Photoperiod and temperature interactively drive spring phenology in multiple species

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Understanding the sensitivity of forest plants to abiotic drivers of plant phenology is critical for developing predictions of community composition, changes in community composition resulting from climate change, and resulting alterations to ecosystem-level properties such as carbon sequestration. Observational studies are limited in the ability to separate plant responses to different climatic factors, with phenological responses known be based on the combination of three environmental cues plants receive: chilling temperatures in fall and winter, photoperiod, and spring forcing temperatures. For a handful of well-studied temperate woody species these cues appear to be interactive, meaning predictions of plant responses to climate change will be complex and non-linear [1]. Other work however has suggested many species may be dominated by one of the three possible cues [2], with a tradeoff between photoperiod and forcing temperature sensitivities, making some species responses simple to predict. However, the range of responses across species within a forest community to winter chilling temperatures, photoperiod, and spring forcing temperatures have received relatively limited attention. Given the wide range of budburst and leaf out across temperate woody species [3], these species differences may be crucial in scaling up to ecosystem-level responses. Here we present results from an experimental manipulation of spring forcing temperatures, photoperiod, and intensity of winter chilling with dormant clippings of 28 woody plant species from forest communities at two latitudes (42.5°N and 46°N). We show photoperiod sensitivity is common across northeastern woody plants and phenological sensitivity to photoperiod and temperature appears largely coordinated across species; namely, species highly sensitive to temperature were also highly sensitive to photoperiod. Budburst and leaf out were more sensityve to temperature than to photoperiod. Winter chilling exerts a large role in driving advances in spring phenology, for both budburst and leaf out stages, yet more intense chilling at 1.5°C resulted in less pronounced effects than at 4°C. Latitude of origin exerted surprisingly small effects on sensitivity to abiotic factors in driving spring phenology, indicating that local adaptation—at least across 4°of latitude—may

not necessarily constrain woody plant responses to climate change. Shrub and small tree species were less sensitive to changing temperatures or photoperiod, but consistently earlier in their phenology. These results indicate that under warming conditions, communities could shift to a more canopy-tree dominated system with generally later phenologies, counteracting advances in phenology at the ecosystem scale.

Woody plant spring phenology drives global carbon cycles and local ecosystem properties, from the length of the growing season to energy balance between land and atmosphere. Timing of spring phenology in temperatue woody plants is critical for understanding net ecosystem assimilation at the forest scale, as maximizing the length of the growing season and minimizing risk of tissue loss due to early spring freezing depends on accurate timing of budburst and leaf out [4]. The crucial role that phenology plays in these ecosystem processes, and the indications that plant and animal phenology are advancing as rapidly as 2.3°C per decade [5] have led to increased attention to tracking the patterns of phenology at large temporal scales. Observational studies of long-term trends are crucial for understanding how climate affects timing of such phenological events, and in combination with field and growth chamber studies, it is clear that spring phenology for woody plants in temperate ecosystems is driven by a combination of increasing spring temperature (forcing), length and intensity of winter temperature (chilling), and changing daylength (photoperiod). Observational studies generally show stronger signs of phenological advance in response to temperature than experimental manipulations [6], yet experimental manipulations are necessary for disentangling otherwise covarying environmental factors and directly assess species- and individual-level responses to climate change factors.

Adaptive pressues drive temperate woody plants to balance the maximization of carbon gain with minimization of freezing risk in spring phenology [2]. Strong selective rpessures should be expected to mitigate damage done by frost events to non-evergreen tree species, given the dramatic consequences of even a single frost event, which if timed after leaf out, can substantial reduce ecosystem productivity [7] and potentially shift the composition of temperate forests [8]. Spring frost events have been increasing in North America [9], with greater probability of freezing events occuring after budburst. The ways that species manage such risks can vary in both when on average in the spring they begin their growth, and also how flexible they are around that average timing.

Two tradeoffs have been described for spring phenology of woody plants: tolerance versus avoidance of

freezing, and opportunistic versus conservative strategies in response to a variable environment. The former describes how early or late in a season species carries out bud burst and leaf out, while the latter describes how flexible a species or individual may be in respose to unusually early warm-up events. While related, these tradeoffs may combine to produce contrasting changes in phenology and may be related to different plant functional traits. For the tolerance-avoidance axis, plants may either tolerate risk of spring freezing by investing in tissue which can withstand freezing, or avoid freezing with later phenology. For perennial plants, it has been found that leaves of species which have later phenologies can be more sensitive to frost damage [10] [11], supporting the notion of a tradeoff between tolerance and avoidance of freezing risk. Avoidance should be an adaptive strategy when the risks of freezing damage is high and damage severe enough to make the benefits of early spring phenology not worth the cost of tissue loss [12]. Physiologcially, tolerance to freezing is driven by resistance to rupturing of biomembranes, and is related to dehydration stress [13]. Plant functional traits related to freezing resistance thus are likely to include high tissue density, both of leaves and stems. In particular, wood density is postively related with leaf longevity and resistance of xylem conduits to freezing-induced cavitation [14]. Thus high wood density would be advantageous for high-tolerance (early season) plant species. In contrast, avoidance-strategy plants would be expected to express lower tissue densities, with the shorter growing season being made up for by faster growth rates, less investment in structural elements of tissue, and relatively greater percent nitrogen in leaves.

The other key tradeoff that can be expected is between opportunistic plant strategies, where temperature is the dominant driver of spring phenology, and conservative strategies, where photoperiod and chilling are the key drivers. Opportunistic strategies should benefit species in a non-stationary environment, as in a warming world where mild winters are less an unusual occurance. It has been found for sevearl cases that short-lived, early successional species typically exhibit such opportunistic strategies, and late-successional species are more typically chilling- and photoperiod-controlled in breaking of dormancy [2] [15] [16]. However, opporunisitc and conservative strategies may not be synonymous with tolerance and avoidance strategies.

Opportunistic species, showing greater ability to respond to early warm temperatures in their timing of spring events, would be predicted to exhibit lower tissue densities, greater leaf nitrogen concentrations, and . Drought-tolerance, which can be related to freezing-tolerance in the ability to resist cavitation,

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has been show to relate to low wood density in a semi-arid forest, with low-wood density species having increased ability to store water in the dry season and ability to flush leaves in the dry season [17]. Similarly, for temperate deciduous trees, experimental warming of has been shown to both increase total growing season length for species which have higher specific leaf area [18]. Finally, for deciduous trees, traits can exhibit variation in expression over the growing season, with higher leaf tissue density and allocation of nitrogen following cessation of growth in late summer [19].

Tests of how these two tradeoff axes drive phenology across a co-occuring community of species have not previously been carried out. As the abiotic environment is not the sole contributor to plant performance, considering a suite of co-occuring species together is key for making progress in understanding the role phenology plays in shifts in community composition and ecosystem functioning. Temporal separation in resource use is an imporant driver of plant species coexistence [20] and such temporal separation can drive ecosystem properties such as biomass accumulation [21], thus understanding both the current order of phenology for co-occuring species and propensity to change in future climates is an important goal of plant phenology science.

The role of latitude in how abiotic drivers determing spring phenology has largely been investigated in single-species studies across many sites. Given suffcient distance, more pole-ward sites have lower minimum annual temperatures and shorter growing seasons, making accurate timing of spring phenology even more important. Since daylength differences from winter to spring are also greater for higher latutitudes, populations of northern plants may be expected to rely more on photoperiod as a cue for spring phenology.

For temperate trees, species can be limited at their northern range by inability to develop mature fruit in a given growing season, while limited at their southern range by inability to break dormancy due to insufficient chilling [22]. Thus phenology can drive range limits. Common garden studies have shown that southern-adapted species, when translocated to a more northern location, exhibit later leaf out compared to species adapted to northern sites [23]. If species remain relatively fixed in their timing of leaf out, then northward migration of such late-phenology species may act to counteract community-wide advances in phenology under a warming climate.

Photoperiod has long been known to be a critical driver of the onset of endormancy, in combination with cooling temperatures [24]. However, the role of photoperiod in determining the breadking of

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dormancy has been debated, with various authors finding that the strength of daylength as a driver may depend on phenological stage, species and location [25] [26]. Photoperiod and winter chilling can interact, as long photoperiod enhances cell growth, compensating for a lack of chilling during the endodormancy phase [27] [28] [29]. In the few experimental studies that have directly manipulated both forcing temperature and photoperiod, photoperiod has been shown to act to moderate advances in phenology due to warming, with reduced advances due to temperature when daylength was short [30] [27].

In addition to photoperiod, winter chilling requirements also act as a conservative strategy to avoid damage from early spring freezing, allowing woody plants to avoid breaking bud during unusually early warm spells [31]. To an extent, these three factors of temperature, photoperiod, and chilling are interchangeable, such that plants experiencing mild winter with insufficient chilling can still break bud given sufficiently long photoperiods and warm temperatures [27]. Chilling requirements are known to vary substantially across species, with some needing relatively little winter chilling to initiate budburst, and others not bursting bud even in long-day, warm envronments unless sufficient chilling has taken place [2].

Knowing species-specific sensitivies of temperate plant phenology to chilling and forcing alone can predict regional-scale phenology [32]. Substantial variation exists at the species level in the magnitude of the temporal advance of spring phenology [33], such that the presence of species highly sensitive to temperature change can strongly drive community-level phenology [34].

Early phenological events, such as initial swelling of buds and budburst (separtion of budscales) are challenging to study from remote sensing, with little obvious change in color or reflectance. requiring experimental work at the individual level. Different phenological stages may be driven by different environmental cues. The period between budburst and leaf out is critical for leaf development, as this is a period when plants are highly sensitive to damage from late freezing events, with freezing resistance increasing as leaves expand [12].

To test the interactive effects of the three controlling drivers of spring phenology, temperature, photoperiod, and chilling across latitudes, we carried out a study of 28 woody plants. We assessed both budburst and leafout to account for the potential different sensitivies of these phenological stages to abiotic drivers, and analyzed responses across all species to examine the support for how well the

tolerance-avoidance and opportunistic-conservative tradeoff axes represent temperature plant spring phenology.

Results

Temperature and photoperiod individually and interactively determined timing of leaf-out, with the strongest effects of temperature in short-day conditions. We found photoperiod sensitivity was common and strong across all of the woody plants studies, consistently reducing time to phenological responses for each species, across sites of origin.

For the 28 species studied, sensitivity to temperature and photoperiod cues for leaf-out times varied substantially, and—in contrast to our hypotheses [that we set up in the intro]—co-varied overall. The coordinated response to warming temperatures and longer photoperiod was consistent with overall pace of phenological events; earlier-leafing out species (namely the shrubs *Spiraea alba*, *Viburnum cassanoides*, and *Vaccinium myrtilloides*) exhibited relatively limited advances to either warming or longer days, while later leafing-out species showed ability to advance their phenology by in response to both warming and longer days. Thus, no trade-off was observed between photoperiod-cued and temperature-cued species, but rather species exhibit coordinated responses to both environmental factors (Fig. 1). Of the other species, *Fagus grandifolia* exhibits relatively limited response to warming but substantial photoperiod sensitivity, while *Rhamnus frangula* shows relatively limited response to photoperiod but substantial warming sensitivity; if only a small subset of species including these two had been included in the study, it might have been concluded that a tradeoff between photoperiod sensitivity and warming sensitivity would exist.

While both photoperiod and temperature cues were important for driving woody plant phenology, responses to chilling were also substantial. Budburst day was accelerated most by the chilling treatments. Tables 1 and 2 summarizes hierarchical mixed-effects model analysis of day of budburst and leaf-out, with negative values indicate earlier day of experiment for each event. Overall the 5°C experimental warming resulted in 6.8 days earlier budburst and 21.9 days earlier leaf out. Such advance was delayed by the each chilling treatment, as indicated by the positive coefficient for the temperature x chilling interactions. Latitude of origin (Site) overall had little direct effect on budburst

173 or leaf-out, but populations from the northern site tended to exhibit slower budburst and leaf-out, with

174 a more rapid budburst and leaf out in response to the chilling treatments (indicated by negative

175 coefficients for site x chilling treatments).

176 Warming, photoperiod, and chilling individually and interactively acted to drive budburst and leaf out

177 earlier across species. The strength of the acceleration in budburst due to both warming and

178 photoperiod were similar, but the acceleration of leaf out due to warming exceeded that of

179 photoperiod for both phenological stages. Surprisingly, site of origin exerted limited effect on either

180 budburst or leaf out across species.

Effect of chilling

182 The cuttings were harvested in late January 2015, and thus experienced substantial natural chilling by

183 the time they were harvested. Using weather station data from the Harvard Forest and St. Hippolyte

184 site, chilling hours (below 7.2°C), Utah Model chill portions (hours below 7.2°C and between 0°C and

185 7.2°C) and Dynamic Model [35] chill portions were calculated both for the natural chilling experienced

186 by harvest and the chilling experienced in the 4°C and 1.5°C treatments. The Utah Model and

187 Dynamic Model of chill portions account for variation in the amount of chilling accumulated at

188 different temperatures, with the greatest chilling occurring approximately between 5-10°C, and fewer

189 chill portions accumulating at low temperatures and that higher temperatures can reduce accumulated

190 chilling effects. The two differ in the parameters used to determine the shape of the chilling

191 accumulation curve, with the Dynamic Model being shown to be the most successful in predicting

192 phenology for some woody species [36]. With both the Utah and Dynamic model, the more severe

193 chilling treatment resulted in fewer calculated chilling portions.

194 Species varied widely in response to chilling treatments, with some exhibiting strong chilling

195 requirements (*Acer saccharum*, *Fagus grandifolia*), while others exhibited little change in phenological

196 advancement under experimentally manipulated chilling. Overall, budburst and leaf-out advanced by

197 22.1 or 26.4 days under additional 30 d of vernalization at 4°C, and advanced by a reduced amount of

198 19.7 or 26.1 days under 30 d of vernalization at 1.5°C. The reduced chilling effect at the lower

199 temperature chilling is consistent with the Dynamic Model of chilling accumulation.

Species-specific responses to chilling demonstrate that chilling requirements are not uniform across species, with of *Fagus grandifolia* to increasingly strong vernalization varies by latitude of origin and by phenological stage; winter chilling reduced day to budburst and leaf-out, but more strongly for individuals from the northern site.

While nearly all species showed advances in spring phenology in response to the experimental chilling treatment, as indicated by fewer days to phenological events for the 4°C and 1.5°C treatments, the majority of species (e.g. *Populus grandidentata*) showed delays in both budburst and leaf out at the more severe chilling treatment. Of the species exposed to the additional chilling, only *Fagus grandifolia* was consistently advanced by the more severe chilling.

Species-specific responses

Species traits partly explain variation in warming and photoperiod sensitivities of leaf out. Plants with high nitrogen leaves, as well as high SLA (thinner, less dense) leaves, were significantly later in both budburst and leaf out. Thus early leaf out species tended to be tougher, less N-dense, and have higher carbon investments than later species. Greater wood density had inconsistent effects as a driver, with higher wood density driving later budburst but tending to drive earlier leaf out.

Ring-porous species (*Fraxinus sp.*, *Lonicera*, *Myrica*, and *Quercus*; lower values of Pore Anatomy variable) exhibited significantly later budburst and leaf out compared to diffuse-porous species, in line with previous work on wood anatomy and freezing risk [37].

Shrubs with low specific leaf area (thick/dense leaves) and high stem density were more likely to leaf out earlier. For trees, with an overall later leaf out pattern,

Rank order of leaf out and budburst was stable across warming and photoperiod treatments. Chilling treatments shifted the order, for example *Fagus grandifolia* was the 23-28th species to burst bud with no additional chilling, but advanced to the 10-11th species to burst bud in with additional chilling. Within chilling treatments, the consistency of the rank order was high, with standard deviation of the rank order ranging from 2.05 d (budburst, no additional chilling) to 0.75 d (leaf out, additional chilling at 4°C). Compared to field observations, rank order of leaf out was generally most related in the cool, short-day treatment with no additional chilling (Fig. S10).

Nonleaf outs

Across all treatments, 20.2% of the cuttings did not break bud or leaf out. Across species, there was no overall predictive effect of temperature, photoperiod, chilling, or site on the propensity to fail to leaf out. Species ranged from complete leaf out (*Hamamaelis*) to only 50% leaf out (*Fagus grandifolia*, *Acer saccharum*) across all treatments. The percent of nonleaf outs by site was similar, with 20.6% of Harvard Forest and 19.7% of St. Hippolyte samples failing to leaf out. Examining individual species, there was an interaction of temperature by day length for selected species, with greater failure to leaf out in cool, short-day conditions for *Acer pensylvanicum* and *Acer saccharum*. Site effects were inconsistent, with greater failure to leaf out for cuttings from St. Hippolyte in *Acer rubrum* and *Fagus grandifolia*, and from Harvard Forest in *Acer saccharum*.

Discussion

Photoperiod sensitivity is common in northeastern woody plants, and greater photoperiod sensitivity is related to, not instead of, temperature sensitivity. Taken together, this result shows that the opportunism-conservatism tradeoff is not supported by the data for this suite of species. The most sensitive species to both cues, namely the species which could advance their phenology in response to both longer days and warmer temperatures, were the later-successional tree species, rather than the shrubs. The trait data indicate partially that the species earliest to leaf out, namely the shrubs and small trees, also had lower SLA and lower leaf %N, indicating greater investment in tissue structures. These results support the tolerance-avoidance tradeoff, with the early phenology species being tolerant to freezing but relatively less able to advance their phenology in a warming environment. These results also indicate that the later-successional species have potentially the most to gain from a warming world, as they can extend their growing seasons

While both photoperiod and temperature sensitives were common, chilling sensitivity greatly outweighed both of these factors. It is important to note that the results from the chilling part of this experiment are derived from 11, not 28 species, but the strength of this effect is notable. Strong chilling requirements were detected both for budburst and leaf out responses, and the most substantial advance in spring phenology came from the more mild chilling treatment, at 4°C, with reduced

254 effectiveness of chilling at 1.5°C.

255 These three factors did show some degree of substituability, meaning for example that a lack of chilling

256 could be made up for by an increase in temperature. These are indicated by the positive two-way

257 interactions; chilling and forcing temperature are more substitutable than chilling and photoperiod, for

258 both budburst and leaf out.

259 We found only limited support for the northern populations showing more conservative

260 (photoperiod-cued) strategies in these 28 species was found, with small delays in both phenological

261 events for populations from the more northern site. The latitudinal range studied here is within the

262 range of the phenotypic flexibility of these species. Of these study species, we should not be overly

263 concerned about being photoperiod limited at the more northern sites; given sufficient pace of

264 dispersal, they will be able to track a changing climate.

265 Budburst is sensitive to the same environmental cues as leaf out, but species show idiosyncratic

266 orderings of their sensitivity to environmental cues at these two phenological stages; leaf out responses

267 can not necessarily be used to back-cast budburst responses. Budburst showed a more limited total

268 response to environmental cues, and species were more tightly clustered in those responses.

269 Surprisingly, the smaller statured, earlier-leafing out shrubs and small trees exhibited reduced

270 sensitivity to all three factors of temperature, photoperiod, and chilling. They are relatively more fixed

271 in their timing of both budburst and leaf out, perhaps indicating an alternative mechanism for timing

272 of spring phenology in these plants [38].

273 Given these results, the future of the northeastern forests may shift towards later-phenology, canopy

274 trees, as these species demonstrated a greater ability to lengthen their growing seasons

275 opportunistically in response to warmer temperatures.

Methods

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Field sampling

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278 Woody plant cuttings were made in January 2015 for 28 species which occurred in both Harvard

279 Forest (HF, 42.5°N, 72.2°W) and the Station de Biologie des Laurentides in St-Hippolyte, Quebec

(SH, 45.9°N, 74.0°W). The typical late January temperatures are -3.4 and -22°C, respectively; day length between these two sites differs by a maximum of 45 minutes. Weather station data from each field site was obtained for calculations of chilling units.

Species were chosen based on the dominant forest vegetation at each site, aiming to maximize the number of shared species between the two sites. Of the 28 species, 19 occurred at both sites. Comparing only shared species, the mean days to budburst and leaf out across all treatments for Harvard Forest and St. Hippolyte was 25.6/36.8 and 24.8/36.1 days, respectively (Table S1). For each species, up to 15 representative healthy, mature individuals with branches accessible by pole pruners from the ground were tagged in late summer and fall 2014. In winter 2015, six individuals were located and 4-16 cuttings taken from each individual, depending on size of the individual and number of treatments to be applied. Cuttings were kept cold and transported back to the Arnold Arboretum in Boston, MA.

Growth Chamber Study

Cuttings were placed in growth chambers at the Arnold Arboretum in Erlenmeyer flasks distilled water, with water changed every 7-10 days. The base of cuttings was re-cut at each water change under water to prevent callusing. For 11 of the 28 species, sufficient cuttings were obtained from each individual tree to apply the full set of 12 experimental treatments: 2 temperature (20°C / 10°C warm vs. 15°C / 5°C cool) × 2 photoperiod (12 vs. 8 h) × 3 chilling (no additional chilling, additional 33 d at 4°C, or 33 d at 1.5°C) treatments. For the remaining 17 species, only sufficient cuttings were obtained to apply the temperature and photoperiod treatments, without the additional chilling levels. The total number of cuttings for a given species thus ranged from 24 to 144, depending on presence at each site and application of the chilling treatment.

Phenology of the cuttings was assessed using a modified BBCH scale [39], with observations on each of the 2,136 cuttings made every 2-3 days for the course of the 82-day experiment, a total of 48 observation days. The phenological stages assessed in the present study are budburst, defined as beginning of sprouting or bud breaking or shoot emergence (Code 07 in [39]) and leaf out, defined as first leaves unfolded (Code 11 in [39]). Additional stages up to flowering and stem elongation were also recorded. In total, we made 19,318 phenological observations at the cutting level.

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Functional trait collection In summer 2015, the same individuals previously tagged in the field were revisited as part of an additional study. Six individuals of each species were sampled for several plant functional traits, following standard protocols [40]. In some cases, the individual used in the growth chamber study was missing, in poor condition, or had no remaining branches to sample, and was replaced by a nearby representative individual. For each individual, height and diameter at breast height (DBH) were recorded, and leaf and stem material were sampled from the middle of the canopy or the greatest height reachable with pole pruners. Leaf material was kept cool and moist, and within several hours was scanned for leaf area and weighed fresh. Stem volume was measured using a water-displacement method. Samples were oven dried at 70°C and weighed within several days of sampling, and specific leaf area (SLA) were calculated stem density. Leaf tissue was further processed for carbon:nitrogen ratio using an elemental analyzer (Perkin-Elmer Elemental Analyzer) at Harvard Forest. Since in not all cases the same individual used for the growth chamber experiments was the individual sampled for functional traits.

Statistical analysis

For the two phenology responses measured, we fit mixed effect models separately for day of year, using site, warming, photoperiod, and chilling treatments as predictors and species as a modeled groups (random effects). For each model, two-way interactions for effects of site, warming, and each of the chilling treatments were included. Simplified versions of models were initially fit using the *lme4* package in the statistical programming environment R, then full versions of the model were fit using a Markov Chain Monte Carlo sampling approach in the programming language Stan (www.mc-stan.org).

Phylogenetic methods

We tested the influenced of phylogenetic relatedness on the relationship between functional traits and sensitivities to warming, photoperiod, and chilling treatment. Sensitivities were extracted as the slopes of the species-level responses of leaf out day to each of the experimental factors; more negative values indicate greater advance in leaf out in response to that factor. Using a phylogenetic tree resolved at the genus level from Phylomatic (www.phylodiversity.net), and the *caper* package in R, we fit phylogenetic generalized linear models between the sensitivities at the species level to the functional traits of stem density, SLA, and percent leaf nitrogen (%N). In this type of model, the parameter λ

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represents the strength of the phylogenetic symbol, with values close to 1 indicating that closely

related species have more similar responses to the abiotic drivers.

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436 **Figures and Tables**

Figure 1: Coordinated responses of 28 woody plant species to photoperiod and temperature cues for leaf out. Color of circle reflect average leaf out day across treatments, across sites of origin, while size of circle represents the total number of clippings in the experiment—this varies mainly based on whether the species was found at both sites and whether it was exposed to all three chilling treatments, see Supp X for more details.
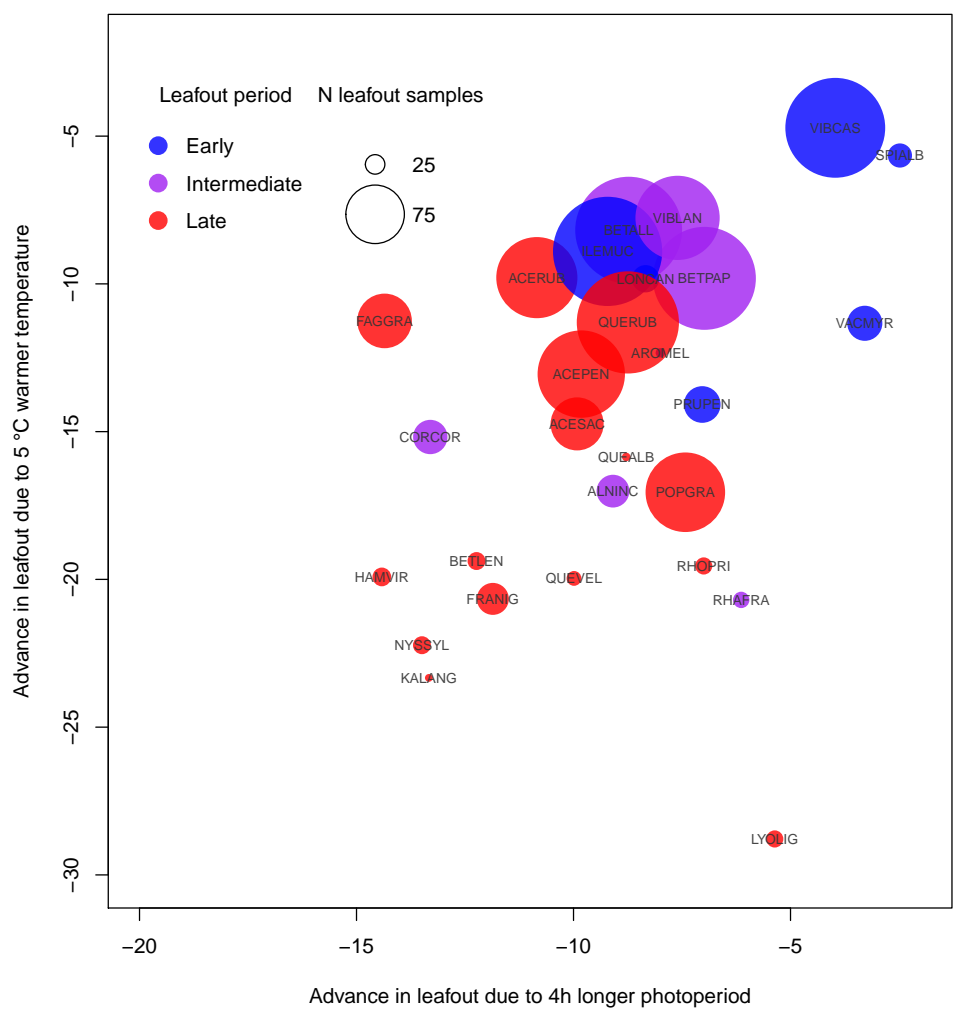
Figure 2: Modeled effects plots, Budburst and leaf out

a. Budburst

b. Leafout

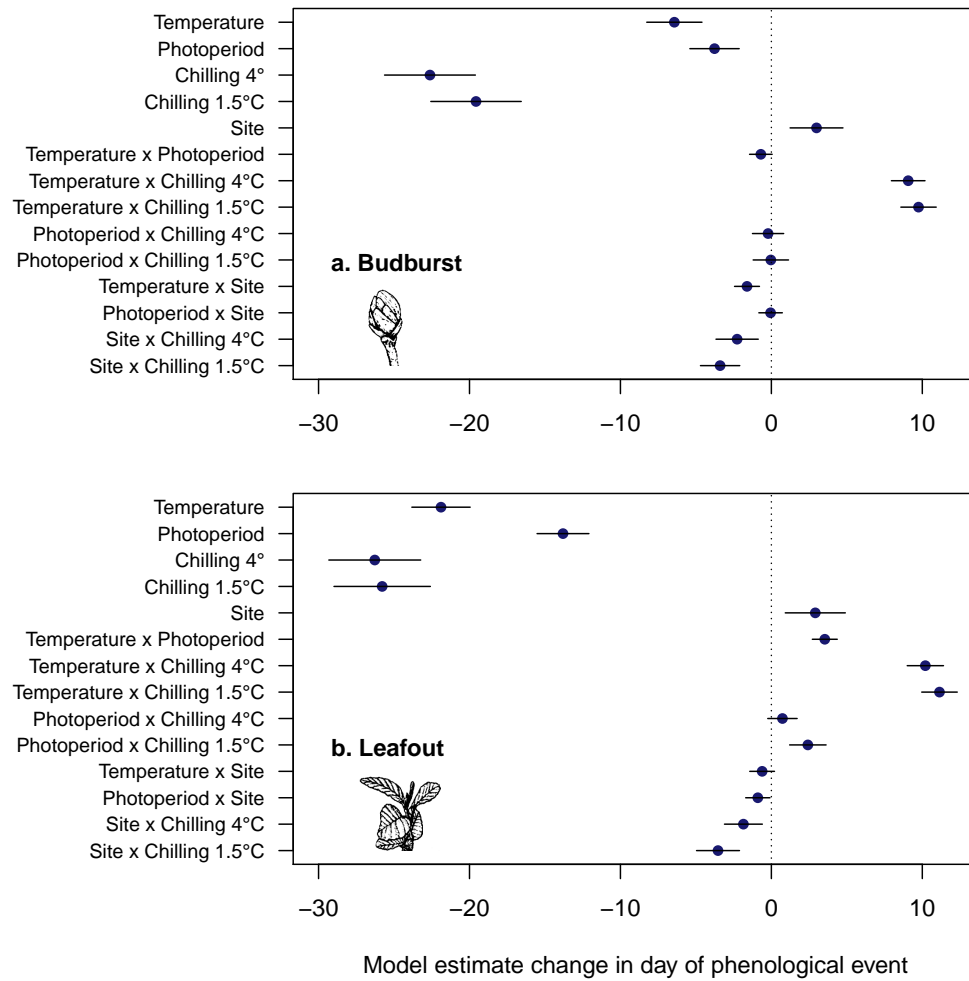Model estimate change in day of phenological event

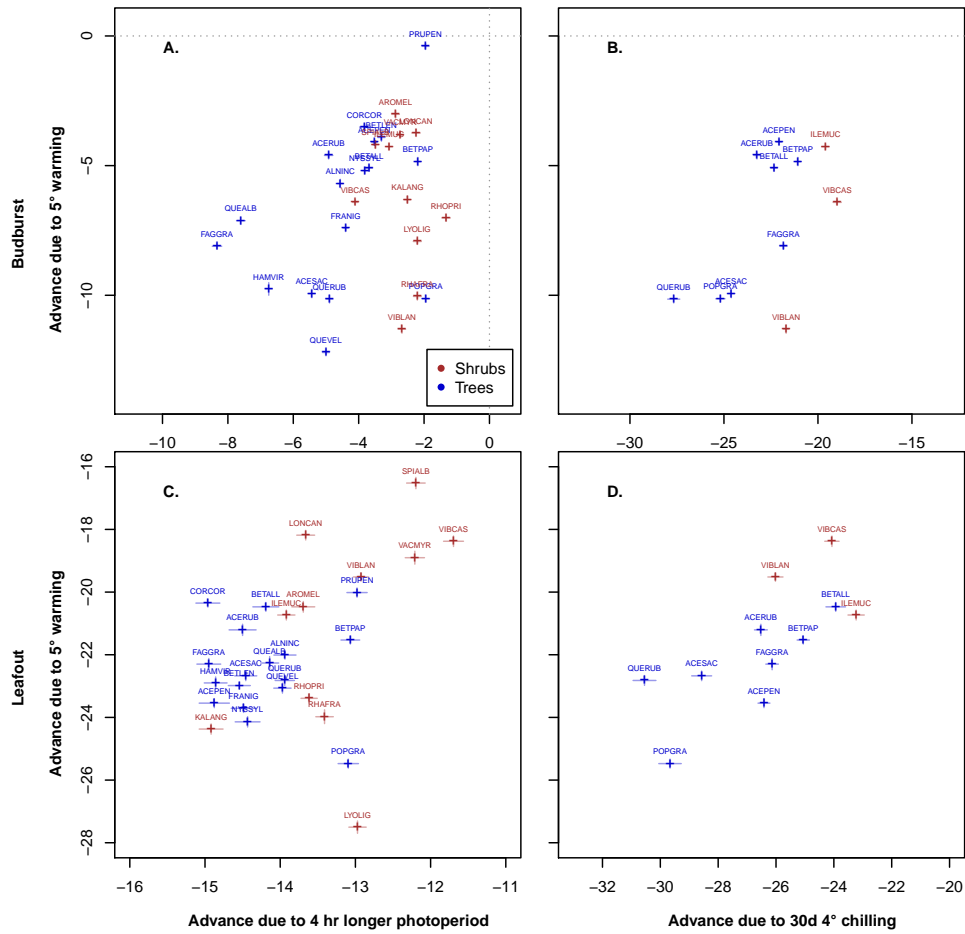Figure 3: Sensitivity of budburst and leaf out to warming, leaf out, and chilling.

Table 1: Chill units in field and field and growth chamber conditions.

Site	Treatment	Chilling Hours	Utah Model	Chill portions
Harvard Forest	Field chilling	892	814.50	56.62
	4.0 °C x 30 d	2140	2062.50	94.06
	1.5 °C x 30 d	2140	1702.50	91.17
St. Hippolyte	Field chilling	682	599.50	44.63
	4.0 °C x 30 d	1930	1847.50	82.06
	1.5 °C x 30 d	1930	1487.50	79.18

Table 2: Phylogenetic signal in timing of budburst and leaf out and species specific traits, as estimated in the caper package with simultaneous fitting of lambda. Pore anatomy (ring- versus diffuse-porous species) was highly clustered phylogenetically, but no other trait examined demonstrated significant phylogenetic signal

Relationship	Lambda
SLA - Temperature	0.000
SLA - Photoperiod	0.000
SLA - Chilling 4 °C	0.000
SLA - Chilling 1.5 °C	0.000
Wood Density - Temperature	0.000
Wood Density - Photoperiod	0.000
Wood Density - Chilling 4 °C	0.000
Wood Density - Chilling 1.5 °C	0.000
% N - Temperature	0.313
% N - Photoperiod	0.228
% N - Chilling 4 °C	0.127
% N - Chilling 1.5 °C	0.130
Pore anatomy - Temperature	1.000
Pore anatomy - Photoperiod	1.000
Pore anatomy - Chilling 4 °C	1.000
Pore anatomy - Chilling 1.5 °C	1.000

Table 3: Trees, budburst

	est	se	stat	p	lwr	upr
Intercept	29.45	0.37	78.70	0.00	28.72	30.19
Stem density	2.16	0.48	4.47	0.00	1.21	3.11
SLA	1.70	0.38	4.52	0.00	0.96	2.44
Pore anatomy	-4.81	0.37	-12.89	0.00	-5.55	-4.08

Table 4: Trees, leaf out

	est	se	stat	p	lwr	upr
Intercept	42.91	0.44	97.56	0.00	42.04	43.77
Stem density	-2.81	0.60	-4.68	0.00	-3.98	-1.63
SLA	2.07	0.44	4.74	0.00	1.21	2.92
Pore anatomy	-3.52	0.42	-8.35	0.00	-4.35	-2.70

Table 5: Shrubs, budburst

	est	se	stat	p	lwr	upr
Intercept	23.76	0.53	45.07	0.00	22.72	24.79
Stem density	-4.59	0.79	-5.84	0.00	-6.13	-3.04
SLA	0.29	0.52	0.55	0.58	-0.74	1.32
Pore anatomy	1.58	1.27	1.25	0.21	-0.91	4.07

Table 6: Shrubs, leaf out

	est	se	stat	p	lwr	upr
Intercept	27.16	0.68	39.69	0.00	25.82	28.50
Stem density	0.56	0.93	0.60	0.55	-1.28	2.39
SLA	2.32	0.57	4.06	0.00	1.20	3.45
Pore anatomy	-1.11	1.63	-0.68	0.50	-4.32	2.10