change clearly shifts both simultaneously in many regions. We expect that our fundamental predictions of an increasing advance of spring phenology for many temperate trees will remain robust, unless cues begin to change highly asynchronously. However, a better understanding of the physiology processes involved, as well as more precise metrics for estimating chilling and applications of nonlinear models, will improve accuracy of regional forcasting, and our ability to manage ecosystems in the future.

Figures

model

Legend:
- Abies_alba
- Acer_complex
- Acer_pseudoplatanus
- Acer_saccharum
- Aesculus_hippocastanum
- Alnus_glutinosa
- Alnus_incana
- Betula_complex
- Betula_pendula
- Betula_pubescens
- Carpinus_betulus
- Cornus_alba
- Cornus_mas
- Corylus_avellana
- Fagus_sylvatica
- Fraxinus_complex
- Fraxinus_excelsior
- Larix_decidua
- Picea_abies
- Populus_complex
- Populus_tremula
- Prunus_avium
- Prunus_complex
- Prunus_padus
- Pseudotsuga_menziesii
- Quercus_complex
- Quercus_petraea
- Quercus_robur
- Quercus_rubra
- Robinia_pseudoacacia
- Salix_complex
- Sorbus_aucuparia
- Symphoricarpos_albus
- Syringa_vulgaris
- Tilia_cordata
- Ulmus_complex
- Vaccinium_complex

Axis labels: mu_b_force_sp, mu_b_photo_sp, mu_b_chill_sp

X-axis: Model estimate change in days to BB (−30, −20, −10, 0, 10)
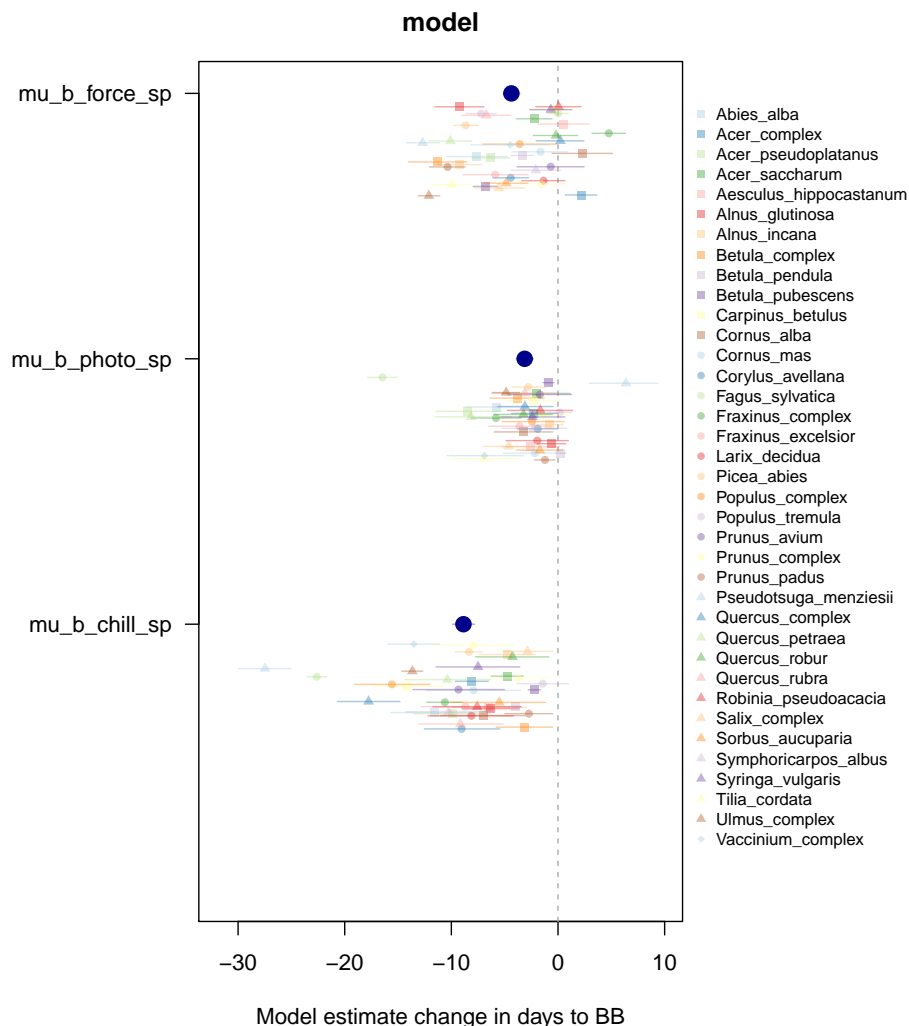
Figure 1: **Estimates for effects of chilling exceeded forcing and photoperiod estimates** in the budburst models fit to data from the OSPREE database. Here we show estimates from the model fit to centered data, enabling comparisons of effects sizes across predictors, and using Utah units to quantify chilling. Estimates to models fit to uncentered data and using Chill Portions were qualitatively similar and can be found in the Supplemental Materials.
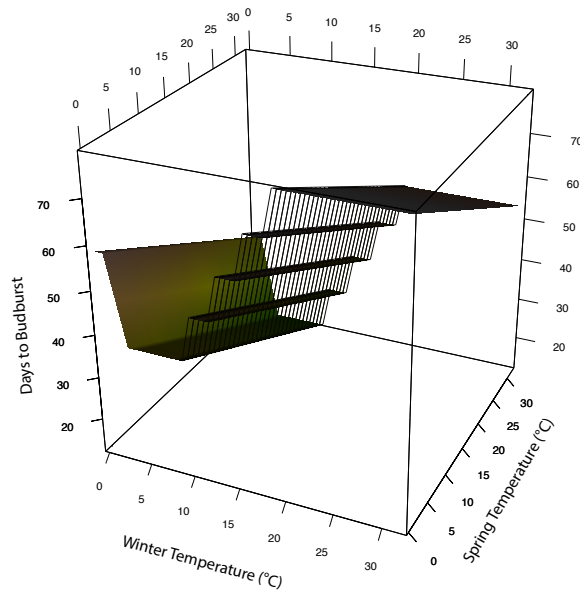
Figure 2: **Based on the OSPREE model, days to budburst decrease linearly with forcing temperature and vary nonlinearly with chilling temperature** due to the way that chilling is modeled (in this case, the Utah model; the model with Chill Portions is shown in the Supplemental Materials). Treatment temperatures in growth chamber experiments ranged from 0-30 °C (see Table 1S for details). A) The full range of experimental conditions and budburst response predicted by the OSPREE model. B) The range of experimental conditions for *Betula pendula*, a European species that is one of the most common in OSPREE (AILENE NEEDS TO DO THIS!).
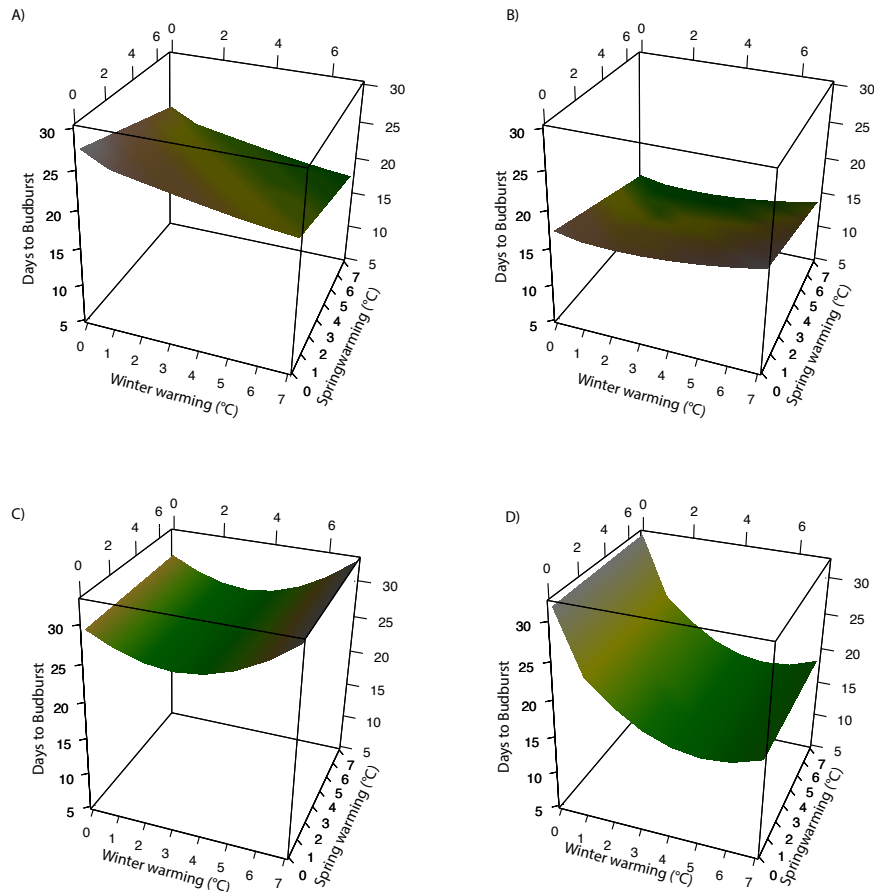
Figure 3: Implications of global warming on budburst varies by site, depending on pre-warming climate for the two most common species in the OSPREE database: *Betula pendula* (A,B) and *Fagus sylvatica* (C,D), as predicted by the OSPREE model. For sites in A and D, chilling increases with warming, whereas chilling decreases with warming for the sites in B and C. See Supplemental Materials, especially Figure 5S, for details. Could add a map of where these sites are? Or just show on the Fig 5S..

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