Chilling outweighs photoperiod and forcing cues for 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., 2012a). 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 suggest that responses to other environmental cues underlie these declining temperature sensitivities.

Fundamental research in phenology outlines three major cues, chilling, forcing, and photoperiod, 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 require a lower amount of forcing to trigger budburst, compared to a warmer winter that results in significantly lower chilling (Harrington and Gould, 2015). In other species daylength may help 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). 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).

Given the declining response to temperature observed in long-term observational studies (Fu et al., 2015), a number of studies have tried to tease out evidence that chilling or daylength cues are playing an increasingly important role 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: e.g., during the transition from winter to spring at temperate latitudes, air temperatures increase (i.e., forcing increases) at the same time that daylength increases. In contrast to observational studies, controlled environment experiments can break 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, yet, to date, they have identified contrasting effects of the three major budburst cues. Some studies report 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 state that photoperiod is not a strong cue (Zohner et al., 2016; Laube et al., 2014) and that chilling is more important to current and future trends.

Resolving these discrepencies to identify which cues most strongly affect spring phenology is critical for forecasting future phenological changes. 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).

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 (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, 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 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 -2.5 days per 10 Chill portions, Fig. 2), followed by forcing (-4.83 days/standard unit or -0.85 days per degree of warming, Fig. 2), and photoperiod (-3.17 days/standard unit or -0.54 days per hour of daylength). 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. Only *Fagus sylvatica*, a species well-known for having a large response to photoperiod deviated far from the overall estimate (Figure 1). Species also showed fairly consistent responses to chilling (sigma = 7.88, 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 and observational studies have observed (Wolkovich et al., 2012b; 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 and photoperiod effects (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 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 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 is the rarity of studies designed to test interactions. 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 in future research will be critical to understanding and predicting budburst. For example, the most commonly observed interaction between chilling and forcing—that lower amounts of chilling increases forcing requirements for budburst (cite)—is the hypothesized cause of declining sensitivities in European trees (cites). As more data become available, it would allow additional tests of important interactions, such as how responses vary across latitudes (see Supp).

A simple interpretation of our model supports hypotheses that chilling and photoperiod cues may underlie declining sensitivities to warming in long-term European data (cite papers, ref our pep fig?). 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 budburst (cite our photoperiod paper? or something else...). Our model supports this in that it predicts that increased forcing advances budburst whereas less chilling and shorter photoperiods both delay budburst (Fig. 3). This superficial agreement, however, integrates across experimental conditions—a more robust test of the model's implications requires examining our model in situations closer to those in natural systems.

Reinterpreting our model using the climate and phenology data that has led to observations of declining temperature sensitivities across Europe suggests instead that chilling and photoperiod cues are unlikely to underlie the observed declines. Our model predicts such declines for most sites only at extreme warming (Supplemental Materials for details). In contrast to the common hypothesis that chilling declines with warming we found that chilling often increased with small amounts of warming, though this varied with local climate prior to warming (Fig. 3 A-D, supp heat map fig). 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!). 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. 3 E,F).

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 (cite Vitasse and other paper?). Physiologically budburst is triggered by the accumulation of forcing temperatures

(cites). Yet, researchers today often estimate temperature sensitivities from long-term observational data using a linear regression of annual budburst date data versus mean or other aggregate spring temperature measures. This approach has the benefit of yielding an easily interpretable metric—days change per °C—but will systematically estimate lower sensitivities given warmer average temperatures (supp figures), even with no change in the underlying cues. We found the declining sensitivities observed in European data are in magnitude with those predicted from a statistical artifact, and the data also show a related decline in variance that would not be immediately predicted from shifting cues (supp figures).

Our results suggest most or all studied species are responsive to chilling, forcing, and photoperiod, and we expect climate change to continue to have dramatic effects on spring phenology, especially because the two temperature-derived cues (chilling and forcing) 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. Our results comparing experiments to observations are only for one region, but highlight the critical nature of accurate forecasts of shifts in forcing and chilling at local scales. To do this, we desperately need to better understand chilling (i.e., the process of dormancy release), so that we can accurately predict it in the future. Current common models for chilling (i.e., Utah which was developed for XX species, chill portions which was developed for XX species) are *hypotheses* for how chilling may accumulate to affect the process of dormancy release, but are likely to be inaccurate for many species. Our model highlights how the choice of chill units can affect model estimates and associated forecasts (reference supplemental figure with utah units vs chill portions in main manuscript). Alongside this, we need improved fundamental understanding of the way these three cues interact. This requires larger studies across diverse species. 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 (Gauzere et al., 2017), unless cues are changing very asynchronously.
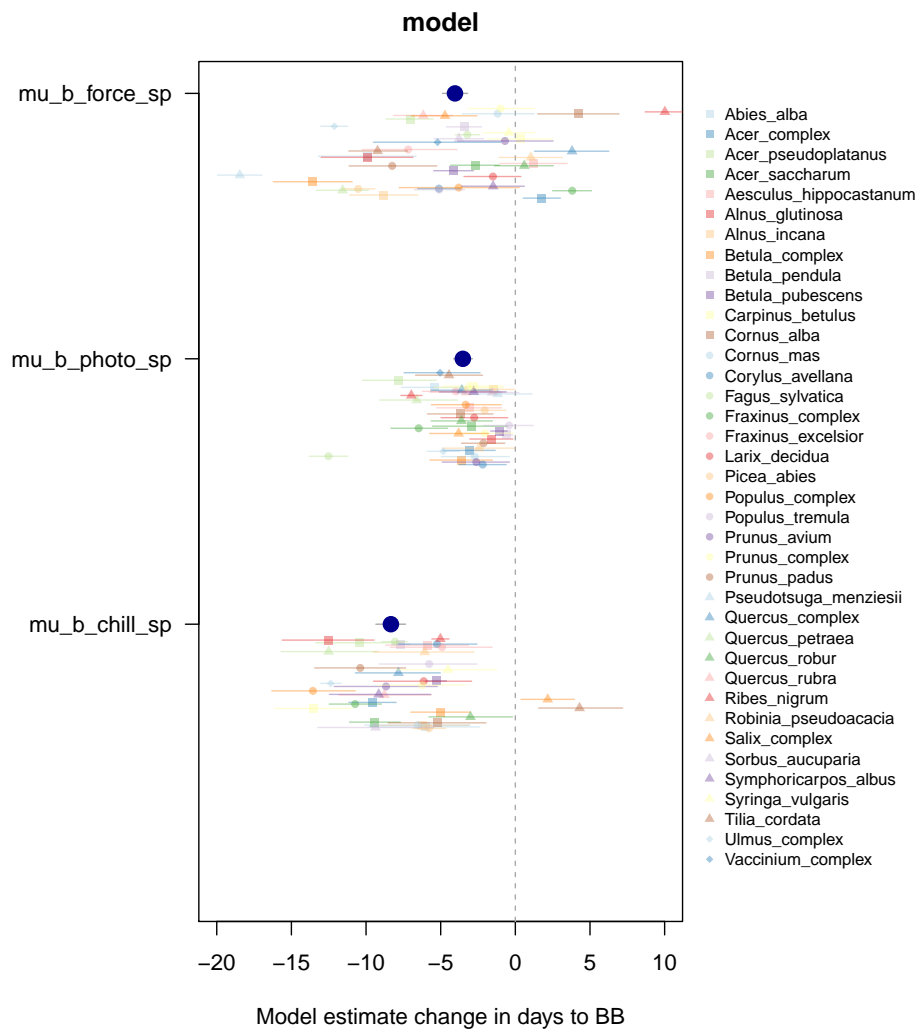
Figures

model

■	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
▲	Ribes_nigrum
▲	Robinia_pseudoacacia
▲	Salix_complex
▲	Sorbus_aucuparia
▲	Symphoricarpos_albus
▲	Syringa_vulgaris
▲	Tilia_cordata
●	Ulmus_complex
◆	Vaccinium_complex

Model estimate change in days to BB

Figure 1: Budburst model estimates

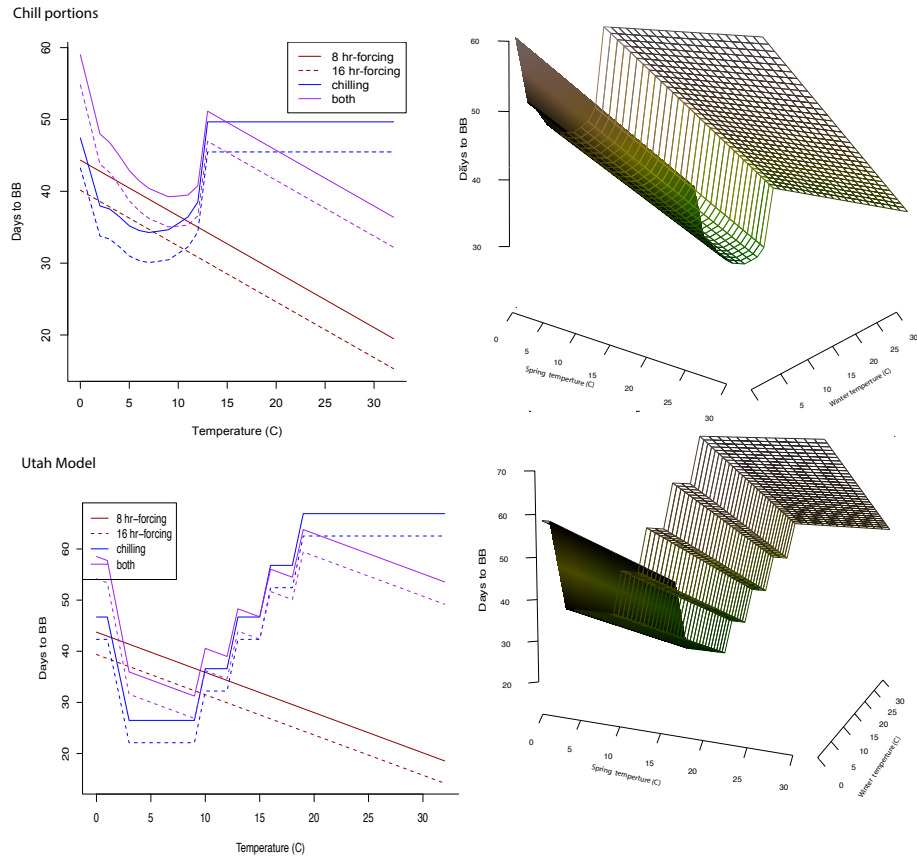for model fit to centered data with Chill Portions.

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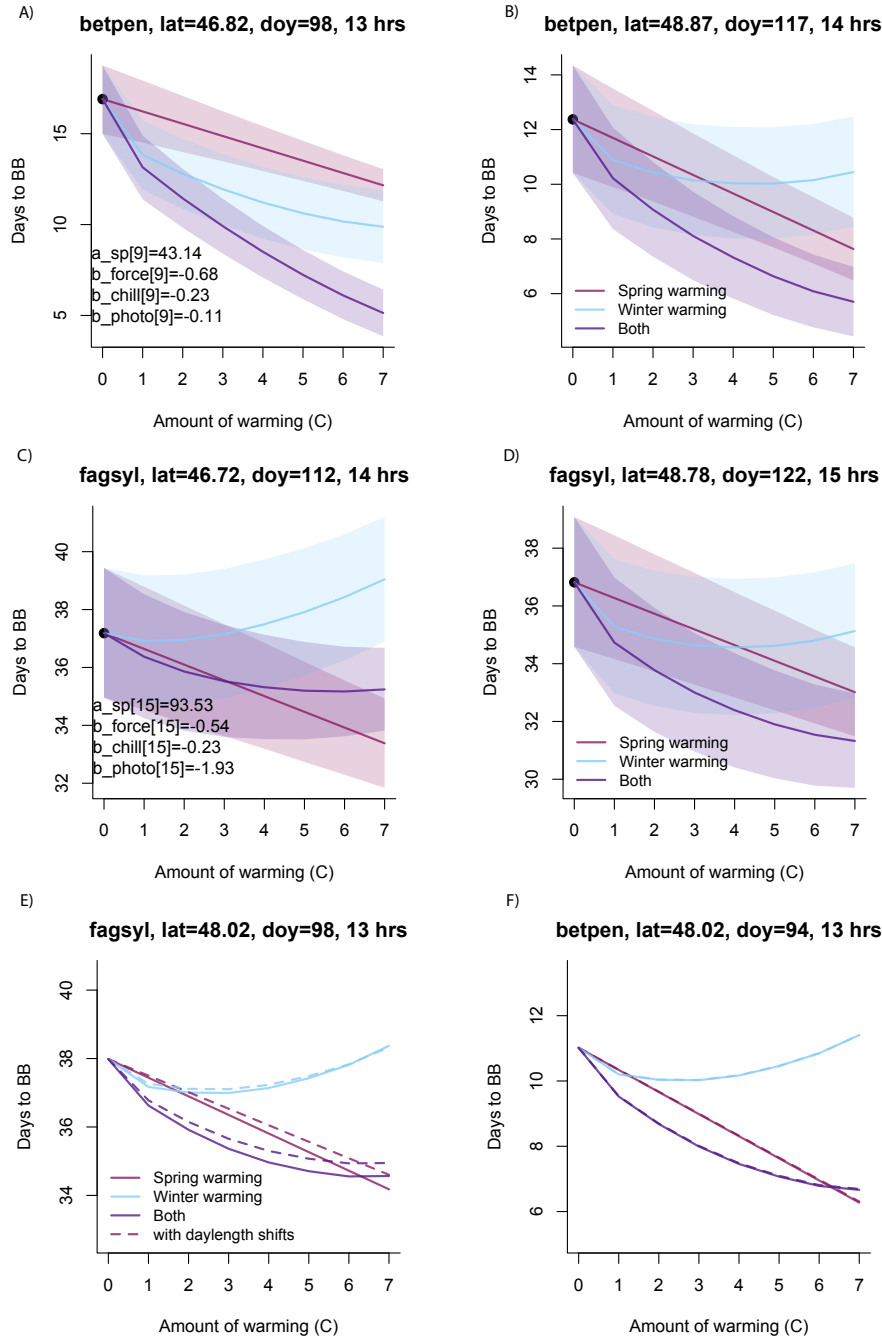
Figure 3: Implications of global warming on budburst of *Betula pendula* (A,B) and *Fagus sylvatica* (C,D) as predicted by the OSPREE model. We show the maximum and minimum latitudes at which each species occurred in the PEP database for Germany as examples; these locations differ in current climate.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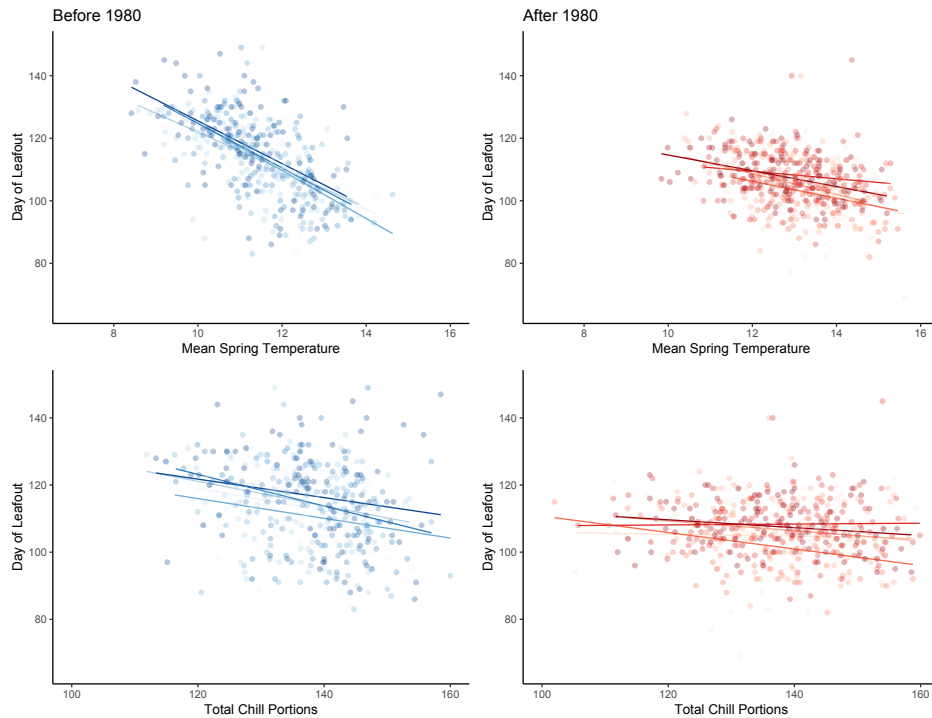
Figure 4: Implications of global warming on budburst of *Betula pendula* (A,B) and *Fagus sylvatica* (C,D) as predicted by the OSPREE model. We show the maximum and minimum latitudes at which each species occurred in the PEP database for Germany as examples; these locations differ in current climate.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

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. (2011*a*); Caffarra and Donnelly (2011); Caffarra et al. (2011*b*); Heide and Prestrud (2005); Koerner and Basler (2010*b*); 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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