Photoperiod and temperature interactively drive spring phenology in multiple species

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Understanding the sensitivity of forest plants at the species level 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. While observational studies of long-term trends are essential for understanding how climate affects timing of phenological events, experimental manipulations are necessary to disentangle otherwise covarying environmental factors and directly assess species- and individual-level responses to climate change factors. Observational studies have additionally known difficulties in teasing out plant responses to climate, with responses expected to be based on one or several major cues plant receive from the fall to spring: chilling temperatures, 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, 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 (i.e., species highly sensitive to temperature were also highly sensitive to photoperiod), with greater sensitivity of budburst and leaf out 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

54 increasing spring temperature (forcing), length and intensity of winter temperature (chilling),

55 and changing daylength (photoperiod). Observational studies generally show stronger signs of

56 phenological advance in response to temperature than experimental manipulations [6], yet

57 experimental manipulations are necessary for disentangling otherwise covarying environmental

58 factors and directly assess species- and individual-level responses to climate change factors.

59 Balancing the maximization of carbon gain with minimzation of freezing risk can be

60 Spring frost events have been increasing in North America [**?**], with greater probability of

61 freezing events occuring after budburst. A single frost event, if timed after leaf out, can

62 substantial reduce ecosystem productivity and potentially shift the composition of temperate

63 forests [**?**].

64 Plants may either tolerate risk of spring freezing by investing in tissue which can withstand

65 freezing, or avoid freezing with later phenology. For perennial plants, it has been found that

66 leaves of species which have later phenologies can be more sensitive to frost damage [7],

67 supporting the notion of a tradeoff between tolerance and avoidance of freezing risk.

68 Winter chilling requirements can act as additional conservative strategy to avoid damage from

69 early spring freezing [8], as .

70 Do populations at northern sites, with more severe winters and shorter winter daylength, exhibit

71 more conservative phenological strategies?

72 For temperate trees, species can be limited at their northern range by inability to develop

73 mature fruit in a given growing season, while limited at their southern range by inability to

74 break dormancy due to insufficient chilling [9]. Thus phenology can drive range limits.

75 Common garden studies have shown that southern-adapted species, when translocated to a

76 more northern location, exhibit later leaf out compared to species adapted to northern

77 sites [10]. If species remain relatively fixed in their timing of leaf out, then northward migration

78 of such late-phenology species may act to counteract community-wide advances in phenology

79 under a warming climate.

80 Photoperiod has long been known to be a critical driver of the onset of endormancy, in
81 combination with cooling temperatures [11]. However, the role of photoperiod in determining
82 the breadking of dormancy has been debated, with various authors finding that the strength of
83 daylength as a driver may depend on phenological stage, species and location [12] [13].
84 Photoperiod and winter chilling can interact, as long as photoperiod enhances cell growth,
85 compensating for a lack of chilling during the endodormancy phase [14] [15] [16]. In the few
86 experimental studies that have directly manipulated both forcing temperature and photoperiod,
87 photoperiod has been shown to act in contradictory ways

88 A literature review (see Supplemental Materials) shows that at most four species have been
89 examined for photoperiod and temperature cues in a manipulative study to date.

90 Knowing species-specific sensitivies of temperate plant phenology to chilling and forcing alone
91 can predict regional-scale phenology [17]. Substantial variation exists at the species level in the
92 magnitude of the temporal advance of spring phenology (Primack 2009), such that the presence
93 of species highly sensitive to temperature change can strongly drive community-level
94 phenology [18].

95 Early phenological events, such as initial swelling of buds and budburst (separtion of budscales)
96 are challenging to study from remote sensing, with little obvious change in color or reflectance.
97 requiring experimental work at the individual level.

98 Different phenological stages may be driven by different environmental cues. The period
99 between budburst and leaf out is critical for leaf development, as this is a period when plants are
100 highly sensitive to damage from early frosts . Thus we carried out our tests for both budburst
101 and leaf out. We predicted that budburst would be generally less predictable than leaf out.

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 or leaf-out, but populations from the northern site tended to exhibit slower budburst and leaf-out, with a more rapid budburst and leaf out in response to the chilling treatments (indicated by negative coefficients for site x chilling treatments).

Warming, photoperiod, and chilling individually and interactively acted to drive budburst and leaf out earlier across species. The strength of the acceleration in budburst due to both warming and photoperiod were similar, but the acceleration of leaf out due to warming exceeded that of photoperiod for both phenological stages. Surprisingly, site of origin exerted limited effect on either budburst or leaf out across species.

Effect of chilling

The cuttings were harvested in late January 2015, and thus experienced substantial natural chilling by the time they were harvested. Using weather station data from the Harvard Forest and St. Hippolyte site, chilling hours (below 7.2°C), Utah Model chill portions (hours below 7.2°C and between 0°C and 7.2°C) and Dynamic Model [19] chill portions were calculated both for the natural chilling experienced by harvest and the chilling experienced in the 4°C and 1.5°C treatments. The Utah Model and Dynamic Model of chill portions account for variation in the amount of chilling accumulated at different temperatures, with the greatest chilling occuring approximately between 5-10°C, and fewer chill portions accumulating at low temperatures and that higher temperatures can reduce accumulated chilling effects. The two differ in the parameters used to determine the shape of the chilling accumulation curve, with the Dynamic Model being shown to be the most successful in predicting phenology for some woody species [20]. With both the Utah and Dynamic model, the more severe chilling treatment resulted in fewer calculated chilling portions.

Species varied widely in response to chilling treatments, with some exhibiting strong chilling requirements (*Acer saccharum*, *Fagus grandifolia*), while others exhibited little change in phenological advancement under experimentally manipulated chilling. Overall, budburst and

6

leaf-out advanced by 22.1 or 26.4 days under additional 30 d of vernalization at 4°C, and advanced by a reduced amount of 19.7 or 26.1 days under 30 d of vernalization at 1.5°C. The reduced chilling effect at the lower 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 inconsitent 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 [21].

Shrubs with low specific leaf area (thick/dense leaves) and high stem density were more likely to

177 leaf out earlier. For trees, with an overall later leaf out pattern,

178 Rank order of leaf out and budburst was stable across warming and photoperiod treatments.

179 Chilling treatments shifted the order, for example *Fagus grandifolia* was the 23-28th species to

180 burst bud with no additional chilling, but advanced to the 10-11th species to burst bud in with

181 additional chilling. Within chilling treatments, the consistency of the rank order was high, with

182 standard deviation of the rank order ranging from 2.05 d (budburst, no additional chilling) to

183 0.75 d (leaf out, additional chilling at 4°C). Compared to field observations, rank order of leaf

184 out was generally most related in the cool, short-day treatment with no additional chilling (Fig.

185 S10).

Nonleaf outs

187 Across all treatments, 20.2% of the cuttings did not break bud or leaf out. Across species, there

188 was no overall predictive effect of temperature, photoperiod, chilling, or site on the propensity

189 to fail to leaf out. Species ranged from complete leaf out (*Hamamelis*) to only 50% leaf out

190 (*Fagus grandifolia*, *Acer saccharum*) across all treatments. The percent of nonleaf outs by site

191 was similar, with 20.6% of Harvard Forest and 19.7% of St. Hippolyte samples failing to leaf

192 out. Examining individual species, there was an interaction of temperature by daylength for

193 selected species, with greater failure to leaf out in cool, short-day conditions for *Acer*

194 *pensylvanicum* and *Acer saccharum*. Site effects were inconsistent, with greater failure to leaf

195 out for cuttings from St. Hippolyte in *Acer rubrum* and *Fagus grandifolia*, and from Harvard

196 Forest in *Acer saccharum*.

Discussion

198 • Photoperiod sensitivity is common in northeastern woody plants; Phenological sensitivity

199   to photoperiod and temperature are largely coordinated across species.

- Chilling is the most important factor, even of greater importance than forcing. Mild winters spur greater phenological advancement than colder winters. Chilling much more important than temperature or photoperiod in driving earler budbreak, and still relatively more important for leaf out. Chilling and forcing temperature are more substitutable than chilling and photoperiod, for both budburst and leaf out.

- Only limited support for risk-avoidance strategies for northern populations of these 28 species was found, with small delays in both phenological events for populations from the more northern site. The latitudinal range studied here is within the range of the phenotypic flexibility of these species. Of these study species, we should not be overly concerned about being photoperiod limited at the more northern sites; given sufficient pace of dispersal, they will be able to track a changing climate.

- Budburst is sensitive to the same environmental cues as leaf out, but species show idiosyncratic orderings of their sensitivity to environmental cues at these two phenological stages; leaf out responses can not necessarily be used to back-cast budburst responses. Budburst showed a more limited total response to environmental cues, and species were more tightly clustered in those repsonses.

- Surprisingly, the smaller statured, earlier-leafing out shrubs and small trees exhibited reduced sensitivity to all three factors of temperature, photoperiod, and chilling. They are relatively more fixed in their timing of both budburst and leaf out, perhaps indicating an alternative mechaism for timing of spring phenology in these plants, such depending on carbohydrate metabolism to time budburst [22].

- Given these results, the future of the northeastern forests may shift away from shrubs and small trees, as late-successional, later-event species demonstrated a greater ability to lengthen their growing seasons opportunistically in response to warmer temperatures.

Methods

Field sampling

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

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; daylength 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 occured 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 Erlenmyer 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) x 2 photoperiod (12 vs. 8 h) x 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 sufficnet 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 [23], 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 [23]) and leaf out, defined as first leaves unfolded (Code 11 in [23]). Additional stages up to flowering and stem elongation were also recorded. In total, we made 19,318 phenological observations at the cutting level.

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. 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 At each individual, Leaf and stem material

Statistical analysis

For the two We fit mixed effect models separtely for budburst and leaf out 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.

Phylogenetic methods

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Figures and Tables

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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.
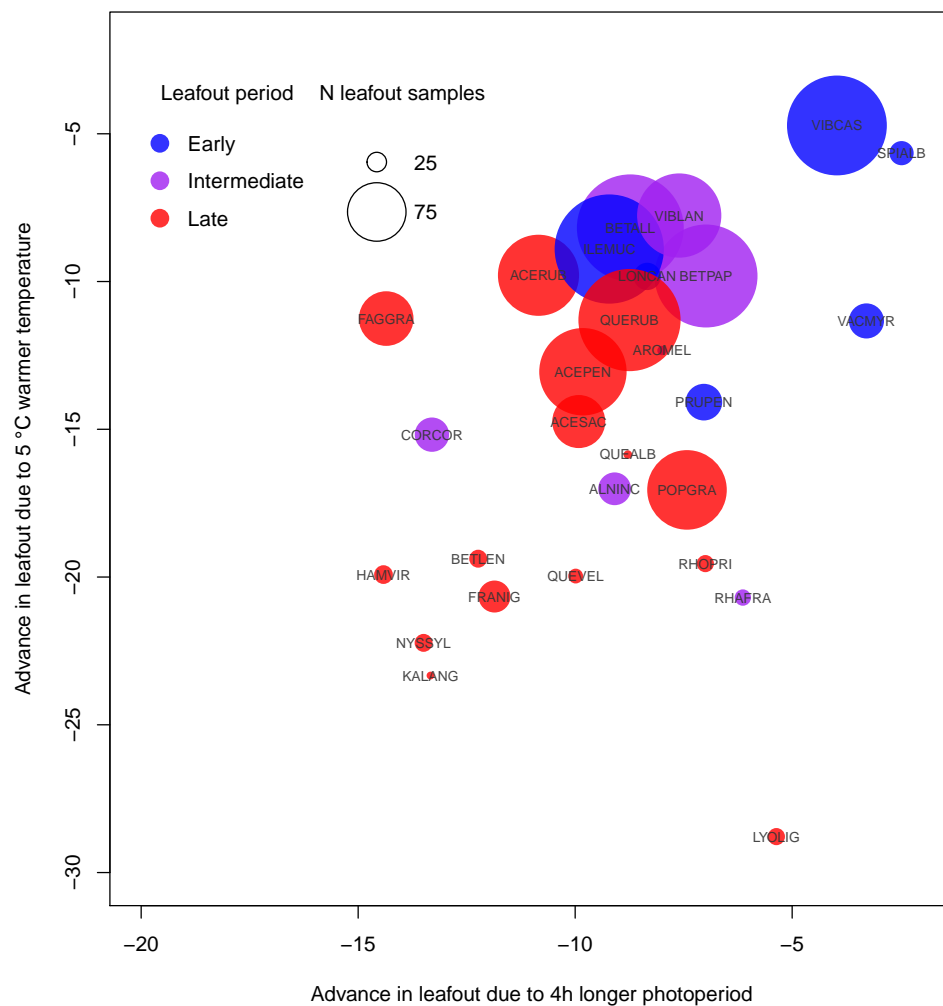
Figure 2: Modeled effects plots, Budburst and leaf out

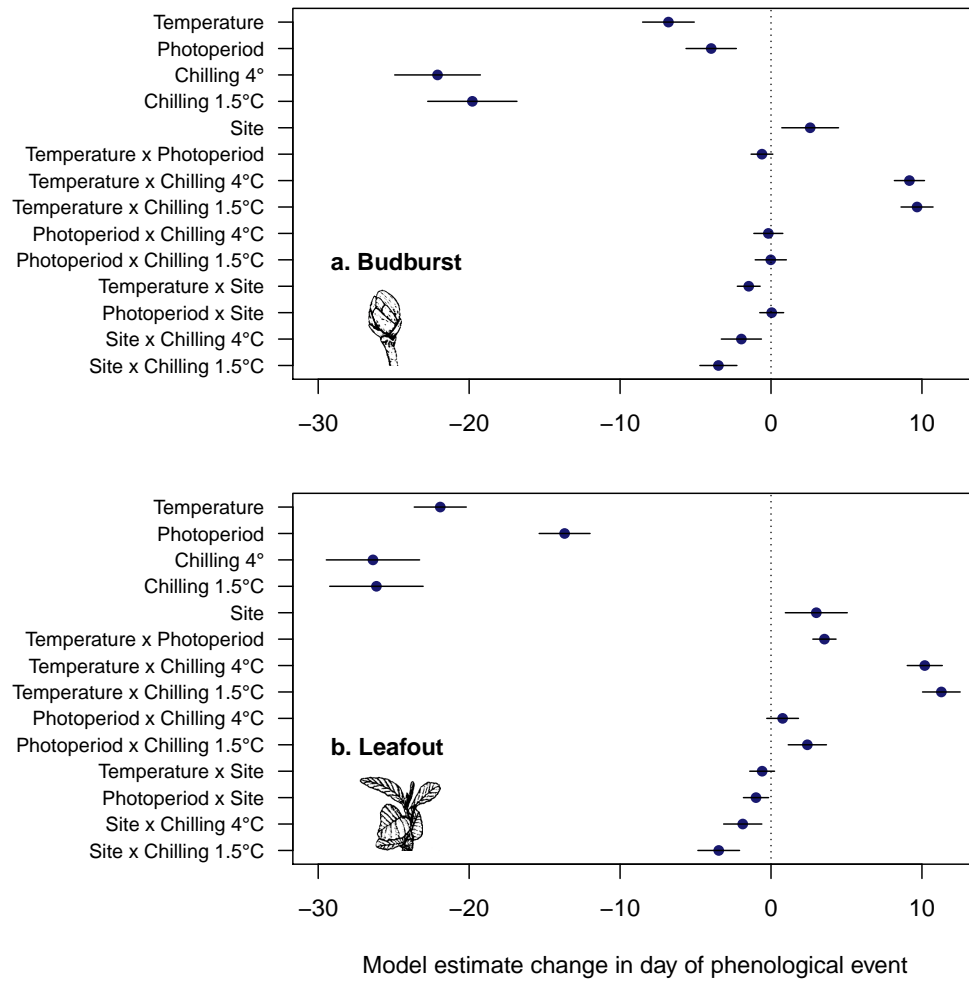Model estimate change in day of phenological event

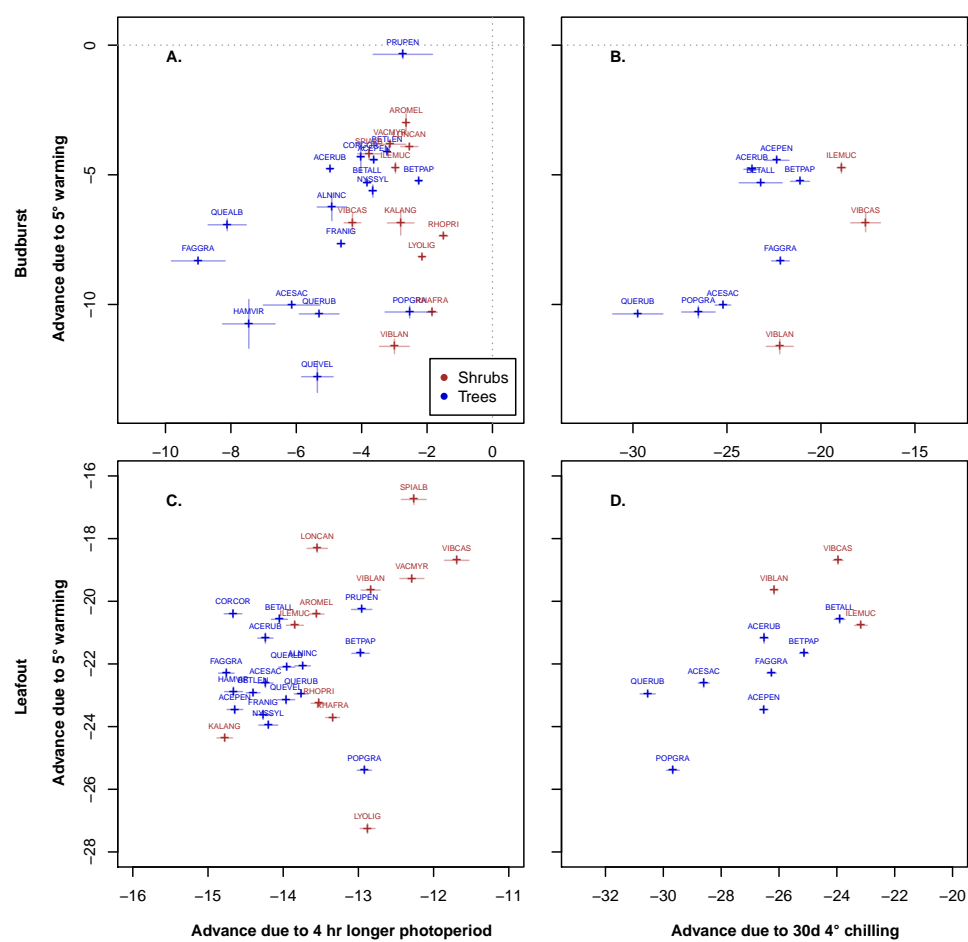Figure 3: Sensitivity of budburst and leaf out to warming, leaf out, and chilling.

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	0.285
% N - Photoperiod	0.203
% 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