

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

A.K. Ettinger, C. Chamberlain, I. Morales-Castilla, D. Buonaiuto, D. Flynn, T. Savas, J. Samaha & E. Wolkovich

May 13, 2019

Abstract

Decades of fundamental research on woody plant species highlight how three major cues shape spring phenological events: forcing (warm temperatures, generally occurring in the late winter and early spring), daylength, and chilling (cool temperatures, generally occurring in the fall and late winter). As research on the biological impacts of climate change has grown it has led to debate over whether forcing cues may dominate in nature for some or many species, while fewer respond to chilling and/or daylength. 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. 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 almost all species show strong responses to all three cues, with chilling being the strongest cue (numbers), followed by forcing (numbers) and daylength (numbers). 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 may not have a major impact on projections in well-studied areas (e.g., Central Europe) without warming of 4°C or more. Our results, thus, 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 Diez et al. (2012); 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*a*). 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, forcing, 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 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).

Resolving this debate requires overcoming major hurdles to estimate responses to each cue. While a number of studies have tried to do this using long-term observational data (CITES), these studies 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 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. To date, however, they have identified contrasting effects of the three major cues (Zohner et al., 2016; Laube et al., 2014; Basler and Körner, 2012; Caffarra et al., 2011b; Caffarra and Donnelly, 2011)

Resolving these discrepancies 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 chilling limits budburst, then we may see delays in spring phenology as further global warming reduces 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 reported budburst responses, 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 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 pennindula*) 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—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, in contrast, 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 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 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 the timing of 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 cause 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, our results suggest 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 versus mean or other aggregated metrics of spring temperature. 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 echo the growing call in phenological research to better understand chilling and its related physiological stage of endodormancy (cite CHUINE-GCB). Despite chilling being the strongest cue, we found few studies manipulate it 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 and exposure to ‘forcing’ conditions (cite Weinberger), with the assumption that tissues collected later experienced more chilling. The challenge with this method multifold: first, as we know little about what temperatures actually accumulate chilling it possible that in many systems time does not always co-vary with chilling, and, second, photoperiod and other factors will 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. Estimating chilling from field conditions is further confounded because 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. Despite their wide use neither has been robustly tested in forest trees, highlighting a major gap in our understanding, especially compared to perennial crops where research has more often identified the key physiological stages (endo- versus eco-dormancy) that formally differentiate

whether a plant is experiencing forcing or chilling, or both.

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. More accurate forecasts will need a greatly improved understanding of chilling and an improved fundamental understanding of the way these three cues interact (see supp). 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

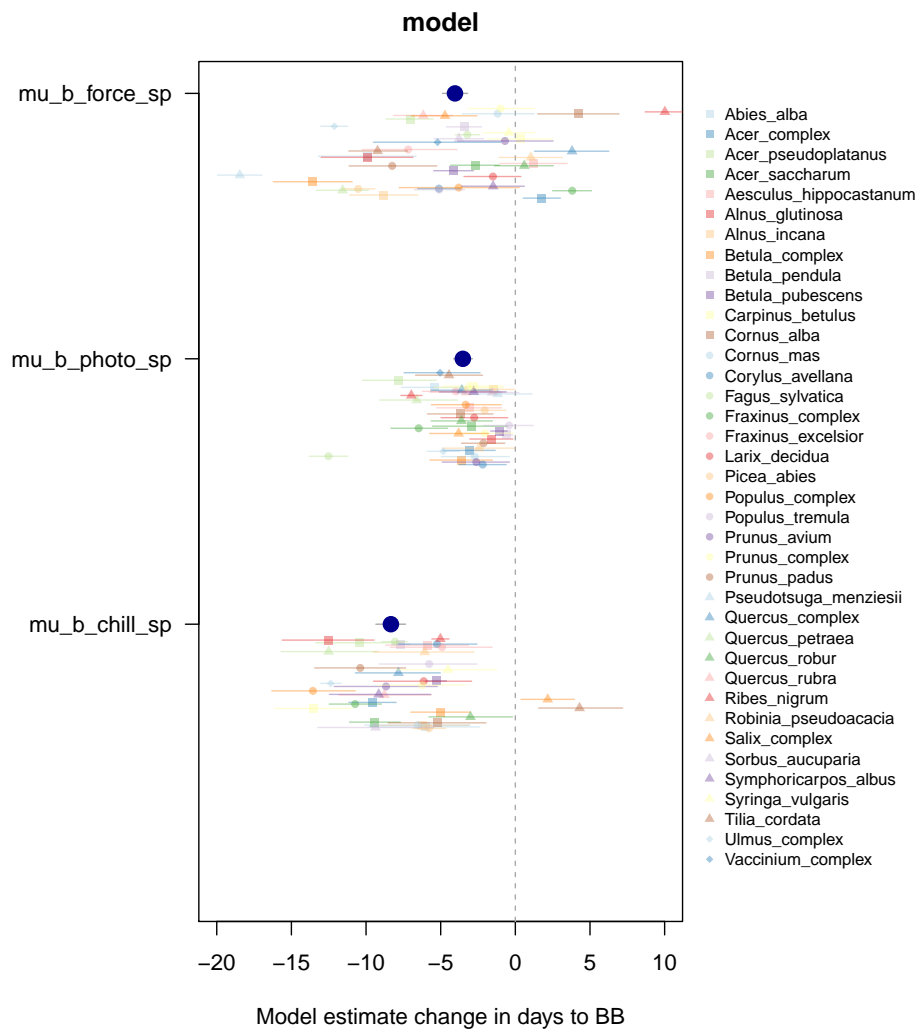


Figure 1: Budburst model estimates
for model fit to centered data with Chill Portions.

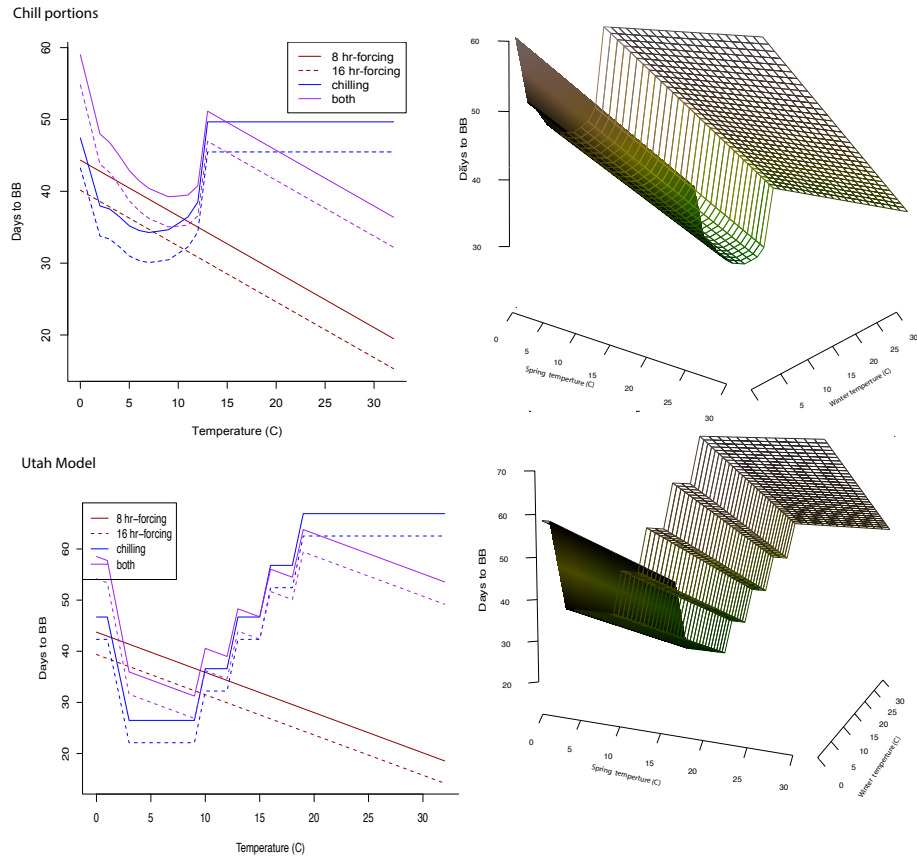


Figure 2: Effects of chilling, forcing, and photoperiod, across the experimental conditions in the OS-PREE database. Make this part of a 2-panel figure with 1?

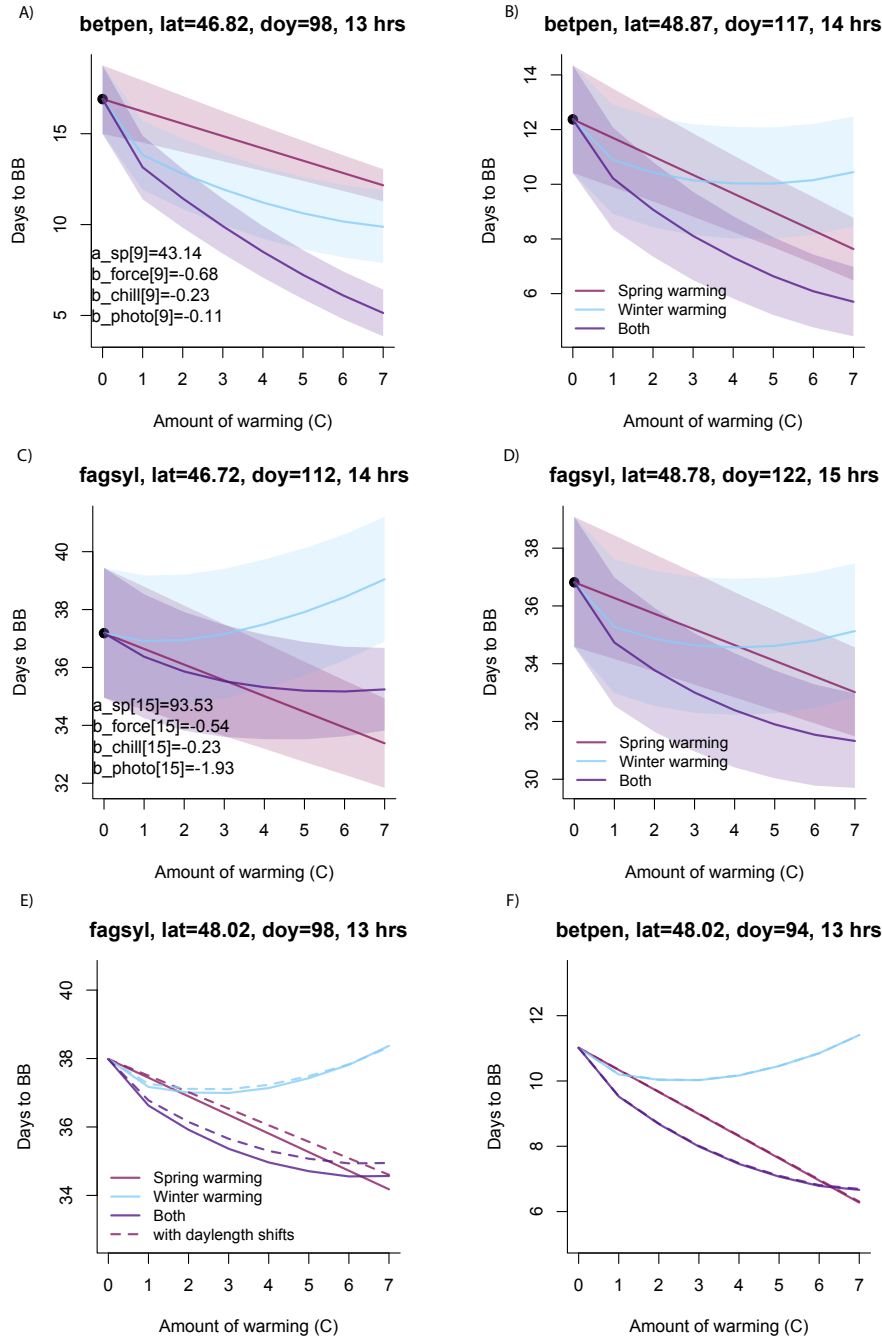


Figure 3: Implications of global warming on budburst of *Betula pendula* (A,B) and *Fagus sylvatica* (C,D) as predicted by the OSPREE model. We show the maximum and minimum latitudes at which each species occurred in the PEP database for Germany as examples; these locations differ in current climate.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

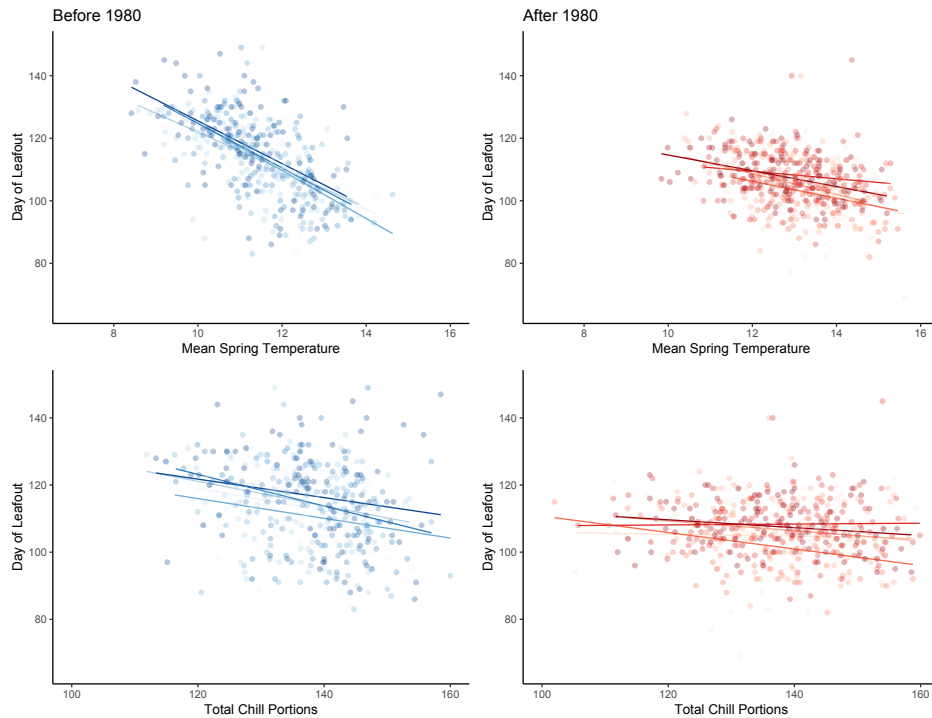


Figure 4: Implications of global warming on budburst of *Betula pendula* (A,B) and *Fagus sylvatica* (C,D) as predicted by the OSPREE model. We show the maximum and minimum latitudes at which each species occurred in the PEP database for Germany as examples; these locations differ in current climate. For all sites effects of potential shifts in photoperiod with advancing budburst 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. (2011a); Caffarra and Donnelly (2011); Caffarra et al. (2011b); Heide and Prestud (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)

References

- Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* 165:73–81.
- . 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree physiology* 34:377–388.
- Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change in wisconsin. *Proceedings of the National Academy of Sciences* 96:9701–9704.
- Caffarra, A., and A. Donnelly. 2011. The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *International journal of Biometeorology* 55:711–721.
- Caffarra, A., A. Donnelly, and I. Chuine. 2011*a*. Modelling the timing of *Betula pubescens* budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research* 46:159–170. Times Cited: 2 Caffarra, Amelia Donnelly, Alison Chuine, Isabelle.
- Caffarra, A., A. Donnelly, I. Chuine, and M. B. Jones. 2011*b*. Modelling the timing of *betula pubescens* bud-burst. i. temperature and photoperiod: A conceptual model. *Climate Research* 46:147.
- Chuine, I. 2000. A unified model for budburst of trees. *Journal of Theoretical Biology* 207:337–347.
- Diez, J. M., I. Ibáñez, A. J. Miller-Rushing, S. J. Mazer, T. M. Crimmins, M. A. Crimmins, C. D. Bertelsen, and D. W. Inouye. 2012. Forecasting phenology: from species variability to community patterns. *Ecology Letters* 15:545–553.
- Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* 0.
- Fraga, H., J. G. Pinto, and J. A. Santos. 2019. Climate change projections for chilling and heat forcing conditions in european vineyards and olive orchards: a multi-model assessment. *Climatic Change* pages 1–15.
- Fu, Y. S. H., H. F. Zhao, S. L. Piao, M. Peaucelle, S. S. Peng, G. Y. Zhou, P. Ciais, M. T. Huang, A. Menzel, J. P. Uelas, Y. Song, Y. Vitasse, Z. Z. Zeng, and I. A. Janssens. 2015. Declining global warming effects on the phenology of spring leaf unfolding. *Nature* 526:104–107.
- Gauzere, J., S. Delzon, H. Davi, M. Bonhomme, I. G. de Cortazar-Atauri, and I. Chuine. 2017. Integrating interactive effects of chilling and photoperiod in phenological process-based models. a case study with two european tree species: *Fagus sylvatica* and *quercus petraea*. *Agricultural and Forest Meteorology* 244:9–20.
- Harrington, C. A., and P. J. Gould. 2015. Tradeoffs between chilling and forcing in satisfying dormancy requirements for pacific northwest tree species. *Frontiers in Plant Science* 6:120.
- Heide, O., and A. Prestrud. 2005. Low temperature, but not photoperiod, controls growth cessation and dormancy induction and release in apple and pear. *Tree Physiology* 25:109–114.
- IPCC. 2014. *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Koerner, C., and D. Basler. 2010*a*. Phenology under global warming. *Science* 327:1461–1462.
- . 2010*b*. Warming, photoperiods, and tree phenology response. *Science* 329:278–278.

- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- Luedeling, E., and P. H. Brown. 2011. A global analysis of the comparability of winter chill models for fruit and nut trees. *International Journal of Biometeorology* 55:411–421.
- Luedeling, E., E. H. Girvetz, M. A. Semenov, and P. H. Brown. 2011. Climate change affects winter chill for temperate fruit and nut trees. *Plos One* 6.
- Luedeling, E., L. Guo, J. H. Dai, C. Leslie, and M. M. Blanke. 2013. Differential responses of trees to temperature variation during the chilling and forcing phases. *Agricultural and Forest Meteorology* 181:33–42.
- Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kuebler, et al. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.
- Miller-Rushing, A. J., and R. B. Primack. 2008. Global warming and flowering times in Thoreau’s Concord: A community perspective. *Ecology* 89:332–341.
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169:156–173.
- Rutishauser, T., J. Luterbacher, C. Defila, D. Frank, and H. Wanner. 2008. Swiss spring plant phenology 2007: Extremes, a multi-century perspective, and changes in temperature sensitivity. *Geophysical Research Letters* 35:L05703. Rutishauser, This Luterbacher, Juerg Defila, Claudio Frank, David Wanner, Heinz.
- Vitasse, Y., and D. Basler. 2013. What role for photoperiod in the bud burst phenology of european beech. *European Journal of Forest Research* 132:1–8.
- Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau, J. Regetz, T. J. Davies, N. J. B. Kraft, T. R. Ault, K. Bolmgren, S. J. Mazer, G. J. McCabe, B. J. McGill, C. Parmesan, N. Salamin, M. D. Schwartz, and E. E. Cleland. 2012*a*. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485:494–497. Wolkovich, E. M. Cook, B. I. Allen, J. M. Crimmins, T. M. Betancourt, J. L. Travers, S. E. Pau, S. Regetz, J. Davies, T. J. Kraft, N. J. B. Ault, T. R. Bolmgren, K. Mazer, S. J. McCabe, G. J. McGill, B. J. Parmesan, C. Salamin, N. Schwartz, M. D. Cleland, E. E.
- Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau, et al. 2012*b*. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485:494–497.
- Yu, H. Y., E. Luedeling, and J. C. Xu. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America* 107:22151–22156. Yu, Haiying Luedeling, Eike Xu, Jianchu.
- Zohner, C. M., B. M. Benito, J. C. Svenning, and S. S. Renner. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* .