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

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Abstract

Decades of research on woody species highlight how three major cues shape spring phenological events (e.g., budburst and leafout): forcing (warm temperatures, generally occurring in the late winter and early spring), daylength (photoperiod) and chilling (cool temperatures, generally occurring in the fall and late winter). How pervasive these cues are and whether some species are effectively governed by only one or two cues is a critical area of climate change biology research, as it would shape how complex responses to warming will be. Here we use a global meta-analysis of all published growth chamber studies to test for the relative effects of these three major cues across XX species. We find they almost all show these cues, making climate change responses complex.

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 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.

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 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; Fu et al., 2015). In Europe, recent work from many of the most well-studied tree species shows declining responses to temperature, suggesting that the long-term trend towards ever-earlier springs may be stalling (Fu et al., 2015). The authors, and others, suggest that responses to other environmental cues underlie these declining temperature sensitivities.

Fundamental research in phenology outlines three major cues known to shape spring phenology (Chuine, 2000): 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 (photoperiod). These cues are thought to provide mutiple routes to budburst each spring depending on the environment. For example, a cool winter resulting in chilling above some threshold will require some forcing to trigger budburst, whereas a warmer winter may fail to meet the chilling threshold and thus more forcing, or some combination of forcing and longer daylength, will be required to trigger budburst (Harrington and Gould, 2015; ?). 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), but 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).

Given the declining response to temperature observed in long-term observational studies (Fu et al., 2015), a number of papers have tried to tease out evidence of unfufilled chilling or daylength cues in recent years (Basler and Körner, 2014; Zohner et al., 2016; Laube et al., 2014). This work must overcome the fundamental challenge that all three cues are strongly correlated in nature. During the transition from winter to spring at many temperate latitudes, air temperatures increase (i.e., forcing increases) at the same time that daylength is increasing; likewise, winters with low amounts of chilling are often correlated with warmer springs, and thus higher forcing. Identifying which of these cues most strongly affects spring phenology is critical for forecasting future phenological changes. For example, if forcing is the dominant cue (as many observational studies to date have assumed, (Bradley et al., 1999; Menzel et al., 2006; Harrington and Gould, 2015)), then we can expect additional spring advancement as temperatures continue to warm. However, if unfulfilled chilling limits budburst, then we may see delays in spring phenology with additional global warming, which will reduce chilling in many areas (Fraga et al., 2019).

In contrast to observational studies, controlled environment experiments can break correlations between chilling, forcing, and photoperiod to reveal which cues underlie budburst phenology. These experiments— most often conducted in growth chambers or similar systems to control temperature and light—have been conducted for decades as a major method to understand the fundamental drivers of spring phenology. To date, controlled environment experiments have identified contrasting effects of the three major budburst cues. Some studies have proposed that photoperiod is likely to constrain species responses to climatic warming (Basler and Körner, 2012; Caffarra et al., 2011b; Caffarra and Donnelly, 2011), whereas others report that photoperiod is not a strong cue for most species (Zohner et al., 2016; Laube et al., 2014) and suggest chilling may be more important to current and future trends.

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 met XX conditions, yielding data from 74 studies across 39 years and 223 species (reference map of studies). This database includes only studies for which we could identify forcing, photoperiod, and chilling treatments quantitatively. As chilling was only rarely reported, we estimated chilling ourselves 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 partially pools across species to estimate a robust overall effect, and for robust effects for species with lots of data (*Fagsyl, Betpen*) but pools towards the mean for species with fewer data (See Supplemental Materials- mention species complex).

Across studies, all cues—chilling, forcing, and photoperiod—each advance budburst phenology (Fig. 1). Using a standardized scale to allow comparisons of the three cues we found that chilling was the strongest cue (-8.16 days/standard unit or -0.25 days per chill portion, Fig. 2), followed by forcing (-4.83 days/standard unit or -0.85 days per degree of warming, Fig. 2). Photoperiod was the weakest cue (-3.17 days/standard unit or -0.54 days per hour of daylength); however—given an extensive literature that has suggested photoperiod is a weak or non-existent cue for many species (Zohner et al., 2016; Koerner and Basler, 2010a)— it was surprisingly large and consistent across species, with only *Fagus sylvatica*, a species well-known for having a large response to photoperiod deviating far from the overall estimate (Figure 1). Species also showed fairly consistent responses to chilling (Figure 1, though two species delayed budburst with chilling *Tilia codata*, *Salix* complex). Responses to forcing, on the other hand, were the most variable across species (sigma = 6.04).

As temperature is radically altered by anthropogenic 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. 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 (-0.85 days per degree of warming) is consistent with what previous experiments (CITES), and observational studies (CITES) have observed. Our results, however, suggest

chilling has a greater effect on budburst than forcing (Fig. 1). This has not been widely suggested previously, as little work has manipulated chilling directly and that work which has usually contrasts it with photoperiod, not forcing (e.g., Basler and Körner, 2014; Caffarra et al., 2011a; Laube et al., 2014; Zohner et al., 2016).

The paucity of studies directly manipulating chilling—which our results suggest has the greatest effect on budburst—suggests a major gap in current research. While many studies (X out of Y here) directly manipulated forcing, far fewer directly manipulated chilling (Z out of Y). Instead many studies (J out of Y) estimate chilling effects through sequential removal of tissue from the field and exposure to 'forcing' conditions (cite Weinberger), with the assumption that tissue collected later experienced more chilling. The challenge with this method is that photoperiod and other factors may have also changed during this time. Indeed, we found estimates varied in XX way when derived from direct manipulations of chilling versus the sequential 'Weinberger' method. Given the limited manipulation of chilling in studies, we estimated chilling for all studies by combining chilling from the field (i.e., chilling before plants were sampled) and experimental chilling into two widely used metrics of chilling: Utah (citation) and Chill portions (citation). We found the effects of chilling and other cues remain qualitatively the consistent across the two chilling units, though chilling and photoperiod estimates were slightly lower using chill portions compared to Utah (cite supplemental table comparing estimates with both units).

An additional important limitation in most current experiments is the rarity of studies designed to test interactions. While interactions between these cues are widely expected (cites) and, when examined, often found (cites), we were unable to estimate interactions in our meta-analysis because very few studies design experiments to test for interactions between chilling, forcing, and photoperiod (cite table with number of interactions from coding challenge!). The few that do incorporate interactions generally use the Weinberger method, which is not designed to robustly tease out of the effects of multiple cues (cites, Tables, figs). Our estimated effects average over interactions (citeGelman), but identifying them should be an important area of future research. While designing studies to tease out interactions generally requires many additional replicates and careful consideration of the design of treatment combinations, they appear critical to understanding and predicting budburst. For example, the most commonly observed interaction between chilling and forcing— that lower amounts of chilling increase forcing requirements for budburst (cite)—is the hypothesized cause of declining sensitivities in European trees (cites). [Opportunity to sneak in one or two lines on how data limitations meant we could not compare other effects ... then mention latititute x photoperiod?]

We expect climate change to continue to have dramatic effects on spring phenology, because the two temperature-derived cues (chilling and forcing) both strongly affect budburst (Laube et al., 2014). However, the relative importance of chilling versus forcing (i.e., the extent to which a chilling threshold will be reached and cause delays in budburst with additional warming) will vary spatially. Forcing is increasing with climate change and is therefore expected to continue advancing budburst. Chilling, on the other hand, is expected to increase in some locations and decrease in others with climate change (Fraga et al., 2019), so budburst responses may advance less strongly in places where chilling declines. In some locations, budburst may even delay with substantial amounts of warming (e.g. X degrees, as is forecasted for the end of the 21st century, IPCC, Fig. 3) as chilling limitations come into play.

A simple interpretation of our model – especially its chilling and photoperiod effects – predicts declining sensitivities to warming in long-term data with climate change. This is because even though forcing increases, chilling is expected to decrease and photoperiods will often shorten as budburst advances (cite our photoperiod paper? or something else...) – both predicting delays, and thus an overall muted effect of global warming on spring budburst (Fig. 3). Experimental conditions likely differ from those *in situ*, however; for example, photoperiods in experimental treatments ranged from 8 hours to 16 hours, whereas photoperiods during the spring budburst period (e.g., 1 March through 1 May) range from 11 to 14 hours at latitude 45 °. We therefore wanted to put the OSPREE experimental data and model estimates in the context of forecasted and observed environmental conditions.

Interpreting our model with conditions experienced in natural systems in Germany, on the other hand, the OSPREE model predicts a decline in sensitivity only at extreme warming for most sites (Supplemental

Materials for details). Chilling often increased with small amounts of warming, though this varied with current local climate (Fig. 3 A-D, supp heat map fig). We also found that patterns of budburst advancement with warming vary considerably depending on the current climate (e.g. how much advancement will continue with warming depends on how much chilling is currently experienced and whether that will increase or decrease with warming). The decline in sensitivity observed with high warming was due to declines in chilling; photoperiod had little effect on budburst day of year, even for the photosensitive species *F. sylvatica* (Fig. 3 E,F). Portions of Europe have experienced more dramatic warming in winter versus summer (citatopm), but even if warming *only* occurs in the winter, the OSPREE model suggests that delays due to decreased chilling will occur at warming levels of 4°C or more (CHECK THIS!). Given the modest amounts of warming experienced at these sites (XX on average), the OSPREE model predicts a general advance of budburst for Germany.

We compared our model's predictions with observations from the PEP database, and found a different response than predicted by the OSPREE model. The PEP data show declining sensitivities to warming in recent decades (Fig. 4). (Compare advances in our models to PEP725 data?). Our results suggest few sites with delays before 3-4 degrees warming (CHECK) and Germany has warmed X amount. Why do the OSPREE model and PEP observations not match up? Possibly because conditions are different between experiments and natural systems: although forcing conditions are roughly similar between experimental and observed conditions, experimental chilling is generally lower than field chilling. Add:

1. Speeding up a biological process given sampling time resolution could lead to declining estimates of sensitivites, even if unchanged

2. Say something about what to do about this and how to figure out if this is the issue or it's cues.

Our results suggest most or all studied species are responsive to these three cues

1. Our results are only for one region, but highlight how critical accurate forecasts of shifts in forcing and chilling will be at local scales

2. To do this, we desperately need to better understand chilling (dormancy release) so that we can predict it in the future (maybe say need better models for chilling across species).

3. Alongside this, we need more fundamental understanding of interactive cues, which requires larger studies across diverse species. Our results include these complexities but a finer understanding is needed in locations where cues do not change in concert.

4. These complexities are unlikely to alter our fundamental predictions of an increasing advance for many temperate trees in the future, even those with strong chilling or forcing cues (ref Gauzere) [Alt: An improved understanding of interactive cues, however, is unlikely to alter our fundamental predictions of an increasing advance for many temperate trees in the future, even those with strong chilling or forcing cues (ref Gauzere), unless cues are changing very asynchronously.]
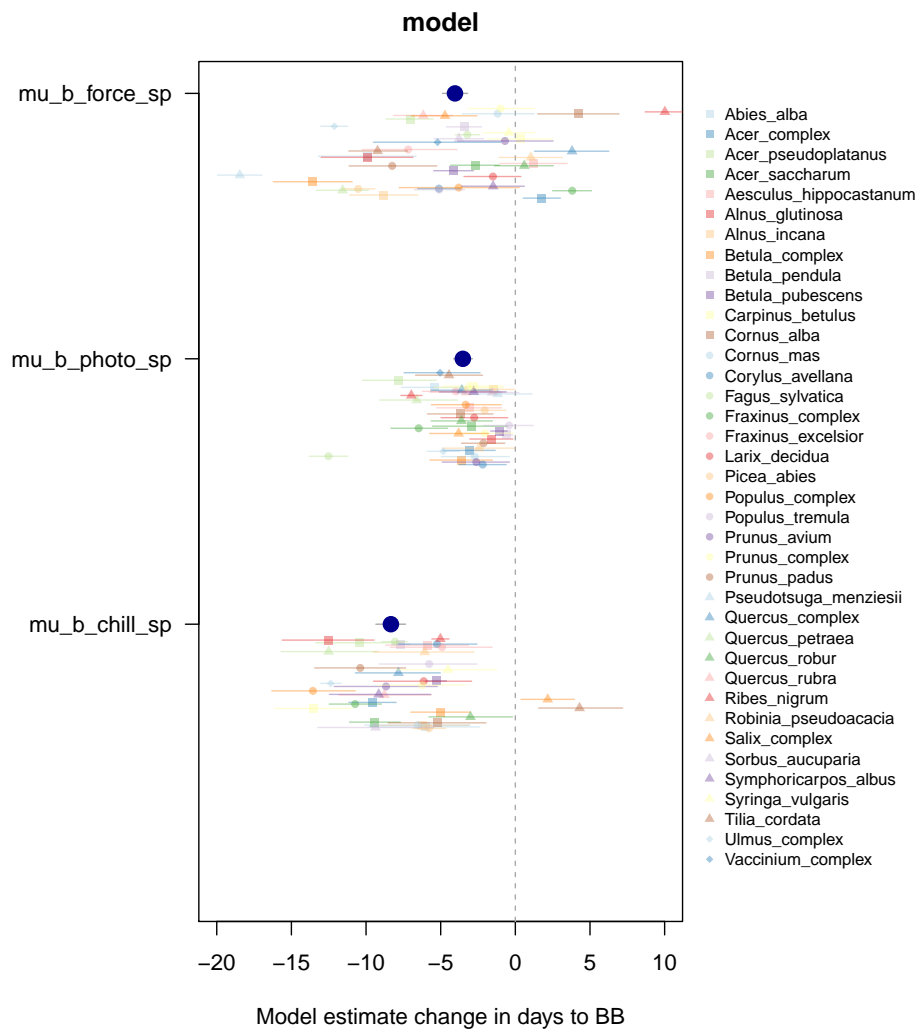
Figures

model

Figure 1: Budburst model estimates

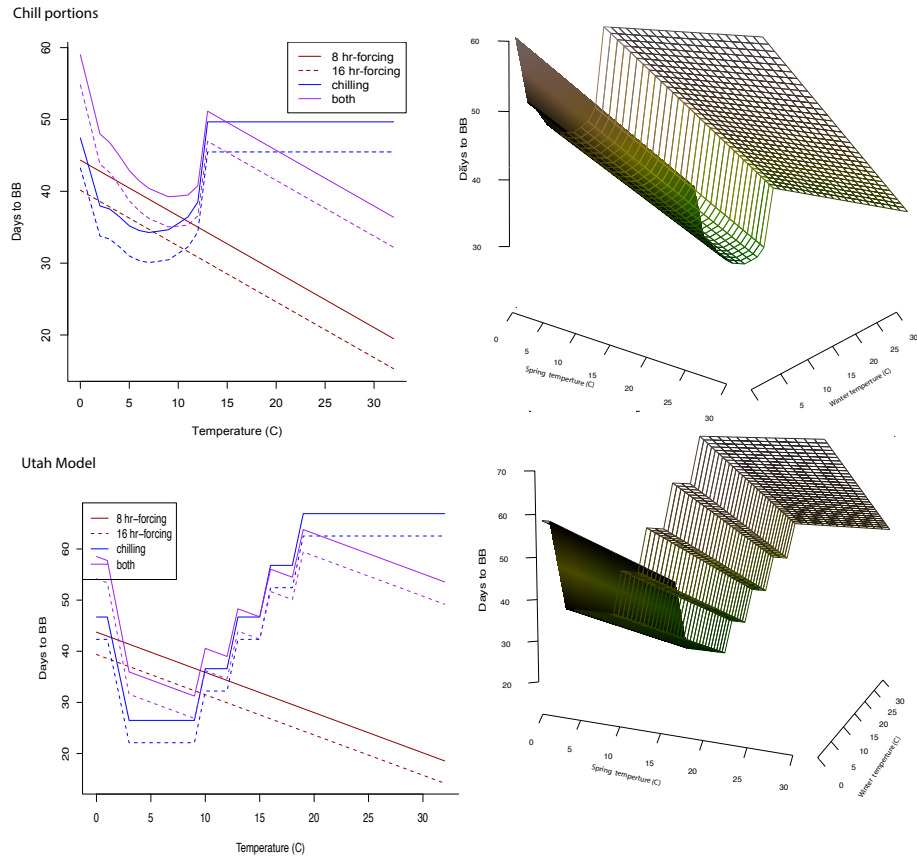for model fit to centered data with Chill Portions.

Figure 2: Effects of chilling, forcing, and photoperiod, across the experimental conditions in the OS-PREE database. Make this part of a 2-panel figure with 1?
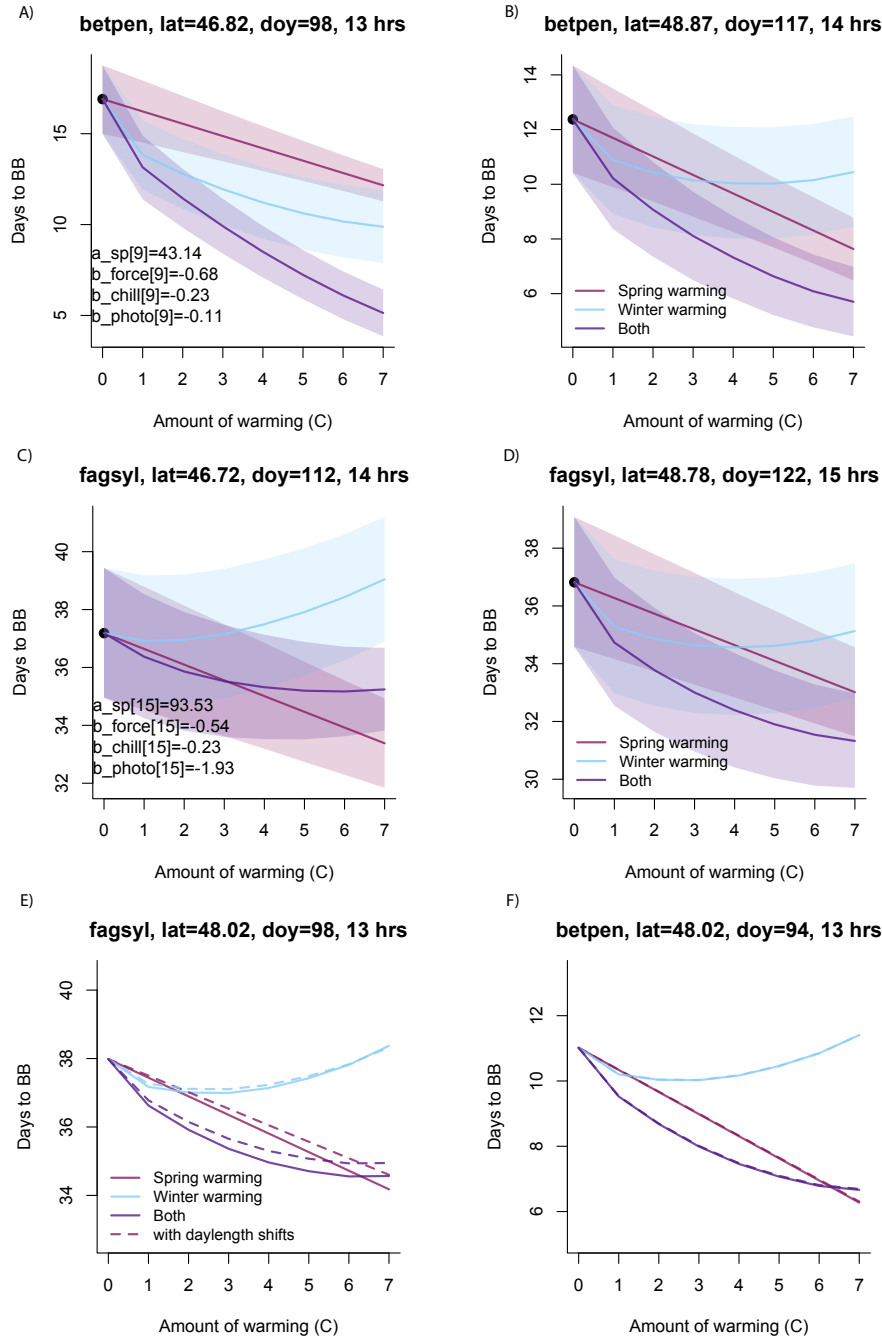
Figure 3: Implications of global warming on budburst of *Betula pendula* (A,B) and *Fagus sylvatica* (C,D) as predicted by the OSPREE model. We show the maximum and minimum latitudes at which each species occurred in the PEP database for Germany as examples; these locations differ in current climate. For all sites effects of potential shifts in photoperiod with advancing budbrst were minimal (E,F), even the photosensitive species *Fagus sylvatica*
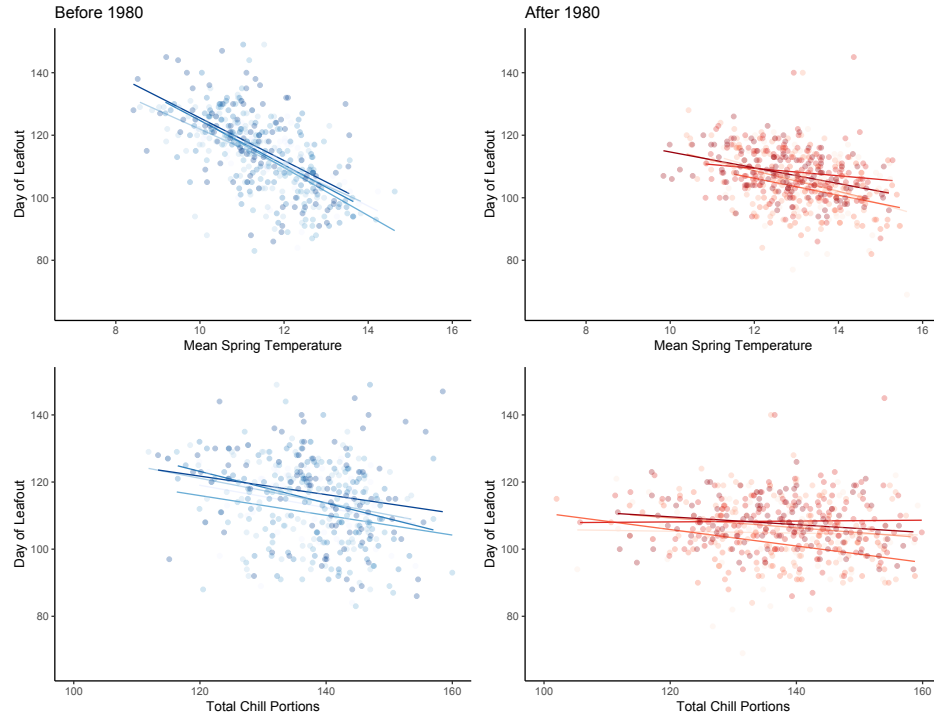
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Figure 4: Implications of global warming on budburst of *Betula pendula* (A,B) and *Fagus sylvatica* (C,D) as predicted by the OSPREE model. We show the maximum and minimum latitudes at which each species occurred in the PEP database for Germany as examples; these locations differ in current climate. For all sites effects of potential shifts in photoperiod with advancing budbrst were minimal (E,F), even the photosensitive species *Fagus sylvatica*

Supplemental Materials

Supplemental methods

1. Forecasting with the OSPREE model: We selected sites in Germany where temperature and budburst have been monitored since the 1950s. We extracted mean temperature data from 1950 through 1980 (pre warming time period) and used these values as baseline data in our model. We then investigated model predictions of budburst given different levels of warming (from 1-7 °C), including altered chilling and forcing as well as potential declines in photoperiod due to advancing phenology. We did this for two common European species: *Betula pendula* (silver birch) and *Fagus sylvatica* at all lat/longs included in the PEP database for Germany.

2. To understand how experimental temperature, photoperiod, and budburst sensitivity compares to past and current conditions in nature, we used data from the PEP database (cite). We summarized forcing, chilling, and budburst doy for two common species: *Betula pendula* (silver birch) and *Fagus sylvatica* (European beech) during a pre-warming time-period (1950-1980) and post-warming period (1981-2014?).

Supplemental figures/tables:

1. Map of study locations, shading or symbol coding for number of cues (Lizzie)

2. Map of species forecasting to justify sites

3. Tables, yes.

4. Heat maps for the main data, including by actual study design and by calculated chilling (our calculations)

5. Photoperiod x latitude effects figure

6. Equation of our model

Reference list

A few categories:

Papers about contrasting results over what cues matter from growth chamber studies: Basler and Körner (2012, 2014); Caffarra et al. (2011a); Caffarra and Donnelly (2011); Caffarra et al. (2011b); Heide and Prestrud (2005); Koerner and Basler (2010b); Laube et al. (2014); Vitasse and Basler (2013); Zohner et al. (2016). Get Nanninga *et al.* 2017: 'Increased exposure to chilling advances the time to budburst in North American tree species' and maybe Malyshev *et al.* 2018 'Temporal photoperiod sensitivity and forcing requirements for budburst in temperate tree seedlings.'

Papers about declining sensitivities (Ailene will update this list): Rutishauser et al. (2008); Fu et al. (2015). Also look for a Wang *et al.* article 'Impacts of global warming on phenology of spring leaf unfolding remain stable in the long run.' Vitasse paper on declining variation across elevation gradient. See Yu et al. (2010), but this is not temperate trees.

Papers about chilling units paper (Lizzie gets a list): Fu 2012 from OSPREE. Harrington and Gould (2015)Luedeling et al. (2011); Luedeling and Brown (2011); Luedeling et al. (2013)

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