# Differences in flower and leaf bud responses to the environment drive shifts in spring phenological sequences of temperate woody plants

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## Introduction

One of the most widely documented biological effects of anthropogenic climate change are shifts in phenology, the timing of life cycle events, in plants (Parmesan & Yohe, 2003; Menzel *et al.*, 2006; Cleland *et al.*, 2007). While phenology is generally advancing with climate change, the strength of these phenological shifts can vary substantially among specific phenological phases (Augspurger & Zaya, 2020). These differences alter the timing of phases relative to each other, changing the the duration of inter-phase periods that make up phenological sequences (Ettinger *et al.*, 2018). Phenological sequences are a major driver of plant fitness that impact plant life history, resource allocation, demography and ecosystem processes (Post *et al.*, 2008). Shifts in phenological sequences will likely alter many of these processes, but the effects these shifts depend both on the direction (whether distinct phases are shifting closer together or farther apart) and magnitude (how much they are shifting relative to each other).

Among deciduous woody plants, the relative timing of flower and leaf phenology, or flower-leaf sequences (FLSs), may be particularly consequential to fitness in temperate regions where flowering prior to leaf development is common (Rathcke & Lacey, 1985; Gougherty & Gougherty, 2018). Long-term phenological observations over the last several decades indicate that, like other phenological sequences, FLSs are shifting due to anthropogenic climate change (Buonaiuto *et al.*, in review)—for several species, the time between flowering and leafing appears to be increasing, but the strength of this trend varies among species and the direction of FLS shifts are not consistent across populations. These changes could affect the important functions of FLSs, which may put some species at greater risk while benefiting others.

Flowering before leaf development may be a critical adaptation for pollination efficiency in wind-pollinated taxa by eliminating pollen interception by the forest canopy (Whitehead, 1969). In insect-pollinated taxa, flowering-first may increase the visibility of flowers to pollinators (Janzen, 1967; Savage, 2019). Species with decreasing FLS interphases with climate change may experience increased pollen limitation as more wind pollen is intercepted by vegetative structures and flowers are obscured by developing leaves. Conversely, pollination efficiency could improve for species with lengthening FLS interphases (direction). A change in the FLS interphase of just a few days would likely have little impact on these processes, but if shifts were on the order of weeks, the impact on the pollination biology of a species could be highly significant (magnitude).

Predicting the direction and magnitude of any FLS shifts requires identifying the underlying mechanisms that drive the different responses to climate change among these phenophases for a diversity of woody plant species. Decades of research suggests that for woody plants in temperate regions, cool winter temperatures (chilling), warm spring temperatures (forcing) and day-length (photoperiod) are the primary drivers of both reproductive and vegetative phenology (Forrest & Miller-Rushing, 2010; Flynn & Wolkovich, 2018). However, observed FLS shifts indicate that there must be differences in how these cues influence phenological activity in floral and leaf buds. Identifying these differences is a necessary step for predicting the direction and magnitude, and ultimately fitness impacts of FLS shifts with climate change.

Studies that have attempted to identify the differences between reproductive and vegetative phenology in woody plants have mostly focused on crop species and two common, yet competing, explanations have emerged:

One hypothesis suggests that reproductive and vegetative buds utilize the same underlying environmental cues, but have different threshold responses to forcing, with whichever bud type bursts later—leaves or flowers—having a higher threshold (Guo *et al.*, 2014; COSMULESCU & CALUSARU, 2020; Cosmulescu & Ionescu, 2018). Under this hypothesis, which we call the precocity hierarchy hypothesis (PHH), leaf and flower buds share the same suite of cues and develop similarly to non-forcing cues but they differ in the thermal units required for budburst.

By contrast, an alternative hypothesis suggests that flower and leaf buds differ in the strength of their phenological responses to the multiple environmental cues (Citadin *et al.*, 2001; Gariglio *et al.*, 2006; Aslamarz *et al.*, 2009; Mehlenbacher, 1991). Under this hypothesis, which we call the differential sensitivity hypothesis (DSH), despite the fact that leaf and flower buds are exposed to similar environmental conditions, each bud type may rely more or less on certain cues, producing different and variable phenological patterns.

While these mechanisms may produce similar phenological patterns under historic climate conditions, they have different implications regarding the potential for FLS shifts with climate change. The PHH suggests that FLS variation is largely a product of climate variation during the interphase. If spring temperatures increase with climate change, the second phenophase of the FLS with be accelerated relative to the first and the FLS interphases will decrease (see Supplement: Response Simulations) , but given the relative auto-correlation of spring temperatures (Di Cecco & Gouhier, 2018), these shifts should be relatively muted.

The DSH suggests that with significant cue use differences among bud types, there will be strongly localized effects of climate change on FLSs. Shifts in FLS variation will depend on the direction and rate of change in cues at specific locations and the differential sensitivity of reproductive and vegetative phenology to cue combinations. This hypothesis allows not only for larger magnitude shift in FLSs, it also suggest that the magnitude of shifts may be highly divergent among populations of the same species.

In this study we test these hypotheses by observing phenological responses to changing environmental conditions for both flower and leaf buds for a suite of temperate shrubs and trees. We subjected dormant twig cuttings of 10 species to multiple levels of forcing, chilling and photoperiod treatments in growth chambers and compared flower and leaf phenological responses to environmental change using a Bayesian hierarchical modeling approach. We then leveraged these data to to make generalized projections for how FLSs may shift with climate change and identify avenues for further research.

# Methods

## Growth chamber study

We sampled all plant material used in this experiment from Harvard Forest in Petersham, MA. On October 25, 2016, immediately after most plants in the area entered dormancy but before they could accumulate any significant chilling in the field, we collected branch cuttings from 7-13 individuals of 12 woody plant species (4-12 cutting per individual for a total of 48-56 per species). The species consisted of a mix of deciduous shrubs, understory and canopy trees commonly found in mesic hardwood forests of the eastern United States (see tab. S1 for species list). We transported all cuttings to the Arnold Arboretum in Boston, MA where they were re-cut in water to prevent callousing and cavitation and placed in 500 ml Erlenmeyer flasks with distilled water.

We randomly assigned cuttings to a full set of eight experimental treatments; two levels of chilling (4 vs 8 weeks at 4°C), two levels of temperature (24°C:18°C (day/night) warm vs 18°:12°C (day/night) cool) and two levels of photoperiod (12 vs 8 hours). We alternated day/night temperature periodicity on a 12 hour schedule to reduce co-variation with photo-periodicity. We re-cut all twig and changed the water every 7-10 days and rotated all treatments between growth chambers every two weeks to minimize chamber effects. We made phenological observations every 2-3 days using a modified BBCH scale for woody plants (Finn *et al.*, 2007) for three month following release from chilling conditions. In this period we assess two phenological phases: budbreak (BBCH phase 07)and first flower open (BBCH 60). At the conclusion of this period we assessed all individuals that did not undergo budbreak and excluded any dead individuals for analysis.

## Data analysis

To assess the sensitivity of each phase, we fit mixed-effect hierarchical models with chilling, forcing, photoperiod and all two-way interactions as the fixed effects and species as a grouping factor on both the slopes and the intercepts. We chose a Bayesian, hierarchical approach in order to identify systematic trends across species' responses while accounting for sample size, variance and the unique effect of each species. Two species *Betula allegheniensis* and *Acer saccharum* produced no flowers in our trial, so we excluded them from our analysis.

We modeled the effects of environmental parameters on flower opening and leaf budburst separately. We also fit a model with FLS interphase (day of budburst- day of flowering) as a response variable to compare these estimates with field observations.

The models we fit appear below:

$$y_{[i]} \sim N(\alpha_{sp_{[i]}} + \beta_{forcing_{sp[i]}} + \beta_{chilling_{sp[i]}} + \beta_{photoperiod_{sp[i]}} + \beta_{forcingxchilling_{sp[i]}} + \beta_{forcingxphotoperiod_{sp[i]}} + \beta_{chillingxphotoperiod_{sp[i]}})$$

Where $y_{[i]}$ is either the day of the experiment leaf budburst, day of first flower opening or FLS interphase length. We modeled the $\alpha$ and each $\beta$ parameter at the species level using the formula:

$$\alpha_{x_{sp}} \text{or } \beta_{x_{sp}} \sim N(\mu_x, \sigma_x^2)$$

It is possible that the PHH is a special case of the DSH that occurs when the chilling and photoperiod requirements of both bud types have been met. To test this hypothesis, we re-ran our models on a subset of our data which included both levels of forcing treatment but only the high photoperiod and chilling treatment levels. This model included forcing as the only main effect but, like our main models written above, included species as a grouping factor on the model slope and intercept.

We fit all models using the R package "brms" (Bürkner, 2018). We ran each model on four chains with 4000 iterations with a 3000 iteration warm up for a total of 4000 sampling iterations. In all models we used weakly informative priors and increasing the priors 5-fold did not affect the model results.

## Climate change predictions

To apply our model results to general climate change projections we chose our environmental treatments in this experiment to broadly reflect historic and future conditions at our sampling site. Our low forcing treatment approximated average spring temperature (March/April) at the site while our high temperature treatment reflects a 5 °C increase. Average field chilling (calculated from 15 Oct - 15 April, measured in Utah units) at Harvard Forest is 979.64, approximately 60% of the difference between our low and high chilling treatment (Fig. S2). Thus, our low chilling treatment represents a feasible estimate for a decrease in chilling with climate change and our high chilling treatment approximate reasonable increase. We should note that our low photoperiod treatment (8 hours of daylight) is well below the photoperiod experienced at Harvard Forest, but given that the photoperiod effects are expected to be small, we chose more extreme values in order to robustly estimate an effect (i.e., increasing statistical power). For this reason, our climate change projections for FLS variation are based on our high photoperiod treatment alone.

We used our flower and budburst models to project for each species in our study:

1. FLSs under average environmental conditions (treatments: low forcing, 6.5 weeks of chilling treatment)
2. FLS shifts with spring warming only (high forcing, 6.5 weeks of chilling treatment)
3. FLS shifts with warming and increased chilling ((high forcing, 8 weeks of chilling treatment)
4. FLS shifts with warming and decreased chilling ((high forcing, 4 weeks of chilling treatment)

To validate our predictions, we compared our FLS interphase model estimates of "average" condition FLS interphases to long term phenological records from Harvard Forest (O'Keefe, 2015) for five species common to both datasets (Fig. S2), and found them to be comparable. Given the variable dynamics of shifts in environmental forcing and chilling with climate change over time and space, these projections should not be treated as absolute predictions of the magnitude of FLS shifts with climate change. Instead, we provide these projections to identify general trends in how FLSs could shift with warming and demonstrate the range of possibilities vary based on individual characteristics of plant species and the specific climate dynamics.

# Results

## Growth chamber study

Both flower and leaf buds advanced with higher forcing and longer chilling duration (flowers: 21 day advance/$\Delta$ chilling duration, 18 day advance/$\Delta$ forcing temperature, leaves: 30 day advance/$\Delta$

chilling, 17 day advance $\Delta$ forcing) , but increases in both of these cues together offset these advances as seen in the delaying effect of their interaction ( by 6 and 12 days for flowers and leaves respectively) (Fig. 1, Tab. **??**). Leaf and flower buds diverged in their responses to increasing photoperiod, with flower phenology advancing and leaf phenology being delayed when the other two cues were at low levels (Fig. 1, Tab. **??**). As seen in the interactions between photoperiod and chilling and photoperiod and forcing, increasing chilling or forcing with longer photoperiod advanced the phenology of both bud types. For both bud types, chilling and forcing were the dominant cues, while increasing photoperiod produced a more muted phenological response (Fig. 1).

While leaf and flower bud phenological responses to environmental cues were qualitatively similar, the strength of their responses to each cue differed substantially. Leaf buds responded more strongly to chilling than flower buds (1.4x) , and had a stronger response to all cue interactions(forcing:chilling 2x, photoperiod:chilling 7.1x, photoperiod:forcing 2.4x) (Fig. 1Tab. **??**). Across all species both bud types displayed a relatively proportionate response to forcing (18 and 17 day advance for flower and leaves respectively) (Fig. 1, Tab. **??**)

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While there was significant variation among species in their strength of their response to forcing between bud types, no species displayed the characteristic sensitivity pattern of the PHH in which the sensitivity to forcing of the second phase twice as strong as the sensitivity of the first phase (Supplement: Simulated Response). Rather, the differences in the strength of the responses of each bud type to each environmental cue combination is signature of the DSH. However, when re-ran our models on the subset of data which included phenological observation at only high levels of chilling and photoperiod, we found the the sensitivity to forcing for all species followed with predicted pattern of the PHH, with the second phase of the FLS showing approximately double the sensitivity to forcing than the first phases (Fig. 2, add a table?).

## Climate change predictions

Our model predicted that both flower and leaf phenology will advance in most of our generalized scenarios for most species, but shifts in FLS depended strongly on how forcing levels change relative to chilling duration (Fig. 3). Following the significant differences in sensitivity to chilling between flowering and leafing phenology we found in our model, FLS interphases were more strongly influenced by changes in chilling exposure than increased forcing alone. The direction and magnitude of shifts in FLS interphases depended on species and the specifics of FLS phase order, with flowering-first and flowering-concurrently species tending to show more profound alterations to FLS patterns than leafing-first taxa. Under some warming scenarios, our model predicted that FLS interphases for some species may effectively disappear or the order of phenophases in the FLS may switch (Fig. 3).

# Discussion

In our study, variation in FLS patterns of deciduous woody plants was dictated by differences in the strength of the response of flower and leaf buds to the primary environmental cues of spring phenology, with differences in the chilling response among bud types being the strongest driver of FLS variation. These result suggest that climate change has potential to significantly disrupt FLSs as global warming alters historic chilling patterns across the temperate zone. Across all of our treatment combinations, there were species level differences in the magnitude of differential sensitivity to environmental cues, but under the high chilling duration and photoperiod treatment, which approximated the historic conditions at our collection site, the FLSs for most species followed the predicted pattern of the PHH, with the sensitivity of the second phase of the FLS to forcing approximately twice as strong as that of the first phase 2. This may explain why the two FLS hypotheses have been difficult to distinguish under current field conditions where in most locations chilling requirements for both bud type were frequently met under historic climate conditions ()(Lizzie: Do you know of any citations for this?). In conjunction with site-specific FLS shifts and species-specific FLS functions, the difficulty of assessing differential sensitivity in contemporary field conditions suggests there is a need for generalizing principles from experimental studies to more fully anticipate the implications of FLS shifts and focus research efforts to the species that may be most affected by FLS shifts with climate change.

## Reconciling the differential sensitivity and the precocity hierarchy hypotheses

The strong differential sensitivity to chilling between flower and leaf buds we found in our study reveals a possible mechanistic link between the DSH and PHH, and offers insight into why these hypotheses have been difficult to differentiate in the past. Our data show that the PHH can be considered to be a special case of the DSH– when the chilling requirement for both flower and leaf buds is met, an an individual appear to follow the predicted pattern of PHH, with temperature during the FLS interphase dictating the inter-annual variability in FLSs. Long term studies suggest that under historic climate conditions, chilling requirements were generally met (), which may explain why support for the PHH most often associated with observational studies (e.g. COSMULESCU & CALUSARU, 2020; Guo *et al.*, 2014). This is consistent with findings in other phenological studies that suggest simple growing degree models (which underlie the PHH) accurately predict phenology under current climate, but under-perform under climate change scenarios when shifts in chilling accumulation become more pronounced (Linkosalo *et al.*, 2008).

By contrast, experimental studies which manipulate chilling levels beyond which was historically observed in the field tend to support the DSH (e.g. Aslamarz *et al.*, 2009; Gariglio *et al.*, 2006). The results of our study in wild species are consistent with experimental manipulations of tree-crop phenology which also found a higher sensitivity to chilling for leaf buds (Gariglio *et al.*, 2006; Citadin *et al.*, 2001). Our findings suggest that as climate continues to change, differential sensitivity to the environment between flower and leaf phenology should become more apparent in field observations. However, the adherence of FLSs to the precocity hierarchy patterning under historic conditions suggest that historical range of FLS variation does not constrain the potential for FLS shifts with climate change.

## Implications of the DSH for flower leaf sequences with climate change

The strong differential sensitivity to chilling the between flower and leaf buds we found in our study suggests complex FLS dynamics with climate change. Predicted shifts in chilling are highly variable across both time and space– because chilling only accumulates at intermediately low temperatures warming may increase chilling at some locations while decreasing it in others (Ettinger & et al.). This suggests that the direction and magnitude of FLS shifts is likely to vary substantially among populations based on the specific cue combinations at a given locality. Long-term phenology records show there was already substantial intra-specific variation in FLSs at the population level (Buonaiuto *et al.*, in review) and our findings suggest that these populations level differences may be further amplified by climate change. In this way, all the three generic FLS climate change scenarios depicted in Fig. 3 should not be considered alternatives to each other, but rather, could occur contemporaneously across a species' range.

Population level heterogeneity has potential to influence patterns of pollen dispersal and gene flow across the landscape (Borycka *et al.*, 2017; Pace *et al.*, 2018). For example, advancing canopy closure relative to flowering impedes long-distance pollen transport (**?**). With divergent FLS shifts at the population level, sires from populations in which climate dynamics are extending FLS interphases may increase their contribution landscape patterns of gene flow relative to populations in which FLSs are reduced. Depending on the spatial arrangement of these populations and other factors such as pollinator movement or prevailing wind directions, this could either facilitate or impeded genetic rescue of climate stressed populations (Kling & Ackerly, 2020). Despite these important implications, there is currently little scholarship regarding how inter-population variation in FLS patterns may impact population biology and this should remain an active area of research inquiry.

The implications of our study's observed differential sensitivity to photoperiod to FLS shifts with climate change are more difficult to characterize. Climate change does not directly impact photoperiod, but warming does shift the time of year when plants become phenologically active, changing the photoperiod they experience. However, depending on the latitude, phenology would have to shifts by at minimum several weeks before the experience photoperiod would change substantially ()(Us, in prep-ish). For this reason we modeled climate change scenarios with a constant photoperiod in our FLS projections with climate change, but at high latitudes where photoperiod changes more rapidly over the season, the experienced photoperiod may mute or amplify the FLS shifts captured in our projections. This may be particularly important as species shift shift their distribution pole ward with climate change and begin to encounter novel photoperiod regimes (WAY & MONTGOMERY, 2015).

Our study also highlights that the direction and magnitude of FLS shifts with climate change are species specific. Not only is it likely that the function of FLS variation differs among species (Buonaiuto *et al.*, in review), but we found that FLSs of some species were very sensitive to changing climate conditions while other remain fairly resilient (Fig. 3). These differences suggest that some FLS shifts will impact some more than others, and researchers should focus their efforts towards species or populations that are likely to be most vulnerable. However, identify vulnerable species is challenging. At present, observational studies cannot capture the magnitude of FLS shifts with climate, and using artificial environments to manipulate FLSs for all species of interest is unfeasible. Therefore, there is a strong need for generalizing principles to aid in identify species with potential for consequential FLS shifts with climate change. While one study cannot hope to represent the taxonomic diversity of a temperate forest, we identified several patterns in the FLS responses of our multi-species experiment that may serve as starting point for further inquiry.

## 0.1 Generalizing principles for species-specific FLS shifts

In our study several species, *Acer rubrum* ,*Ilex verticillata*, *Prunus pensylvanicum*, *Prunus virginiana*, and *Viburnum acerifolium*, had FLSs that were relatively robust to changing environments. For other species, *Acer pensylvanicum*, *Vaccinium corymbosum* and *Ilex mucronata*, which typically begin to produce leaves shortly before flowers open, the magnitudes of projected FLS shifts were moderate. The two species with the most significant FLS shifts in both direction and magnitude across treatment combinations and climate change projections were *Comptonia peregrina* and *Corylus cornuta* (Fig. 3). In all of our climate change scenarios, the FLS interphase was dramatically reduced in these taxa.

It is likely that these three difference response patterns we observed correlate to broader anatomical, physiological and phenological differences among species. The species that maintained FLS structure across climate change scenarios generally shared a strongly leafing-first FLS, with a fairly long FLS interphase. These species tended to have mixed buds so there may be strong physical constraints on their FLSs. By contrast, the species that were most sensitive to FLS shifts were monoecious, flowering-first, wind-pollinated shrubs. This result may reflect other evidence that wind-pollinated species appear to be more sensitive to climate change than biotically pollinated taxa (Ziello *et al.*, 2012). Given the hypothesized function of FLS in wind-pollinated species, the direction and magnitude of FLS shifts we observed could suggest that that these species, and flowering-first, wind-pollinated taxa in general, may face particular risk for reproductive performance reductions.

Much of the conversation around phenology and pollination in the context of global change has centered around trophic mismatches between pollinator and floral phenology (Memmott *et al.*, 2007), which is of little relevance to abiotically pollinated taxa. By contrast, the possibility that the effect of FLS shifts with climate change may be particularly important for wind-pollinated woody plants and the scope and impact of FLS shifts in these taxa suggest they should be explored in greater detail in the future.

# Conclusion:

Our experiment provides strong evidence that while flower and leaf buds respond to the same environmental cues to initiate spring phenological activity, the different bud types rely on each cue with differing strength. This differential sensitivity to cues drives variation in flower-leaf sequences and will dictate the magnitude and direction of FLS shifts with climate change. Shifts in FLSs with climate change are likely to vary across forest communities and depend on the specific combinations of cue levels at a given locality and the species represented there. More research is needed to identify species' traits that may correlate with the potential for FLS shifts, but flowering-first, wind-pollinated species may be particular sensitive to FLS shifts and merit continued research focus.

# References


Aslamarz, A.A., Vahdati, K., Rahemi, M. & Hassani, D. (2009) Estimation of chilling and heat requirements of some persian walnut cultivars and genotypes. *HortScience* **44**, 697–701.

Augspurger, C.K. & Zaya, D.N. (2020) Concordance of long-term shifts with climate warming varies among phenological events and herbaceous species. *Ecological Monographs* **n/a**, e01421.

Borycka, K., Ortyl, B. & Kasprzyk, I. (2017) Temporal variations and spatial differentiation in the black alder and silver birch pollination pattern-the impact of local climate or something more? *AGRICULTURAL AND FOREST METEOROLOGY* **247**, 65–78.

Buonaiuto, D., Moralles-Castilla, I. & Wolkovich, E.M. (in review) Reconciling competeing hypothesis for fls and what not. .

Bürkner, P.C. (2018) Advanced bayesian multilevel modeling with the r package brms. *R Journal* **10**, 395–411.

Citadin, I., Raseira, M.C.B., Herter, F.G. & da Silva, J.B. (2001) Heat requirement for blooming and leafing in peach. *HortScience HortSci* **36**, 305–307.

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology  Evolution* **22**, 357 – 365.

COSMULESCU, S. & CALUSARU, F.G. (2020) Influence of temperature on blackthorn (¡i¿prunus spinosa¡/i¿ l.) phenophases in spring season. **advpub**, –.

Cosmulescu, S. & Ionescu, M. (2018) Phenological calendar in some walnut genotypes grown in romania and its correlations with air temperature. *International Journal of Biometeorology* **62**.

Di Cecco, G.J. & Gouhier, T.C. (2018) Increased spatial and temporal autocorrelation of temperature under climate change. *Scientific Reports* **8**, 14850.

Ettinger, A., Gee, S. & Wolkovich, E. (2018) Phenological sequences: how early season events define those that follow. *American Journal of Botany* **105**.

Ettinger, A.K. & et al. (????) Buburst paper. *in review* .

Finn, G.A., Straszewski, A.E. & Peterson, V. (2007) A general growth stage key for describing trees and woody plants. *Annals of Applied Biology* **151**, 127–131.

Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.

Forrest, J. & Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3101–3112.

Gariglio, N., González Rossia, D.E., Mendow, M., Reig, C. & Agusti, M. (2006) Effect of artificial chilling on the depth of endodormancy and vegetative and flower budbreak of peach and nectarine cultivars using excised shoots. *Scientia Horticulturae* **108**, 371–377.

Gougherty, A.V. & Gougherty, S.W. (2018) Sequence of flower and leaf emergence in deciduous trees is linked to ecological traits, phylogenetics, and climate. *New Phytologist* **220**, 121–131.

Guo, L., Luedeling, E., Dai, J. & Xu, J. (2014) Differences in heat requirements of flower and leaf buds make hysteranthous trees bloom before leaf unfolding. *Plant Diversity and Resources* **36**, 245–253.

Janzen, D.H. (1967) Synchronization of sexual reproduction of trees within the dry season in central america. *Evolution* **21**, 620–637.

Kling, M.M. & Ackerly, D.D. (2020) Global wind patterns and the vulnerability of wind-dispersed species to climate change. *Nature Climate Change* **10**, 868–875.

Linkosalo, T., Lappalainen, H.K. & Hari, P. (2008) A comparison of phenological models of leaf bud burst and flowering of boreal trees using independent observations. *Tree Physiology* **28**, 1873–1882.

Mehlenbacher, S.A. (1991) Chilling requirements of hazelnut cultivars. *Scientia Horticulturae* **47**, 271–282.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007) Global warming and the disruption of plant–pollinator interactions. *Ecology Letters* **10**, 710–717.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kuebler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatcza, K., Mage, F., Mestre, A., Nordli, O., Penuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach,

S. & Zust, A. (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**, 1969–1976.

O'Keefe, J. (2015) *Phenology of Woody Species at Harvard Forest since 1990.* Harvard Forest Data Archive: HF003., Petersham, MA, USA.

Pace, L., Boccacci, L., Casilli, M., Di Carlo, P. & Fattorini, S. (2018) Correlations between weather conditions and airborne pollen concentration and diversity in a mediterranean high-altitude site disclose unexpected temporal patterns. *Aerobiologia* **34**, 75–87.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37 EP –.

Post, E.S., Pedersen, C., Wilmers, C.C. & Forchhammer, M.C. (2008) Phenological sequences reveal aggregate life history response to climatic warming **89**, 363–370.

Rathcke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**, 179–214.

Savage, J.A. (2019) A temporal shift in resource allocation facilitates flowering before leaf out and spring vessel maturation in precocious species. *American Journal of Botany* **106**, 113–122.

WAY, D.A. & MONTGOMERY, R.A. (2015) Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment* **38**, 1725–1736.

Whitehead, D.R. (1969) Wind pollination in the angiosperms: Evolutionary and environmental considerations. *Evolution* **23**, 28–35.

Ziello, C., Böck, A., Estrella, N., Ankerst, D. & Menzel, A. (2012) First flowering of wind-pollinated species with the greatest phenological advances in europe. *Ecography* **35**, 1017–1023.

# Figures

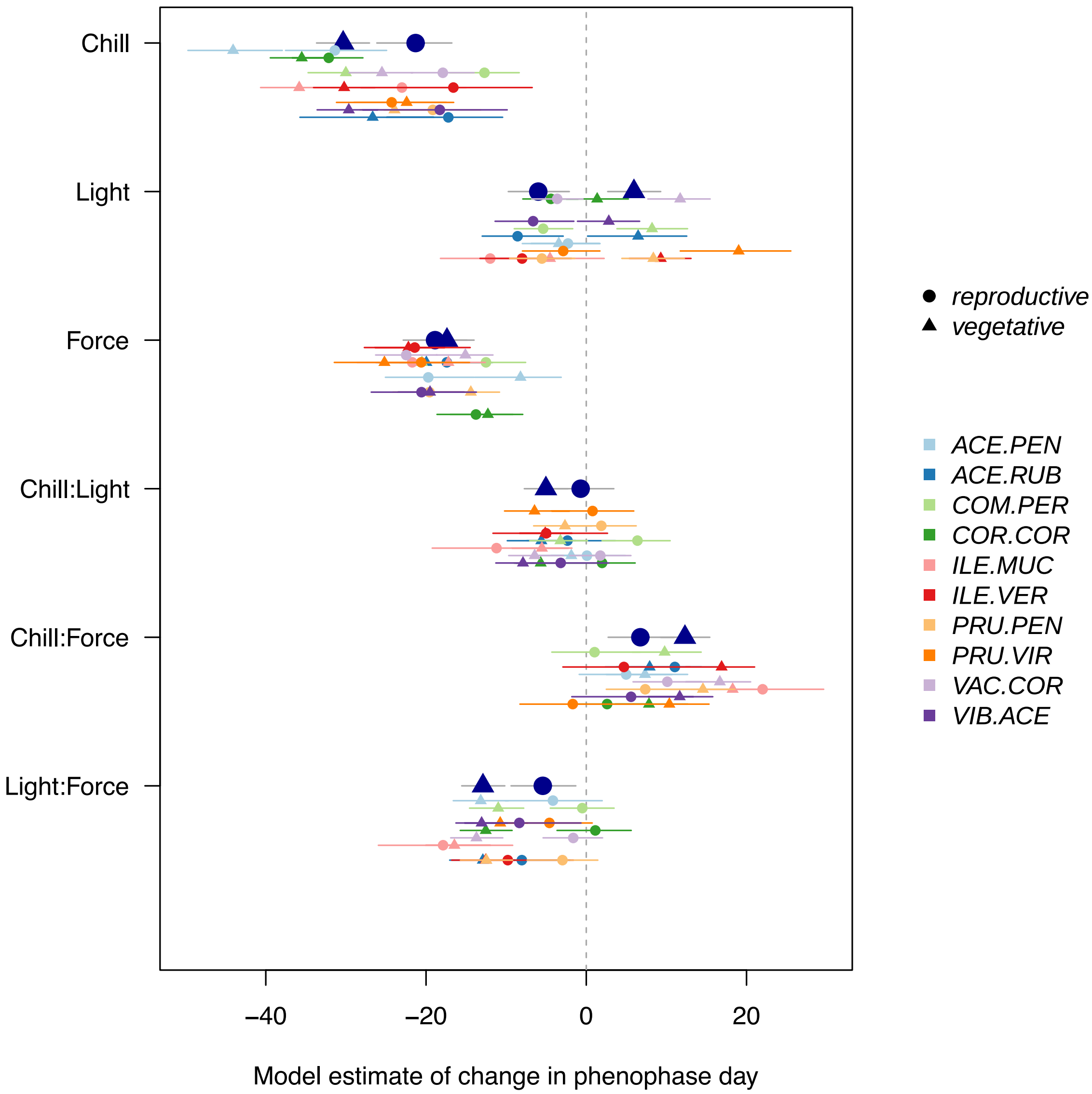


Figure 1: **Experimental results suggest differential sensitivity to environmental cues between flower and leaf buds**. We used a growth chamber manipulation and Bayesian hierarchical models to evaluate the phenological sensitivity ($\Delta$ day of phenological event/ $\Delta$ environmental cue) of flower and leaf buds to varying forcing temperatures, photoperiods, and duration of chilling. Vegetative buds (circles) were more sensitive to chilling and cue interactions. Flower buds (triangles) advanced with photoperiod increases under all treatment combinations but leaf phenology was delayed with increasing photoperiod when chilling and forcing levels were low. Points indicate meaan estimates and lines represent the 50 % credible intervals. These differential sensitivities dictate how FLS patterns vary with changing environmental conditions.

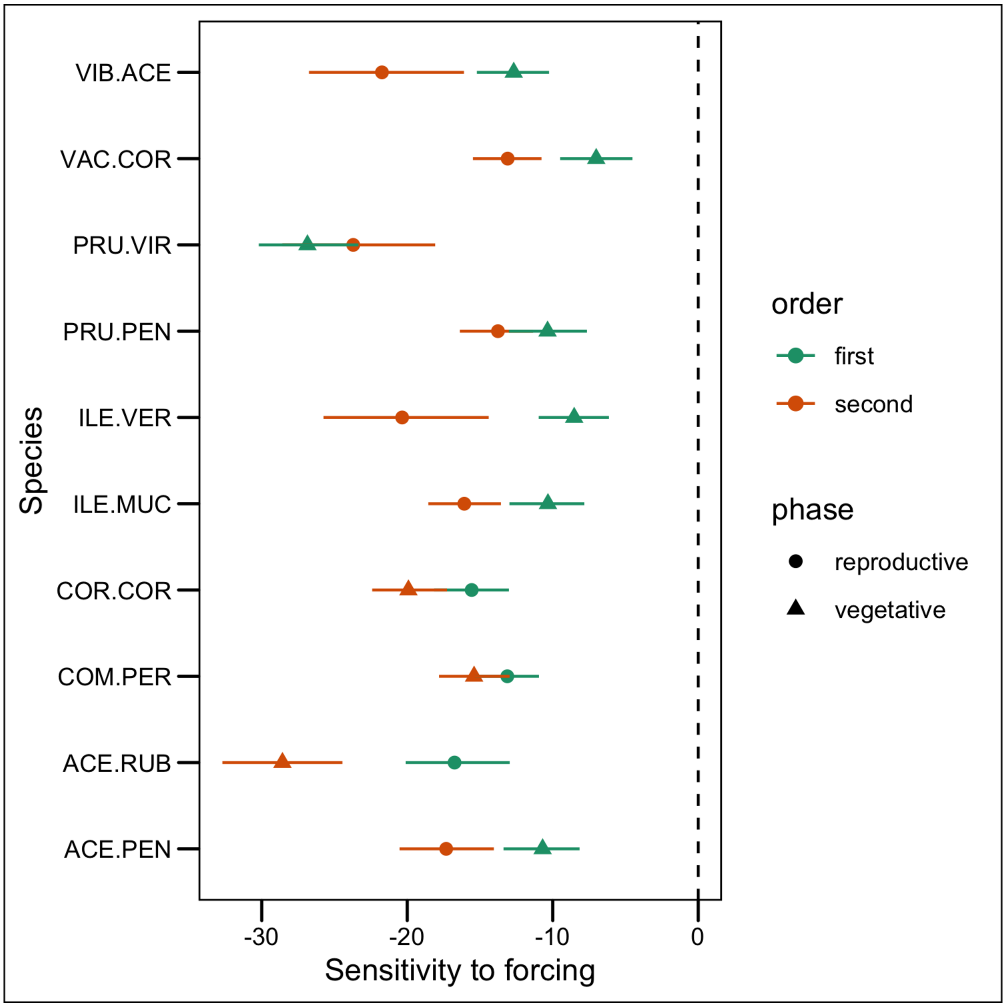


Figure 2: **Under adequately long chilling duration and photoperiods, the phenological sensitivity ($\Delta$ phenological event/ $\Delta$ C°) follow the predicted pattern of the precocity hierarchy hypothesis (PHH), with the second phenophase of the sequence being approximately twice as sensitive to forcing as the first.** After performing a growth chamber manipulation evaluate the phenological sensitivity of flower and leaf buds to varying level forcing temperatures, photoperiods, and duration of chilling, we subset out data to include only observation at high chilling and photoperiod levels. Using Bayesian hierarchical models, we quantified the differences in sensitivity to forcing for all species in our study. Points indicate mean estimates and lines depict 50% Our finding indications that the PHH should be considered a special case of the differential sensitivity hypothesis (DSH) that occurs when the chilling and photoperiod requirements are well met for both bud types.

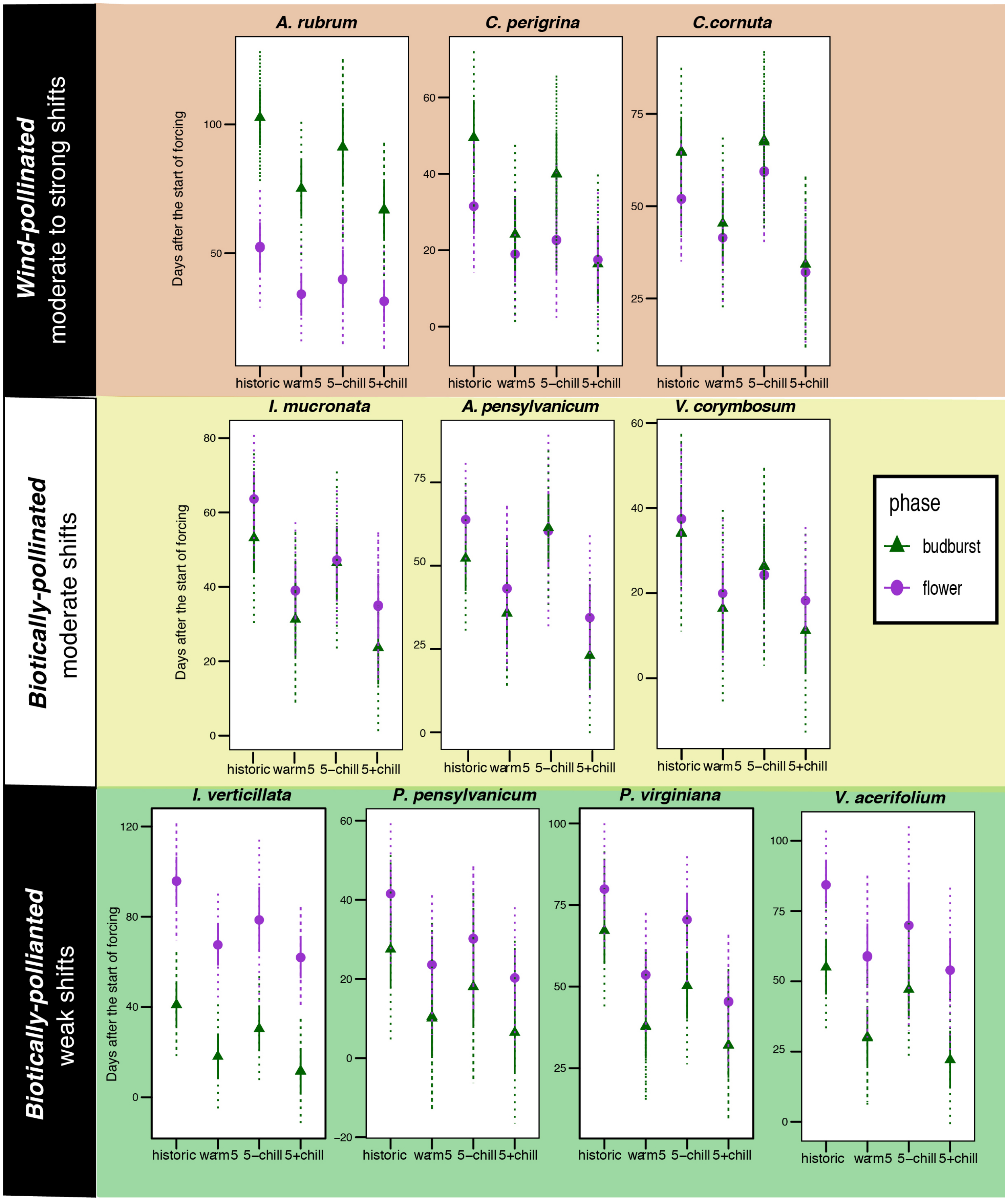


Figure 3: **Flower-leaf sequences (FLSs) of temperate, woody species will shift with climate change, but the magnitudes of these shifts vary by species and depend on the specific dynamics of temperature at a given location**. We used Bayesian, hierarchical models comparing flower and leaf bud responses to variable temperature combinations to predict FLSs patterns under current climate conditions and three climate change scenarios; an increase in spring warming alone (warm 5), increase in spring warming and increase in winter chilling (warm 5 +chill) and an increase in spring warming and decrease in winter chill (warm 5 -chill). The points represent the mean estimates and teh solid and dashed lines represent the 50 and 95% credible intervals respectively. Projected FLS shifts are most pronounced in wind-pollinated, flowering-first shrubs but FLS shifts for all species depend on the relationship between forcing and chilling changes which is likely to vary by location with climate change.