

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, 2010*b*; 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 (CITES). 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 223 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 only have major impact on projections in well-studied areas (e.g., Central Europe) above a warming of 4°C or more. 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*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 (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 (Chaine, 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 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, 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 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 pennsula*) 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). 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). 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 = 2.06 days per 240 Utah units, Figure 1. Responses to forcing, in contrast, were the most variable across species (sigma = 0.91 days per °C of warming).

As temperature is radically 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. 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 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 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 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. 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 (Vitasse et al., 2018; Gusewell et al., 2017). Physiologically budburst is triggered by the accumulation of forcing temperatures (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. 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 (supp figures), even with no change in the underlying cues. We found the declining sensitivities observed in European data are of the same magnitude as 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).

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 poorly understood (Chuine et al., 2016). Models of how species accumulate chilling are poorly developed for forest trees, with few relevant tests of at which temperatures species do or do not accumulate chilling. Instead, researchers generally rely on models developed for perennial fruit trees (i.e., Utah which was developed for peach species (Richardson, 1974), chill portions which was developed for XX species), which 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 multifold: first, chilling time may not always co-vary with chilling (CITE), 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), suggesting estimates from this method may be inaccurate.

An improved understanding of chilling could in turn alter our understanding of forcing. While researchers often define ‘chilling’ and ‘forcing’ treatments based on a temperatures, physiologically plants appear to accumulate forcing only once chilling requirements have been met (?). Our results show that these two

temperature-derived cues strongly affect budburst, thus the an improved physiological understanding of when plants are experiencing and actually accumulating chilling and forcing will be critical for accurate forecasts. With progress in this fundamental area, research may begin to address how these cues interact (see supp)—since climate change clearly altering both at once in many regions. 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

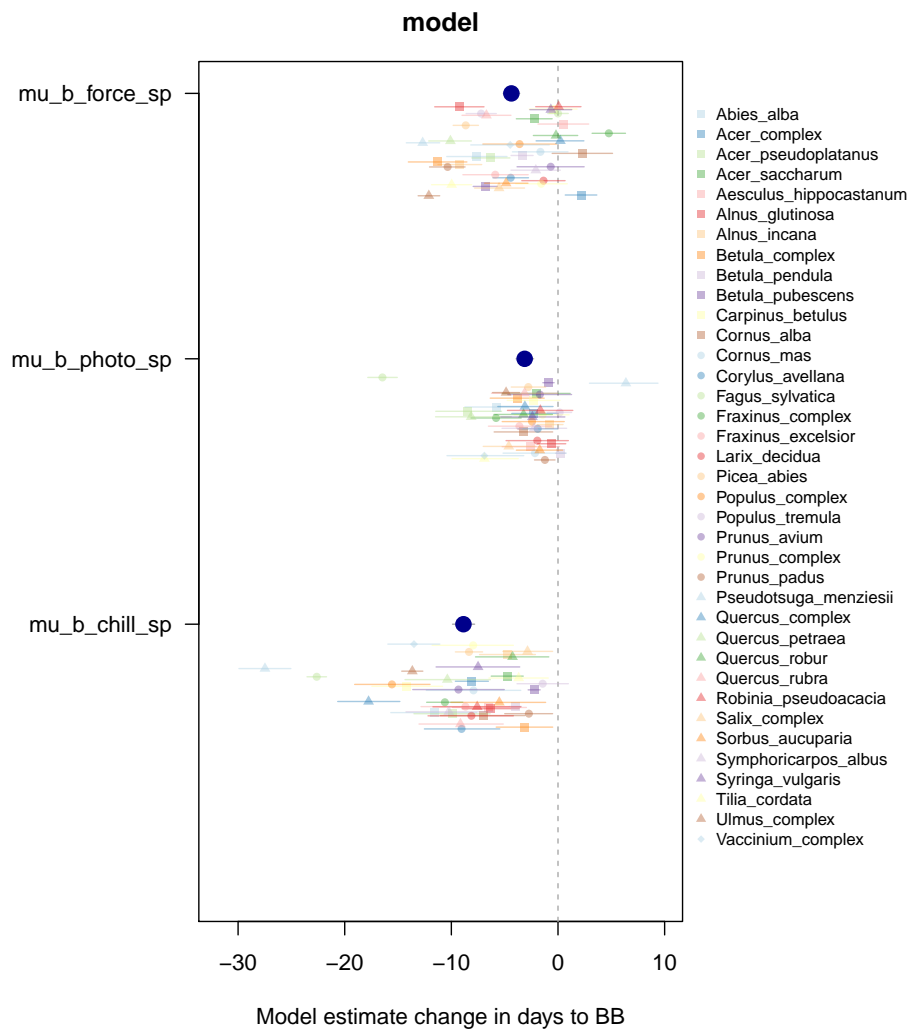


Figure 1: *Estimates for effects of chilling exceeded forcing and photoperiod estimates* in the budburst models fit to data from the OSPREE database. Here we show estimates from the model fit to centered data, enabling comparisons of effects sizes across predictors, and using Utah units to quantify chilling. Estimates to models fit to uncentered data and using Chill Portions were qualitatively similar and can be found in the Supplemental Materials.

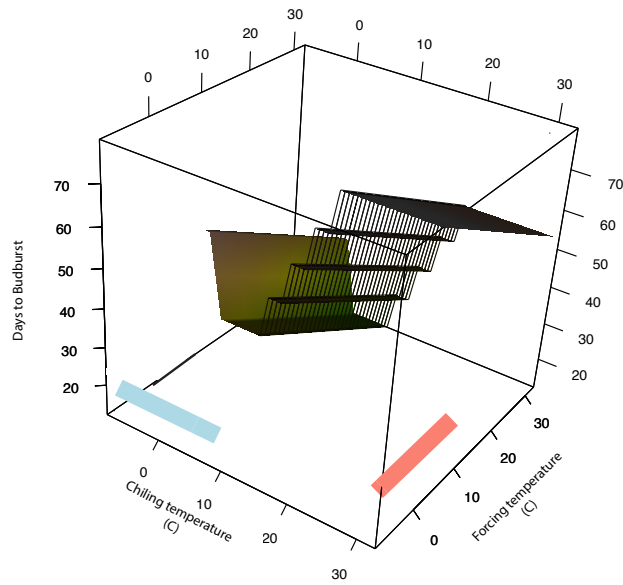


Figure 2: Based on the OSPREE model, days to budburst decrease linearly with forcing temperature and vary nonlinearly with chilling temperature due to the way that chilling is modeled (in this case, the Utah model; the model with Chill Portions is shown in the Supplemental Materials). Treatment temperatures in growth chamber experiments ranged from 0-30 °C (see Table 1S for details). Blue line shows mean winter temperatures in the range of *Betula pendula*, a European species that is one of the most common in OSPREE; pink line shows mean spring temperatures.

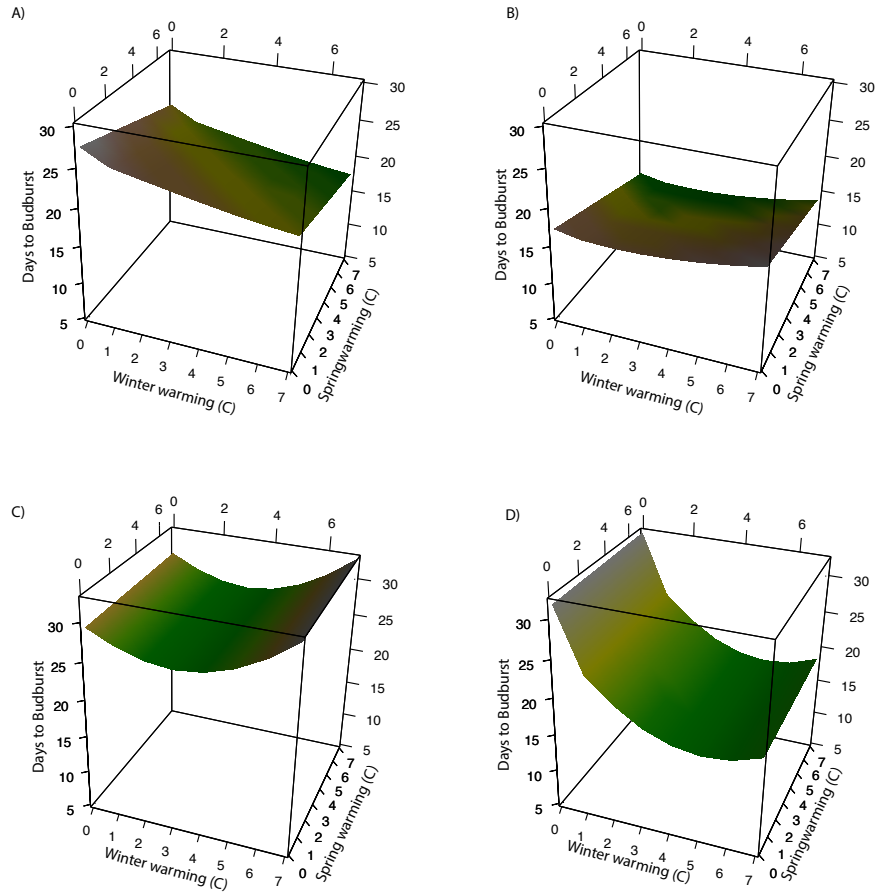


Figure 3: Implications of global warming on budburst varies by site, depending on pre-warming climate for the two most common species in the OSPREE database: *Betula pendula* (A,B) and *Fagus sylvatica* (C,D), as predicted by the OSPREE model. For sites in A and D, chilling increases with warming, whereas chilling decreases with warming for the sites in B and C. See Supplemental Materials, especially Table X, for details.

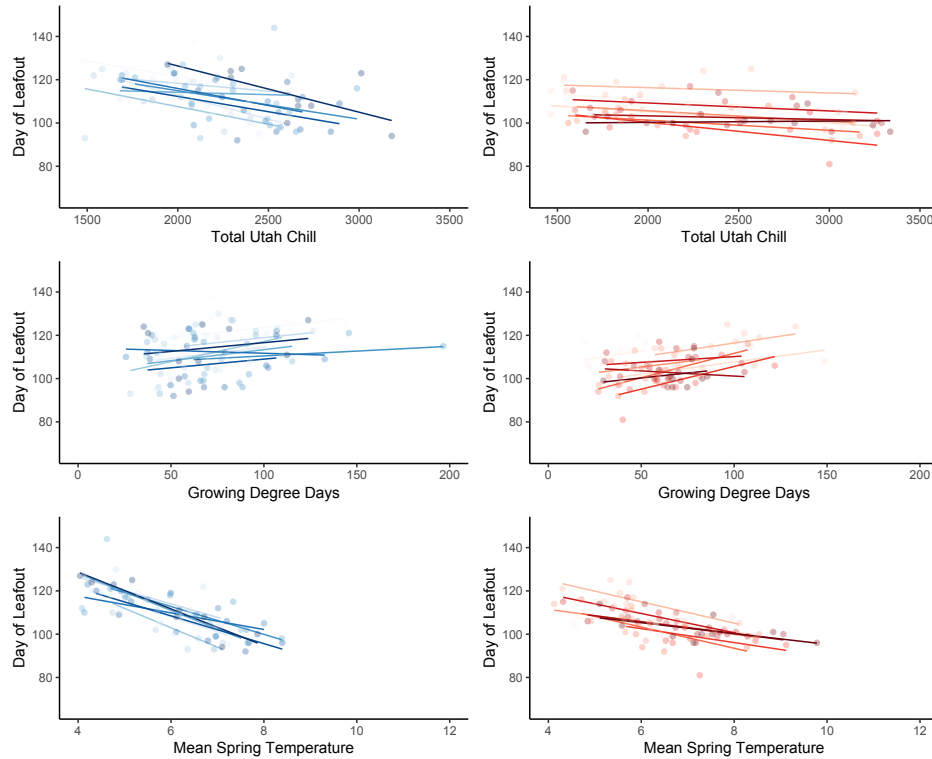


Figure 4: Implications of global warming on budburst of two common species in the OSPREE database, *Betula pendula* (A) and *Fagus sylvatica* (B) at the same site, as predicted by the OSPREE model. We show predicted budburst responses to winter and spring warming at one site where the two species co-occur (lat=48.02, long=) in the PEP database. Budburst day for *Fag syl* is 98, 1minimal effects of photoperiod. advancing budburst were minimal, even the photosensitive species *Fagus sylvatica*

References

- Balling Jr, R. C., P. J. Michaels, and P. C. Knappenberger. 1998. Analysis of winter and summer warming rates in gridded temperature time series. *Climate Research* 9:175–181.
- 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. 2011a. 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.
- Campbell, R. K., and A. I. Sugano. 1975. Phenology of bud burst in douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. *Botanical Gazette* pages 290–298.
- Chuine, I. 2000. A unified model for budburst of trees. *Journal of Theoretical Biology* 207:337–347.
- Chuine, I., M. Bonhomme, J.-M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global change biology* 22:3444–3460.
- Dennis, F. 2003. Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. *HortScience* 38:347–350.
- 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.
- Güsewell, S., R. Furrer, R. Gehrig, and B. Pietragalla. 2017. Changes in temperature sensitivity of spring phenology with recent climate warming in switzerland are related to shifts of the preseason. *Global change biology* 23:5189–5202.
- Hänninen, H. 1995. Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. *Canadian Journal of Botany* 73:183–199.
- 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. M. 2008. Interaction of photoperiod and temperature in the control of growth and dormancy of *Prunus* species. *Scientia Horticulturae* 115:309–314.
- . 2011. Temperature rather than photoperiod controls growth cessation and dormancy in *Sorbus* species. *Journal of experimental botany* page err213.
- 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.

- 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.
- Polgar, C. A., R. B. Primack, E. H. Williams, S. Stichter, and C. Hitchcock. 2013. Climate effects on the flight period of lycaenid butterflies in Massachusetts. *Biological conservation* 160:25–31.
- 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.
- Richardson, E. 1974. A model for estimating the completion of rest for ‘redhaven’ and ‘elberta’ peach trees. *HortScience* 9:331–332.
- 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.
- Vitasse, Y., C. Signarbieux, and Y. H. Fu. 2018. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences* 115:1004–1008.
- WEINBERGER, J. H., et al. 1950. Chilling requirements of peach varieties. Pages 122–28 *in* *Proceedings. American Society for Horticultural Science*. Vol. 56.
- 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* .