

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

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5 Possible ways to go with this: Brief Communication in AJB (3000-4000 words), AoB PLANTS
6 (up to 6000 wrds).

7
8 **Abstract**

9 The order and duration of vegetative and reproductive phenological growth in the spring is an
10 important fitness character for deciduous woody plants in the temperate zone. These flower-leaf
11 sequences (FLSs) are shifting with climate change, but the magnitude of future shifts are difficult
12 to predict without an improved understanding of how flower and leaf phenological responses may
13 differ in a changing environment. We used growth chambers to compare the phenological responses
14 of flower and leaf buds to varying temperature and light conditions for a suite of temperate woody
15 species. We found that flower and leaf buds respond with differential sensitivity to changes in tem-
16 perature and photoperiod, and that these differences dictate species-specific variation in FLS shifts
17 under different climate change scenarios. FLS shifts were strongest in wind-pollinated, flowering-
18 first species that may rely of a long period of time between flowering and leafing for successful
19 pollination, suggesting that climate change may impact the reproductive fitness of these species.

Introduction

Phenological sequences, the temporal relationships among distinct life-cycle events and transitions, strongly influence plant fitness (Ettinger *et al.*, 2018; Post *et al.*, 2008). Among deciduous woody plants, the relative timing of flower and leaf development, or flower-leaf sequences (FLSs), may be particularly consequential to fitness in temperate regions where flowering prior to leaf development is common (Gougherty & Gougherty, 2018; Buonaiuto *et al.*, in review). It has been suggested that this adaptation may enable efficient pollen transfer for wind-pollinated species (Whitehead, 1969), increase floral visibility in biotically-pollinated taxa (Janzen, 1967), improve hydraulic functioning (Gougherty & Gougherty, 2018; Reich & Borchert, 1984) or facilitate early flowering (Primack, 1987).

Long-term phenological observations indicate that FLSs are shifting with anthropogenic climate change, suggesting that some of these critical functions of FLSs may be at risk. However observed FLS shifts vary among species (Buonaiuto *et al.*, in review), which may put some species at greater risk while benefiting others. The effects of FLS shifts on woody plant fitness depends on their direction and magnitude, which is dictated by the particularities of how flower and leaf buds respond to climate.

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 in the spring (Forrest & Miller-Rushing, 2010; Flynn & Wolkovich, 2018). Yet, high levels of reported inter-annual variation in FLSs (Buonaiuto *et al.*, in review) indicate that there must be differences in how these cues influence phenological activity in floral and leaf buds.

While there are also developmental and architectural constraints to FLS variation (Diggle, 1995;

Lechowicz, 1995), research has shown that the flower and leaf buds of many spring flowering woody species of the temperate zone can be relatively physiologically independent (Savage, 2019). This suggests that FLS variation is strongly influenced by differences in cue utilization among flower and leaf buds but the specifics of these responses have not been thoroughly investigated. Identifying these differences is a necessary step for predicting the direction and magnitude, and ultimately fitness impacts of FLS shifts with climate change.

In this study, we perform experimental climate manipulations in growth chambers to compare phenological response to changing environmental conditions between flower and leaf buds. We then leverage these data to make generalized projections for how FLSs may shift with future climate change and interpret these predictions in the context of the functional hypotheses of FLS variation to assess how FLS shifts may impact species in the future.

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 chill-

ing (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 photoperiodicity. 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 three phenological phases: budbreak (BBCH phase 07), leaf unfolding (BBCH phase 15) 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 for 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 appears below:

$$y[i] \sim N(\alpha_{sp[i]} + \beta_{forcing_{sp[i]}} + \beta_{chilling_{sp[i]}} + \beta_{photoperiod_{sp[i]}} + \beta_{forcing \times chilling_{sp[i]}} + \beta_{forcing \times photoperiod_{sp[i]}} + \beta_{chilling \times photoperiod_{sp[i]}})$$

97

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

100

$$101 \quad \alpha_{x_{sp}} \text{ or } \beta_{x_{sp}} \sim N(\mu_x, \sigma_x^2)$$

102

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

107

108 **Climate change predictions**

109 To apply our model results to general climate change projections we chose our environmental treat-
 110 ments in this experiment to broadly reflect historic and future conditions at our sampling site. Our
 111 low forcing treatment approximates average spring temperature (March/April) at the site while
 112 our high temperature treatment reflects a 5 °C increase. Average field chilling (calculated from 15
 113 Oct - 15 April, measured in Utah units) at Harvard Forest is 979.64, approximately 60% of the
 114 difference between our low and high chilling treatment (Fig. S2). Thus, our low chilling treatment
 115 represents a feasible estimate for a decrease in chilling with climate change and our high chilling
 116 treatment approximate reasonable increase. We should note that our low photoperiod treatment
 117 (8 hours of daylight) is well below the photoperiod experienced at Harvard Forest, but given that
 118 the photoperiod effects are expected to be small, we chose more extreme values in order to robustly
 119 estimate an effect (i.e., increasing statistical power). For this reason, our climate change projections
 120 for FLS variation are based on our high photoperiod treatment alone.

121

122 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

We found that that flower and leaf buds response to environmental cues with differential sensitivities (Fig. 1). Specifically, while both bud types had a proportionate response to forcing, leaf buds were more sensitive to chilling. At low levels of chilling and forcing, flower buds tended to advance with increasing photoperiod while leaf buds were delayed. Leaf buds were more sensitive to cue interactions, demonstrating stronger responses to increases in multiple cues than flower buds. While the order of the FLSs remained consistent across treatment combinations in most species, we found that one species, *Vaccinium corymbosum* switched FLS order across chilling treatments (Fig. S1).

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. 2). 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. 2).

Discussion

Differential sensitivity to environmental cues

Our experimental results suggest that flower and leaf buds are differentially sensitive to the primary environmental cues of spring phenology. Specifically, vegetative buds are more sensitive to chilling and cue interactions, and flower buds more sensitive to photoperiod.

We are not aware of any previous studies that systematically compare the phenological responses of flower and leaf buds within individuals of wild species. However, because FLS variation has implications for fruit production, several studies have investigated these responses in crops (see Guo *et al.*, 2014; Gariglio *et al.*, 2006; Citadin *et al.*, 2001). Our findings are consistent with much of the tree crop literature. Like studies in peaches (Gariglio *et al.*, 2006; Citadin *et al.*, 2001) we found that the heat requirements for phenological activity are dictated by cue combinations, with leaf buds responding more strongly to chilling than flower buds. Similarly, we also found that like peaches, flowers in some species (e.g. *Vaccinium corybosum*) tend to emerge before the leaves at low chilling levels. We found no crop literature that evaluated the differential sensitivity of flower and leaf

buds to photoperiod. However, consistent with our findings, genetic work in the model genus *Populus* suggests that flowering may be under stronger photoperiodic control than leafing (Glover, 2014).

In the highly seasonal and variable environments of the temperate zone, this differential sensitivity to cues between flower and leaf buds generates the high level of inter-annual FLS variation observed in nature. Differential sensitivity will also dictate the direction and magnitude of FLS shifts with climate change. In our study, we identified differences in the reaction to cues (Fig. 1) and predicted responses to climate change scenarios (Fig. 2) among species. While we studied only a small subset of species from temperate forest communities, we identified several patterns that may be useful for predicting FLS shifts in taxa beyond the ones investigated in our study.

Patterns in FLS responses

The FLSs of several species were relatively robust to changing environments (Fig. 2). These species, *Ilex verticillata*, *Prunus pensylvanica*, *Prunus virginiana*, and *Viburnum acerifolium*, all share a strongly leafing-first FLS, with a fairly long FLS interphase. These species all have mixed buds so there may be strong physical constraints on their FLSs. This pattern suggests that the FLSs of other leafing-first species with long interphases, or those with architectural or physiological constraints (i.e. reliance on current season's photosynthesis rather than stored reserves for the production of flowers) may change very little under altered climate conditions.

Our models predicted moderate shifts in FLSs for three species, *Acer pensylvanicum*, *Vaccinium corymbosum* and *Ilex mucronata* (Fig. 2). While these three species typically share a leafing-first FLS, we found that under some environmental combinations, these species may switch to concurrent or flowering-first FLSs (Fig. 2, see "warm -chill" scenario). It is unclear why the predicted shifts in these three species were greater than for the other four species mentioned above. All of

198 them broadly share many reproductive characters– biotic pollination syndromes, mixed buds, and
 199 leafing-first FLSs. One possibility is that these three species have shorter inter-phases to begin
 200 with, so small shifts have a larger proportionate impact on the duration of the FLS interphase.
 201 For example, for the sister taxa *Ilex mucronata* and *Ilex verticillata*, warming reduced the FLS
 202 interphase of each species by just 4 and 3 days respectively. However, the estimated interphase
 203 under average conditions for *I. mucronata* is considerably shorter than for *I. verticillata*. While
 204 their shifts are comparable in number of days, such a shift results in 35 % reduction in the FLS
 205 interphase duration for *I. mucronata* and a less than 1% reduction for *I. verticillata*. This suggests
 206 that alterations to FLSs due to climate change may be more significant for species with already
 207 shorter FLS interphases.

208
 209 The two species with the most significant FLS shifts across treatment combinations and climate
 210 change projections were *Comptonia peregrina* and *Corylus cornuta* (Fig. 2). In all of our climate
 211 change scenarios, the FLS interphase was dramatically reduced in these taxa. The most obvious
 212 differences between these species and the ones discussed above are that *C. peregrina* and *C. cor-*
 213 *nuta* are both wind-pollinated with a strongly-flowering first FLS. It is likely that the evolution of
 214 a flowering-first FLS may have required greater physiological and structural independence of leaf
 215 and flower buds, allowing their cue-use patterns to diverge strongly.

216
 217 We did not observed these magnitudes of shifts in the other wind-pollinated, flowering-first species
 218 in our study *Acer rubrum*, which maintained a fairly large and consistent FLS interphase in each of
 219 the treatment combinations in our experiment and projections (Fig. 2). While the low sample size
 220 in our study for this species warrants caution in interpreting this finding, it may reflect biological
 221 differences between these species. *Acer rubrum* is a canopy tree while the other two species are
 222 low growing, understory shrubs. Additionally, the genus *Acer*, is ambophilous (Barnes & Wagner,
 223 1981, 2004), and there is evidence that even *Acer rubrum* which is considered largely wind-pollinated
 224 may still rely on insects for pollination as well (Batra, 1985).

226 While the contrasting patterns of FLS variation among our study species species are striking, the
 227 significance of these differences in an era of global change depends on the function of FLSs in these
 228 taxa. Recent inquiries in the evolutionary drivers of FLSs suggest that FLS patterns may be an
 229 example of convergent evolution, serving multiple functions for different species in the the temperate
 230 zone (Buonaiuto *et al.*, in review; Gougherty & Gougherty, 2018). Therefore the significance of
 231 FLS shifts can only be understood in the context of their function, which may vary among species
 232 or plant functional groups.

233 **FLS shifts and FLS function**

234 First, it is important to emphasize that even in species without strong FLS displacement we still
 235 observed substantial phenological shifts— with both flowering and leafing advanced proportionately
 236 to each other. This suggests that with climate change, if there are any impacts of FLS shifts specif-
 237 ically, they will be minor compared to impacts of phenological shifts in general such as alterations
 238 to the growing season (), increased risk of frost or pest damage (Liu *et al.*, 2018), and phenological
 239 mismatches (Mommott *et al.*, 2007).

240

241 For the leafing-first, insect-pollinated species with short FLS interphases for which we observed
 242 moderate shifts (Fig. 2, middle row), the implications of these shifts are no quite clear. If these
 243 species rely on visual pollinators, advancing of flowering relative leafing could, in theory, help pol-
 244 linators locate receptive flower and increase pollination success but we do not know of any studies
 245 that have tested the impacts of FLS variation on pollinator viability. FLS shifts in these species
 246 could also alter an individual’s hydraulic demand, but we would not expect these modest shifts
 247 to strongly affect plant fitness as it is unlikely that plants are water limited in the spring in the
 248 temperate zone (Polgar & Primack, 2011). It is most likely that even moderate FLS shifts in these
 249 species will also have negligible impacts when compared to the more general impacts of phenological
 250 shifts.

251

252 Shifts in FLSs may be most consequential for wind-pollinated taxa. Flowering-first FLS is an im-
253 portant adaptation for wind pollination, reducing barriers for airborne pollen transfer(Rathcke &
254 Lacey, 1985). Decades of research on the physics of particle movement through forest canopies
255 have demonstrated how leaf expansion reduces pollen transport distances and increases the rate
256 that pollen is intercepted by non-reproductive structures (Niklas, 1985; Milleron *et al.*, 2012; White-
257 head, 1969). For example, Tauber (1967) estimated that a single branch with leaves would intercept
258 more than double than what was impacted on a bare branch. It follows that truncation to FLS
259 interphases in flowering-first, wind-pollinated species on the order that we observed in our experi-
260 ment may reduce reproductive success of these species.

261

262 Much of the conversation around phenology and pollination in the context of global change has
263 centered around trophic mismatches between pollinator and floral phenology (Gérard *et al.*, 2020),
264 which is of little relevance to abiotically pollinated taxa. By contrast, we find evidence that the effect
265 of FLS shifts with climate change may be particularly important for abiotically pollinated woody
266 plants. While we investigated just two flowering-first, wind-pollinated species in our study, this
267 FLS is common to the wind-pollinated *Betulaeae*, *Fagaceae* and *Salicaceae*; families that comprise
268 a significant proportion of the biomass of temperate forests. Given their importance to temperate
269 ecosystems, the scope and impact of FLS shifts in these taxa should be explored in greater detail
270 in the future.

271

272 Conclusion:

273 Our study provides strong evidence that flower and leaf buds integrate the same environmental
274 cues differently between them, which drives variation in flower-leaf sequences. As climate change
275 continues to alter temperature cues, species with physiologically independent buds and strongly

divergent temperature sensitivities among bud types will likely experience significant shifts in FLS. This shifts may be particular detrimental to flowering-first, wind-pollinated species that rely on a lengthy leaf-free period for pollination. Because of the prevalence of these taxa in temperate forests, the scope and impact of FLS shifts in these taxa should remain a high research priority.

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348 **Figures**

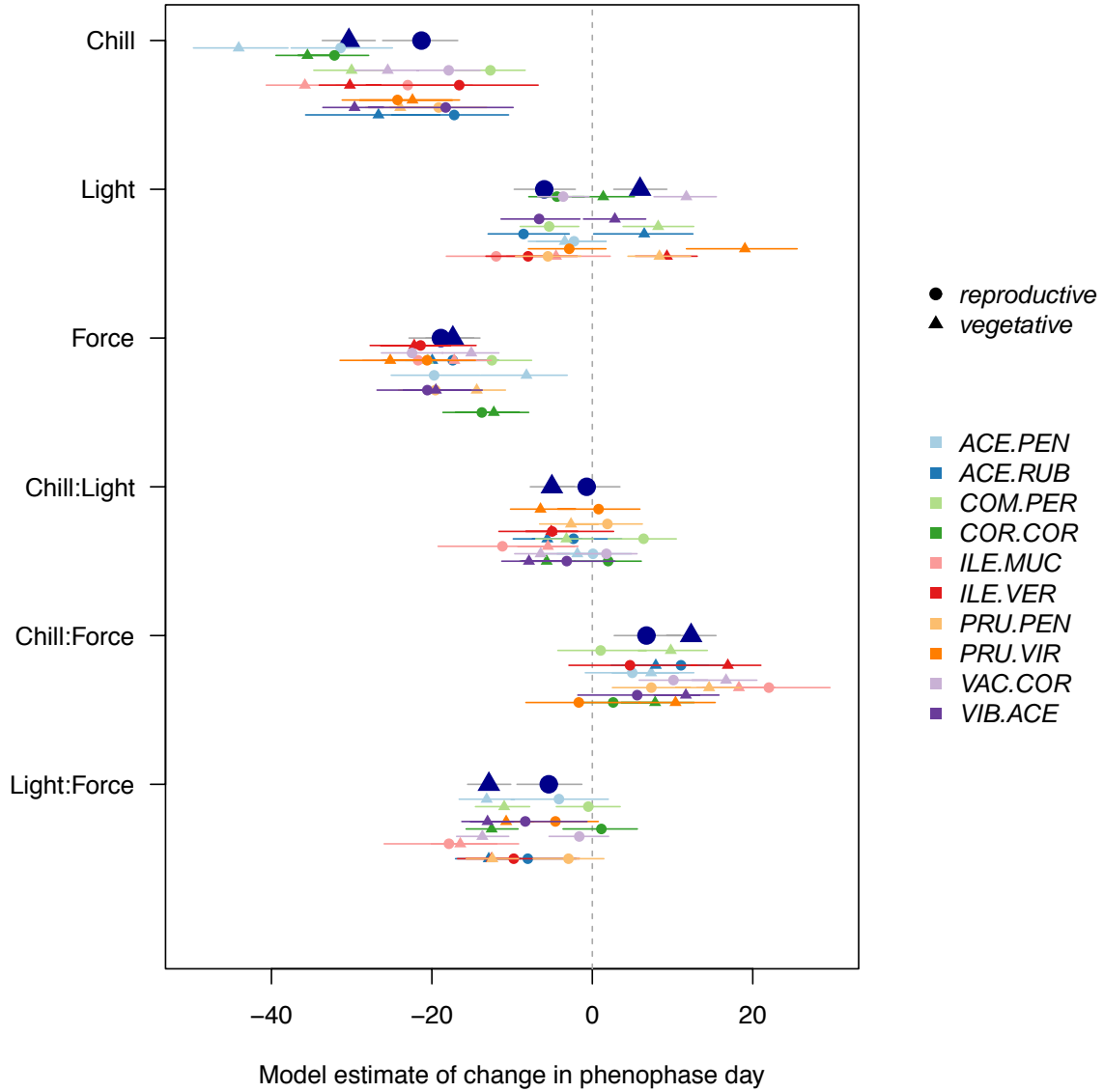


Figure 1: **Experimental results suggest differential sensitivity to environmental cues between flower and leaf buds.** Vegetative buds (circles) as more sensitive to chilling and interaction between chilling and forcing. Flower buds (triangles) advance with photoperiod increases but leaf buds appear to delay. These differential sensitivities dictate how FLS patterns vary with changing environmental conditions.

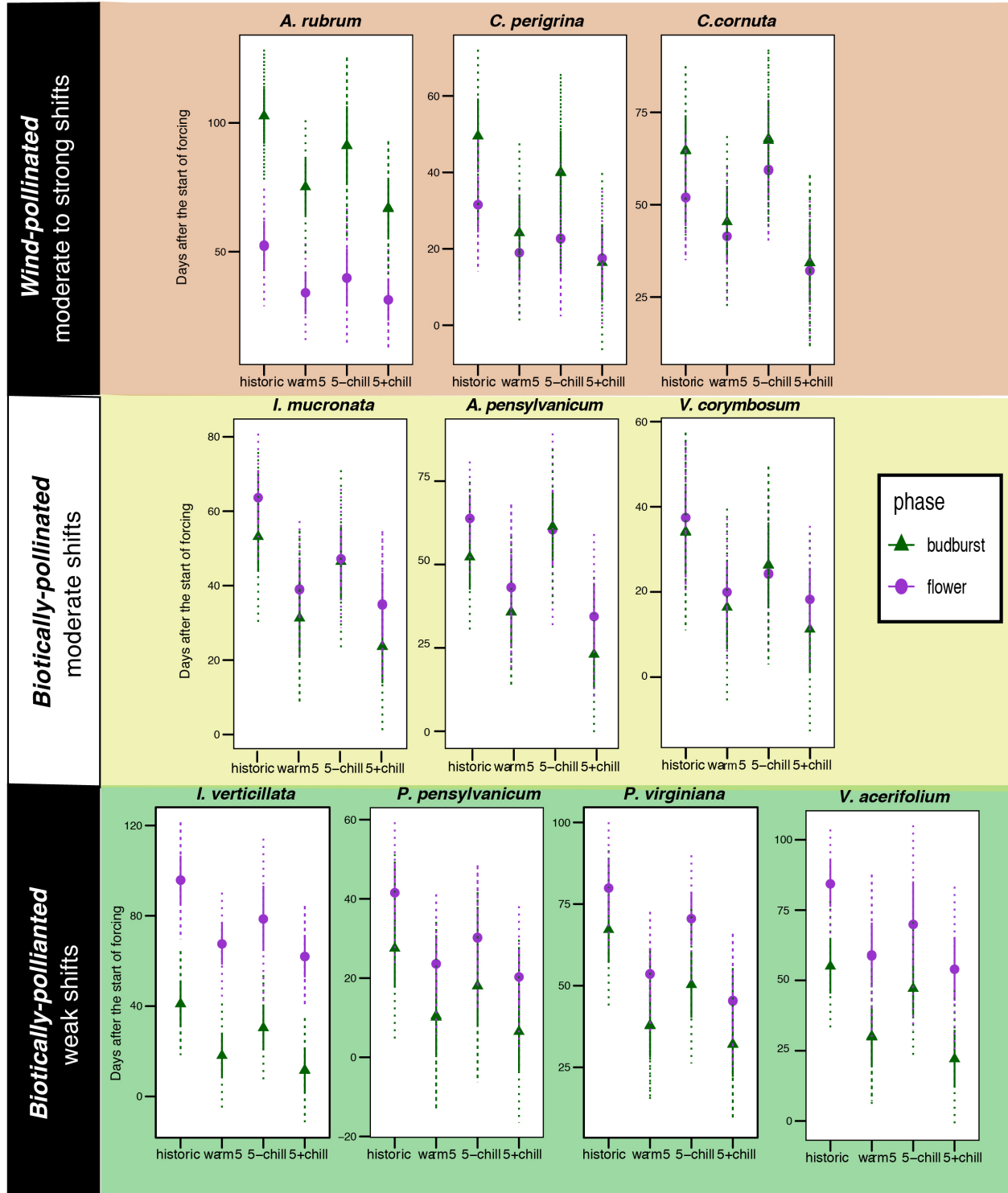


Figure 2: Flower-leaf sequences (FLSs) of temperate, woody species will shift with climate change, but the magnitudes of these shifts vary by species and depend on the specific dynamics of temperature at a given location. We used Bayesian, hierarchical models comparing flower and leaf bud responses to 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). Projected FLS shifts are most pronounced in wind-pollinated, flowering-first species 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.