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Temperature alone does not explain phenological variation of diverse temperate plants under experimental warming

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Abstract

Anthropogenic climate change has altered temperate forest phenology, but how these trends will play out in the future is controversial. We measured the effect of experimental warming of 0.6–5.0 °C on the phenology of a diverse suite of 11 plant species in the deciduous forest understory (Duke Forest, North Carolina, USA) in a relatively warm year (2011) and a colder year (2013). Our primary goal was to dissect how temperature affects timing of spring budburst, flowering, and autumn leaf coloring for functional groups with different growth habits, phenological niches, and xylem anatomy. Warming advanced budburst of six deciduous woody species by 5–15 days and delayed leaf coloring by 18–21 days, resulting in an extension of the growing season by as much as 20–29 days. Spring temperature accumulation was strongly correlated with budburst date, but temperature alone cannot explain the diverse budburst responses observed among plant functional types. Ring-porous trees showed a consistent temperature response pattern across years, suggesting these species are sensitive to photoperiod. Conversely, diffuse-porous species responded differently between years, suggesting winter chilling may be more important in regulating budburst. Budburst of the ring-porous *Quercus alba* responded nonlinearly to warming, suggesting evolutionary constraints may limit changes in phenology, and therefore productivity, in the future. Warming caused a divergence in flowering times among species in the forest community, resulting in a longer flowering season by 10-16 days. Temperature was a good predictor of flowering for only four of the seven species studied here. Observations of interannual temperature variability overpredicted flowering responses in spring-blooming species, relative to our warming experiment, and did not consistently predict even the direction of flowering shifts. Experiments that push temperatures beyond historic variation are indispensable for improving predictions of future changes in phenology.

Keywords: budburst, climate change, flowering, growing season length, leaf senescence, phenology, southeastern United States, temperature sensitivity, warming experiment

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Introduction

Shifts in phenology provide clear evidence that climate change is affecting Earth's biota. Earlier dates of budburst and later dates of leaf senescence have led to an extension of the vegetative growing season by 2.1–4.2 days/decade in Eurasian and North American forests over the past several decades (Menzel *et al.*, 2008; Jeong *et al.*, 2011). Similarly, shifts in first and last flowering dates have resulted in longer community-level flowering seasons (CaraDonna *et al.*, 2014). Despite these mean trends, species vary greatly in their individual responses to climate change. While most species flower earlier with warming (Fitter *et al.*, 1995; Fitter & Fitter, 2002; Primack *et al.*, 2004), other species show no response to warming (Bradley *et al.*, 1999), or even delays, at least in flowering (Sherry *et al.*, 2007; Dorji *et al.*, 2013). Even in responsive species, there are inevitably limits beyond which additional warming fails to produce the same rate of phenological change (Morin *et al.*, 2010; Salk, 2011; Gunderson *et al.*, 2012; Iler *et al.*, 2013; Clark *et al.*, 2014a). Predicting future responses of phenology to climate change in general, and warming in particular, must rely upon the broader perspective offered by considering a range of approaches, including experiments that simulate future climate conditions (Williams & Jackson, 2007; Wolkovich *et al.*, 2012; Clark *et al.*, 2014a).

Timing of leafing and flowering is often consistent within plant genera and families (Kang & Jang, 2004;

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Willis *et al.*, 2008; Davis *et al.*, 2010; Davies *et al.*, 2013), and evolutionary constraints in certain lineages may limit changes in phenology as the climate warms. In theory, the optimal leaf phenology for temperate plants is one which maximizes photosynthetic carbon uptake while minimizing losses to frost damage in the spring and maximizing nutrient resorption in the fall. If plant phenological cues allow such a response to warming, productivity will increase as long as other warming-related stresses (i.e. high temperature or drought stress) do not offset gains from longer growing seasons (White *et al.*, 1999; Saxe *et al.*, 2001; Richardson *et al.*, 2010; Dragoni *et al.*, 2011; Keenan *et al.*, 2014). It has been suggested, however, that plants with phenological responses cued in part by photoperiod or winter chilling may fail to fully track climate warming (Bradley *et al.*, 1999; Yu *et al.*, 2010; Way & Montgomery, 2014). One plant functional group that may under-respond is ring-porous trees, which have large-diameter, early season and smaller diameter, late-season xylem vessels, relative to diffuse-porous species that have consistent vessel diameter throughout the growing season. Ring-porous trees generally burst bud later in the spring than diffuse-porous trees (Wang *et al.*, 1992; Panchen *et al.*, 2014). This may be an adaptive response that limits the risk for frost-induced dysfunction in large-diameter xylem vessels, but it may also reduce the ability of such species to track climatic changes. Advances in budburst with warming can thus be predicted to differ between ring- and diffuse-porous trees (Sanz-Perez *et al.*, 2009; Körner & Basler, 2010; Salk, 2011; Clark *et al.*, 2014b), although such differences have not been detected to date (Way & Montgomery, 2014).

Flowering in temperate regions is restricted to seasons with favorable temperature, precipitation, and presence of pollinators (Rathcke & Lacey, 1985), usually leading to bimodal distribution of flowering times with peaks in spring and late summer (Kochmer & Handel, 1986; CaraDonna *et al.*, 2014). Species from early blooming lineages tend to be more responsive to warming than late spring or summer bloomers (Bradley *et al.*, 1999; Cook *et al.*, 2012; Wolkovich *et al.*, 2012), but the complex interactions among environmental cues and evolutionary history that partition species into temporal niches are poorly understood (Pau *et al.*, 2011). Our current knowledge of how flowering phenology responds to temperature is predominantly restricted to changes in timing of first flowering date, while shifts in last flowering date and length of the flowering season are less commonly measured. However, one recent study has found that flowering season has lengthened by over a month in response to recent warming in a subalpine plant community (CaraDonna *et al.*, 2014).

Warming experiments increase temperatures beyond the range of current variation and are valuable for understanding how future no-analogue climates will affect plant phenology. Mean temperature in the southeastern USA is expected to increase by 2–5 °C by 2100 (IPCC, 2014a). The impact of future warming on temperate forest communities is highly uncertain in part because warming experiments have focused on open ecosystems such as tundra (Chapin & Shaver, 1996; Arft *et al.*, 1999), alpine meadows (Harte & Shaw, 1995; Dorji *et al.*, 2013), and grasslands (Sherry *et al.*, 2007), or have taken place in clearings (Norby *et al.*, 2003). Here, we use a forest understory warming experiment to dissect how temperature affects timing of spring budburst, flowering, and autumn leaf coloring in a diverse suite of 11 temperate forest species (Table 1) with different growth habits, phenological niches, and xylem anatomy. We measured changes in leaf and flower phenology inside actively heated open-top chambers in Duke Forest, North Carolina, USA in 2011 and 2013, 2 years when mean spring temperature differed by about 5 °C, to test the hypotheses that:

1. Warming will lengthen the growing season (by advancing budburst and delaying leaf coloring) and flowering season (by advancing first flowering and delaying last flowering in the community), but these phenology responses will not be linear functions of air or soil temperature.
2. Budburst of diffuse-porous species will be more responsive to temperature than ring-porous species.
3. Flowering of spring-blooming species will be more responsive to temperature than taxa that flower in mid-summer.
4. Observations based on interannual temperature variability will overestimate changes in budburst and flowering phenology relative to a warming experiment simulating future temperatures. This hypothesis is based on recent findings that warming experiments underpredict rates of phenological change relative to long-term historical observations (Wolkovich *et al.*, 2012), although admittedly, we have taken an alternative view. In our study, we were able to analyze phenological changes within the same set of plants, arguably the most appropriate analysis for such a comparison.

Materials and methods

Experimental study site

This study was conducted at an ongoing warming experiment in a ca. 80-year-old deciduous forest stand in Duke Forest (36°2′11″N, 79°4′39″W, 130 m a.s.l.), in the piedmont region near Hillsborough, North Carolina, USA (Lynch, 2006). The

Table 1 Summary of the effect of experimental warming on phenological responses of 11 plant species in the understory community of Duke Forest, NC

					Effects of experimental warming					
Life form	Species	Wood anatomy	Leaf duration	Flowering month	Budburst	Leaf coloring	GSL	First flowering	Last flowering	FSL
Tree	ACRU	Diffuse	Win Decid		Earlier	Later	Longer			
Tree	CATO	Ring	Win Decid		Earlier	Later	Longer			
Tree	QUAL	Ring	Win Decid		Earlier	Later	Longer			
Tree	QURU	Ring	Win Decid		Earlier	None	Longer			
Shrub	VAPA	Diffuse	Win Decid	April–May	Earlier	None	None	None	None	None
Shrub	VAST	Diffuse	Win Decid	April–May	Earlier	None	None	Earlier	Earlier	None
Subshrub	CHMA		Evergreen	May–June				Earlier	Earlier	None
Herb	THTH		Spr Ephem	March–April				None	Earlier	None
Herb	HEAR		Evergreen	March–April				Earlier	Earlier	None
Herb	HIVE		Win Decid	April–May				Earlier	Earlier	None
Herb	TIDI		Sum Decid	July–August				(Later)	None	None

Plant life form, wood anatomy, leaf duration (spring ephemeral, winter deciduous, summer deciduous, evergreen), flowering month, and the direction of observed change relative to controls are given. Nonsignificant phenological responses based on correlations between 2-year response and temperature ($P > 0.05$) are indicated by 'None'; trends ($P < 0.1$) are indicated with parentheses. Species codes: ACRU, *Acer rubrum*; CATO, *Carya tomentosa*; QUAL, *Quercus alba*; QURU, *Quercus rubra*; VAPA, *Vaccinium pallidum*; VAST, *Vaccinium stamineum*; THTH, *Thalictrum thalictroides*, HEAR, *Hexastylis arifolia*; HIVE, *Hieracium venosum*; CHMA, *Chimaphila maculata*; TIDI, *Tipularia discolor*.

mean annual temperature at Duke Forest is 15.5 °C, and the mean annual precipitation is 1140 mm (Duke Forest Remote Automatic Weather Station, Orange County, NC, USA; 8 km from study site). Soil at the site is a Georgeville silt loam (Typic Kanhapludults, Ultisol), and dominant tree species include *Quercus alba*, *Quercus rubra*, *Carya tomentosa*, *Acer rubrum*, and *Oxydendrum arboreum*.

The experimental warming site consists of 15 plots in the forest understory: nine are heated chambers, three are unheated control chambers, and three are control plots that lack chambers but are the same size as the chambers. The octagonal open-top chambers have a volume of 21.7 m^3 (5 m in diameter, 1.2 m wall height) and are located on a north-facing slope (6–15% slope) above a small creek. The chambers are heated by forced air blown over hydronic radiators fed by a closed-loop mixture of hot water and propylene glycol (antifreeze). To control for effects of wind, unheated chambers had the same forced air delivery system minus the radiators. Heat delivery to the chambers began in January 2010, and chambers are heated year-round, both day and night. The experiment uses a regression design of chamber heating, where each chamber is heated to a target of 1.5–5.5 °C above ambient temperature with 0.5 °C increments between chambers. Maintaining a precise target air temperature over long time periods is difficult, and the assigned treatment levels varied by a small amount over time (but were not statistically different from target temperatures, see Fig. S1). This design is particularly useful for revealing potential nonlinearities and threshold effects in plant temperature responses.

Air temperature (two temperature probes per chamber at 22 cm above ground level), soil temperature (two sensors buried 2 cm and two sensors buried 6 cm below the surface), relative humidity (HS-2000V capacitive polymer sensor; Precon, Memphis, TN, USA), soil moisture (Model CS616 TDR probes, Campbell Scientific Inc., Logan, UT, USA), and photosynthetically active radiation (PAR; Model SQ110; Apogee Instruments Inc., Logan, UT, USA) were measured inside each experimental chamber every minute and recorded as hourly means by automated dataloggers (CR1000; Campbell Scientific Inc.). Further details of the warming experiment can be found in Pelini *et al.* (2011).

To determine how environmental conditions varied among experimental chambers, mean air temperature, soil temperature, vapor pressure deficit (VPD), PAR, and relative extractable soil water content (REW) were calculated for each chamber. REW was calculated according to the equation:

$$\mathrm{REW} = (\theta - \theta_{\mathrm{min}})/(\theta_{\mathrm{max}} - \theta_{\mathrm{min}}),$$

where θ is the hourly soil water content, θ_{min} is minimum soil water content, and θ_{max} is the mean maximum volumetric soil water content over the study period. Readings from three saturating rainfall events per year were averaged to determine θ_{max}. To account for soil macropore drainage and thus avoid over-estimating θ_{max}, volumetric soil water content from 2 h after the peak θ of each saturating rainfall event was used.

Large-scale warming experiments unavoidably alter additional environmental factors. Mean spring air temperature (15 February–15 March) of control chambers was about 0.5–0.9 °C above ambient temperature (Fig. S1), so all warming treatments were calculated relative to control chambers to account for this small chamber effect. Our warming experiment heated the air inside chambers by 0.6–5.0 °C above controls (Fig. S1), while the soil was indirectly warmed by 0.1–2.0 °C above controls (Fig. S2a). Many warming experiments unintentionally reduce light availability and soil moisture (Kennedy, 1995; Wolkovich *et al.*, 2012), but PAR and REW were not affected by warming in our experiment (Fig. S2b, d). However, warming inevitably decreased relative humidity by 2–13% (Fig. S2c) and increased VPD by up to 0.5 kPa inside the experimental chambers. Most studies show that plant phenology at temperate latitudes is controlled primarily by temperature and photoperiod (White *et al.*, 1997; Chuine & Cour, 1999). Recently, it was shown that budburst date can be influenced by absolute air humidity (Laube *et al.*, 2014), but this was unaffected by our heating treatments.

Vegetative phenological observations

We visited the experimental site every 4 to 7 days during the period of bud break (early March to mid-April in 2011 and 2013) and weekly during the period of leaf senescence (mid-October to early December in 2011) to observe the vegetative phenological stage of four tree species (*A. rubrum*, *C. tomentosa*, *Q. alba*, *Q. rubra*) and two shrub species (*Vaccinium pallidum*, *Vaccinium stamineum*; Table 1). There was no phenological census in 2012. Each species was present in 8–12 chambers, plus the chamberless control plots (Table S1). Most sampled plants (95%) were seedlings <50 cm tall, although plants up to 1 m tall (still well within the dimensions of the chambers) were sampled if species abundance was low. For each plant, vegetative phenology of terminal buds was divided into five stages: L0, unopened buds (no activity); L1, open buds (buds have broken); L2, emerging, unfolding leaves; L3, fully expanded leaves; L4, senescing leaves (defined as ≥50% of a plant's leaves having changed color). To better capture the continuous budburst response, plants received a score of L0/L1 (swollen buds) or L1/L2 (leaves have just emerged) when relevant and L1 was extrapolated for these individuals. Budburst date (L1) was analyzed for the four tree species, whereas date of leaf emergence (L2) was used for the two *Vaccinium* species due to difficulty in determining L1 on the tiny buds. Leaf emergence of shrubs will hereafter will be lumped with trees and referred to as budburst.

The simplest plausible budburst models are accumulated growing degree days ($\mathrm{GDD_{BB}}$) models (Salk, 2011; Gunderson *et al.*, 2012), which summarize temperature cues for budburst as cumulative heat sums above some threshold level (Rathcke & Lacey, 1985). We calculated the $\mathrm{GDD_{BB}}$ for each plant in 2011 and 2013 to compare differences in budburst between treatments and years. The $\mathrm{GDD_{BB}}$ was calculated from 15 February to the date of budburst using the equation of Cannell & Smith (1983):

$$\mathrm{GDD_{BB}} = \sum_{m=1}^{n} (t_{\mathrm{m}} - x),$$

where $\mathrm{GDD_{BB}}$ is the day degrees above the threshold temperature $x = 5$ °C, n is the number of spring days between 15 February and budburst with a temperature greater than x, and t_{m} is the mean daily temperature or $(T_{\max} + T_{\min})/2$. We used a starting date of 15 February, because this is the beginning of the period in which temperature variation has the most impact on timing of budburst (Clark *et al.*, 2014a). Trees in North Carolina are most sensitive to temperature accumulation in the last several weeks of winter (Clark *et al.*, 2014a), so we used mean air and soil temperature from 15 February to 15 March to summarize chamber-level treatments.

Changes in soil temperature were also examined, as soil temperature could be a better predictor of budburst date than changes in air temperature. The pattern of spring temperature increase is highly variable, with warm and cold spells usually only lasting a few days. Soil temperature changes are muted relative to changes in atmospheric temperature, however, because soils have a greater specific heat. Soil temperatures increased less than half as much as the air inside our experimental chambers (Fig. S2a). Therefore, increased soil temperature is a more conservative indicator than air temperature and is less susceptible to brief mid-winter warm spells. Theoretically, soil temperature could be a safer cue for spring budburst in temperate plants than air temperature.

At the end of the 2011 growing season, the date of leaf coloring (L4) in autumn was compared for all six understory species. Date of leaf coloring was not recorded in 2013. Growing season length was calculated by subtracting the mean date of budburst from the mean date of leaf coloring for each species in each chamber.

Reproductive phenological observations

We visited the experimental site every 4 to 7 days from mid-March through October in 2011 and 2013 to observe the reproductive phenology of four herbaceous species (*Hexastylis arifolia*, *Hieracium venosum*, *Thalictrum thalictroides*, *Tipularia discolor*) and three shrub species (*Chimaphila maculata*, *V. pallidum*, *V. stamineum*; Table 1). Flowering individuals were present in 4–7 chambers, plus the chamberless control plots (except for *H. arifolia*, which was not found in chamberless control plots; Table S1). For each plant, reproductive phenology was divided into seven stages: F0, unopened buds; F1, open buds; F2, flowers; F3, old flowers; F4, initiated fruit; F5, expanding fruit; F6, dehisced/senesced fruit. Plants received multiple scores when relevant, for example, a plant with flowers, old flowers, and initiated fruit was scored as F2/3/4. First flowering (F2) and last flowering (defined as the last date that flowers were present on the plant; scored as F3/F4, no F2) dates were compared for all seven understory species. Flowering season length was calculated by subtracting the mean date of first flowering from the mean date of last flowering for each species in each chamber. The onset of flowering is correlated with mean temperature during the month of flowering for many temperate plants (Sparks *et al.*, 2000; Menzel *et al.*, 2006), so we used the mean air/soil temperature inside each chamber during the month(s) of flowering to compare species responses to warming.

Statistical analyses

Warming effects on day of budburst, leaf coloring, growing season length, first flowering, last flowering, and flowering season length were analyzed by species using mean chamber-level response as the dependent variable. We fitted several types of budburst phenological response models using ordinary least squares regression. The first model had only an intercept and a linear term, while the second model also included these parameters plus a quadratic term. We also implemented models with just year as a predictor, and with year, temperature, and an interaction among these variables. All models were implemented using the 'lm' function in the R statistical package (R 3.0.3; Crawley, 2007). We tested budburst responses to both air and soil warming and chose from among these models using Akaike's Information Criterion (AIC, Akaike, 1974), corrected for small sample sizes (AICc; Hurvich & Tsai, 1989). This is a likelihood-based method that compares the fit of models with a penalty for the number of parameters.

As budburst date varied significantly with year rather than occurring at a constant photoperiod (i.e. the same day in both years), we compared GDD_{BB} to determine whether spring temperature accumulation could explain the variation in timing of budburst among years and warming treatments. Differences in GDD_{BB} for each species were determined using two-ways, full factorial analyses of variance (ANOVA) with year and mean chamber temperature (15 February–15 March) as the main effects. If plants were not constrained by chilling or photoperiod requirements after 15 February, the GDD_{BB} would be constant across chambers. This analysis can also implicate potential mechanisms influencing budburst among species. A different relationship between GDD_{BB} and average temperature between years suggests a species is influenced by variables that are not the same every year (e.g. winter chilling), whereas no difference in this relationship between years would suggest a species is influenced by factors that are invariant from year to year (e.g. photoperiod).

Several types of flowering phenological response models were fitted using ordinary least squares regression, and the best model was chosen using AICc. The first model had an intercept, temperature, and year term, while the second model also included an interaction term; models were fitted separately using air temperature and soil temperature. Chamber means were weighted by the number of plants per chamber.

To facilitate comparisons among species and study years, we calculated the mean phenological sensitivity to temperature (days change per °C in budburst date and first flowering date, relative to control plots) of each chamber for each species. There was no difference in phenological sensitivity between control chambers and chamberless control plots for any species ($t_{1–3} \leq 6.659$, $P \geq 0.123$), so these data were pooled. Mean experimental sensitivities were calculated for each heated chamber and then averaged across chambers for each species. Only data from control chambers and chamberless experimental plots were used to determine whether budburst and flowering date differed between study years; means were compared using the Student's t-test statistic. To determine whether interannual observations overestimated advances in budburst and flowering, relative to experimental warming, we used a paired t-test with mean phenological sensitivity of each species as the dependent variable. These analyses were performed using JMP 11.0 (SAS Institute, Cary, NC, USA).

Results

Vegetative phenology

Unheated chambers had a minimal impact on budburst responses, relative to chamberless controls. Budburst occurred 4–7 days earlier in the control chambers relative to the chamberless control plots for two species (*A. rubrum*, 4 days in 2013: $t_{32} = 2.45$, $P = 0.020$; *V. pallidum*, 7 days in 2013: $t_{27} = 3.36$, $P = 0.002$), but was unaffected in all other species. There was high variability in species budburst date within each chamber in our experiment, as budburst varied up to 31 days among individuals within a single chamber. Warming significantly advanced budburst (Fig. 1; Fig. S3), as mean day of budburst was correlated to air ($r^2 = 0.42$, $P < 0.001$, $n = 132$) and soil temperature ($r^2 = 0.43$, $P < 0.001$) with all six tree and shrub species pooled together. The GDD_{BB} varied among chambers from 230 (in *V. stamineum*) to 370 °C (in *Q. rubra*), with plants growing in warmer chambers accumulating more GDD_{BB} across all species (Fig. 1). Only *Q. alba* had a justifiable (and positive) quadratic term, showing that phenological temperature sensitivity for this species decreases with increased air temperature (Table 2). Budburst was best modeled by differences in air temperature, with no significant improvement when soil temperature was used as the predictor (Table 2).

Budburst responses to experimental warming differed between diffuse-porous and ring-porous species. Budburst of diffuse-porous species was best predicted by a model that included only year, whereas budburst of ring-porous species was best predicted by temperature models (Table 2). In the warmer year (2011) relative to the cooler year (2013), budburst was advanced by 11–13 days in diffuse-porous species ($t_{6–7} \geq 3.05$, $P \leq 0.028$) and by 4–9 days in ring-porous species ($t_{5–7} \geq 2.56$, $P \leq 0.063$) – a 1.7-fold larger shift in diffuse than ring-porous species. Regardless of year, budburst of the ring-porous tree species occurred at the same GDD_{BB} in chambers that had similar temperatures ($t_{19–24} \leq 0.72$, $P \geq 0.477$; Fig. 1). In the diffuse-porous species, budburst occurred at lower GDD_{BB} in control chambers in 2011 than in the hottest chambers in 2013 ($t_{16} \geq 2.72$, $P \leq 0.018$), despite having similar temperatures (Fig. 1).

The effect of warming on timing of autumn color change and growing season length also differed among species. Warming significantly delayed leaf coloring when tested across all six species ($r^2 = 0.15$, $P = 0.002$, $n = 61$), but when tested within species the timing of leaf coloring was correlated with September temperature only in *A. rubrum*, *C. tomentosa*, and *Q. alba*

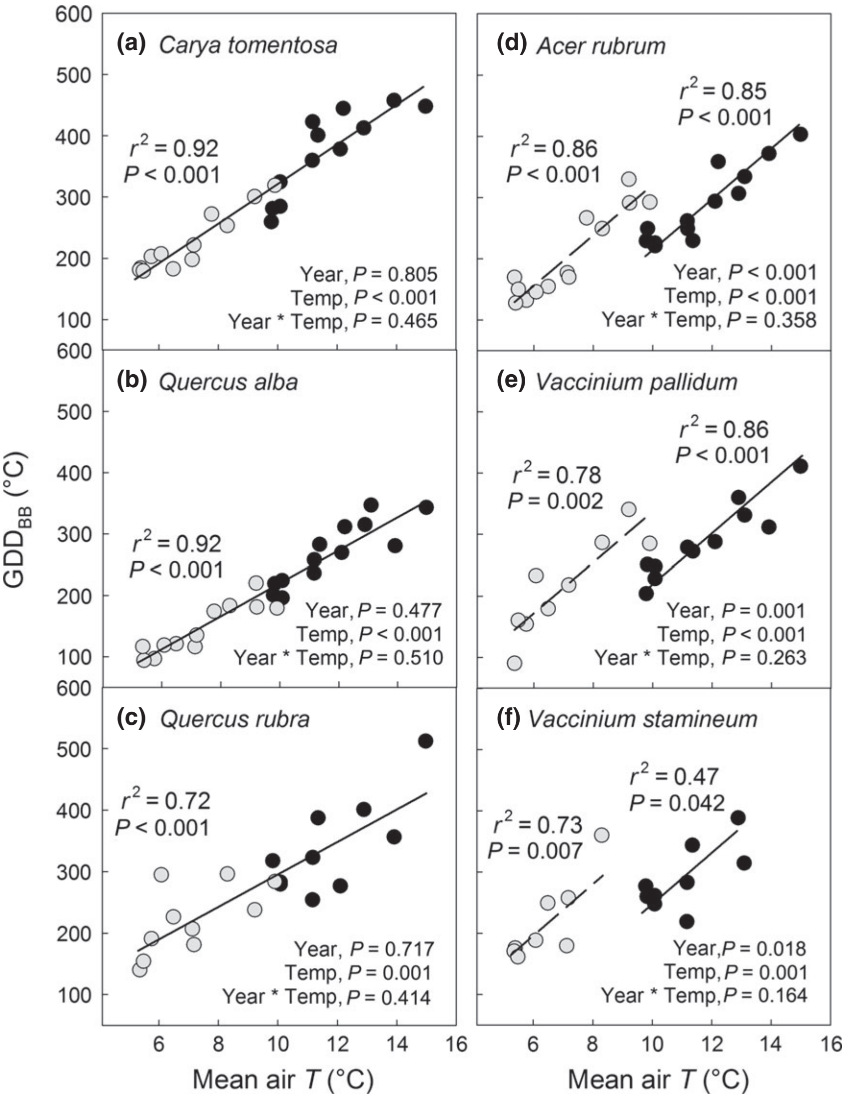

Fig. 1 The effect of air temperature (15 February–15 March) on the observed growing degree days to budburst (GDD_{BB}) in 2011 (black circles) and 2013 (gray circles) for all species. Points represent individual chamber means, and modeled temperature effects are depicted by a single trendline; species with two parallel lines showed significant year effects. Mean 15 February–15 March temperature was 4.6 °C higher in 2011 than in 2013. Ring-porous species (a–c) are shown in the left column, and diffuse-porous species (d–f) are shown in the right column.

($r^2 \geq 0.37$, $P \leq 0.028$; Fig. 2). As a result of advanced budburst by up to 5–15 days and/or delayed leaf coloring in autumn by up to 18–21 days, warming extended the 2011 growing season by as much as 20-29 days in the four tree species ($r^2 \geq 0.38$, $P \leq 0.025$; Fig. 2). There was no significant effect of warming on growing season length of the shrub species *V. pallidum* or *V. stamineum*.

Reproductive phenology

There were considerable differences in the effect of warming on reproductive phenology among the seven understory species examined here (Fig. 3). Four species advanced first flowering (*H. arifolia*, *V. stamineum*, *H. venosum*, *C. maculata*) with warming ($r^2 \geq 0.49$, $P \leq 0.017$), while two species (*T. thalictroides*, *V. pallidum*) did not respond to warming ($r^2 \leq 0.37$, $P \geq 0.061$; Fig. 4). In the orchid species *T. discolor*, there was a trend for delayed first flowering by 10.8 days per °C in 2011 ($t_8 = 1.911$, $P = 0.093$; Table 4). The two most responsive species to warming flowered in late spring and early summer (April–June; Fig. 3). The herb *H. venosum* flowers in April–May, when warming advanced flowering by a mean of 6 days ($t_5 = 2.441$, $P = 0.050$). The evergreen *C. maculata*, which flowers in May–June, had earlier flowering by 23 days ($t_6 = 8.511$,

Table 2 Akaike's Information Criterion (AICc) from five different models predicting the effect of increased air and soil temperature (T, in °C) on GDD_{BB} of six species in Duke Forest, NC in 2011 and 2013

Species	Year	T	$T + T^2$	T + Year	T + Year + T × Year
Air T					
C. tomentosa	137.88	**132.67**	135.57	135.48	138.42
Q. alba	133.61	122.83	**122.15**	125.66	123.68
Q. rubra	132.03	**126.48**	128.78	129.64	132.98
A. rubrum	**131.09**	155.46	157.85	133.49	136.53
V. pallidum	**110.93**	126.67	129.67	113.44	116.86
V. stamineum	**100.64**	106.61	110.01	103.67	107.30
Soil T					
C. tomentosa		132.41	135.31	135.30	138.43
Q. alba		122.66	122.63	125.28	126.46
Q. rubra		125.76	128.83	128.49	131.51
A. rubrum		150.07	152.28	133.29	135.89
V. pallidum		124.66	127.73	113.97	117.05
V. stamineum		106.98	110.46	103.38	106.74

The best model for each species is in bold. The model with just year as predictor is only presented in the air temperature column for convenience.

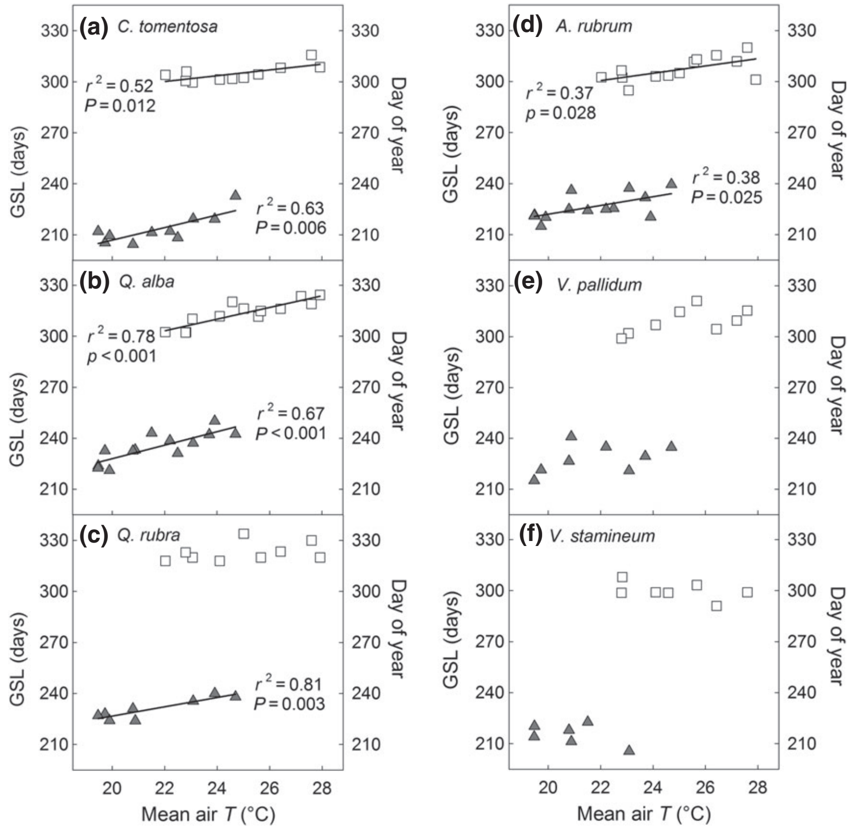

Fig. 2 The effect of warming on growing season length (gray triangles) and day of leaf coloring (white squares) for (a–c) ring-porous species and (d–f) diffuse-porous species in 2011. Points represent individual chamber means, and significant temperature effects ($P < 0.05$) are depicted by a single trendline. Mean September air temperature was used as the predictor for day of leaf coloring, while mean growing season temperature (March–October) was used to predict growing season length.

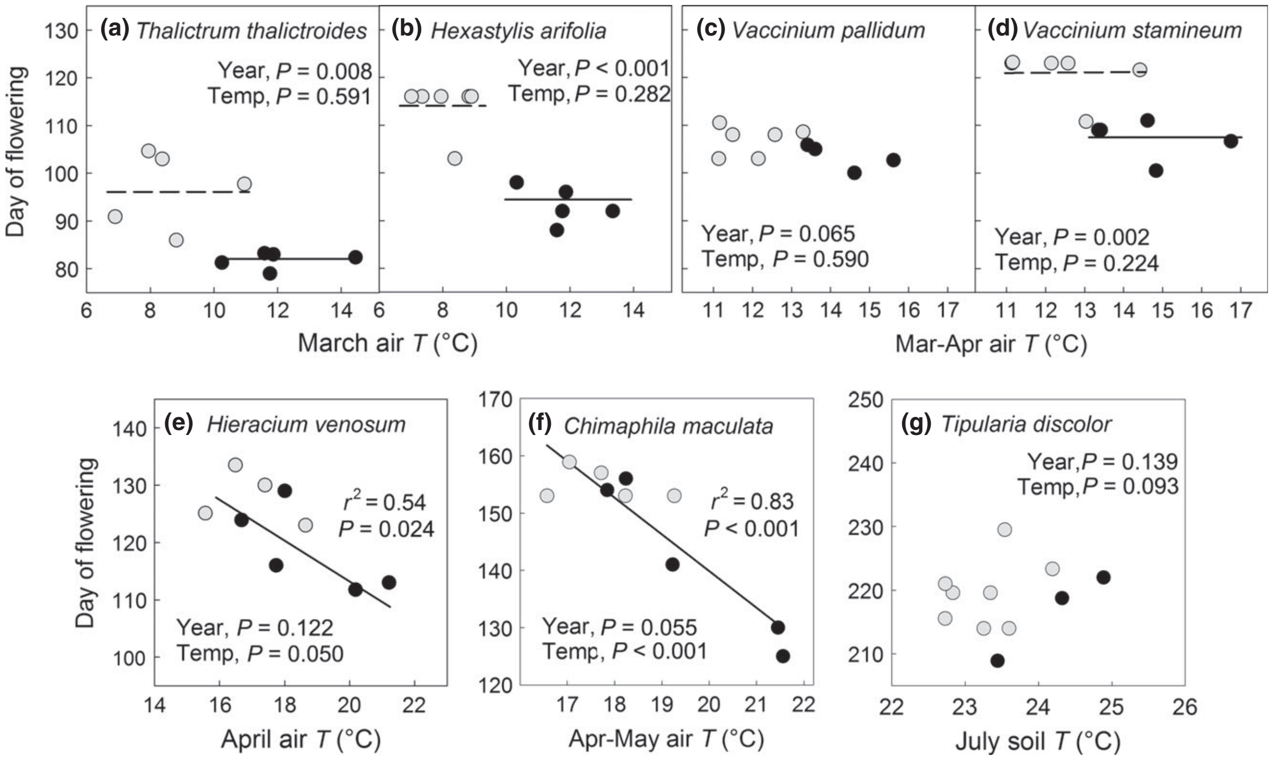

Fig. 3 The effect of air/soil temperature on day of flowering in 2011 (black circles) and 2013 (gray circles) for (a–g) seven species. Circles represent individual chamber means. The best-fitting model as determined by Akaike's Information Criterion (AIC) (see Table 3) was used to determine trendlines for each species. Air temperature effects are depicted by a single trendline. Horizontal lines represent mean flowering date in 2011 (solid line) and 2013 (dashed line) for species with significant interannual differences in flowering date. Soil temperature was only important in predicting flowering of (g) *T. discolor*.

$P < 0.001$). Flowering of all species was best predicted by a model that included only temperature and year; no species was best predicted by a model that also included an interaction term (Table 3). Flowering of most species was best predicted by changes in air temperature, but the flowering response of *T. discolor* was best predicted by changes in soil temperature (Table 3).

Table 3 Akaike's Information Criterion (AICc) from two different models predicting the effect of increased air and soil temperature (T, in °C) on day of flowering of seven species in Duke Forest, NC in 2011 and 2013

	Air T		Soil T	
Species	T + Year	T × Year	T + Year	T × Year
T. thalictroides	**75.63**	84.46	76.03	85.03
H. arifolia	**72.08**	79.17	74.06	79.22
V. pallidum	**62.37**	70.25	62.55	70.92
V. stamineum	**81.86**	89.17	82.17	89.30
H. venosum	**67.43**	75.70	69.34	77.01
C. maculata	**73.25**	73.37	74.40	76.61
T. discolor	81.76	86.59	**79.15**	84.84

The first model had an intercept, temperature, and year term (T + Year), while the second model also included an interaction term (T + Year + T × Year, abbreviated as T × Year). The best model for each species is in bold.

The effect of warming on last flowering date closely followed the response of first flowering to warming (Fig. 4). Warming advanced last flowering in five species ($r^2 \geq 0.40$, $P \leq 0.038$) and had no effect on last flowering of *V. pallidum* ($r^2 = 0.04$, $P = 0.560$). There was a trend for delayed last flowering of *T. discolor* in 2011 ($r^2 = 0.98$, $P = 0.088$, $n = 3$). Warming did not affect flowering season length for any species ($r^2 \leq 0.20$, $P \geq 0.198$), although there was a trend for shorter flowering seasons with increased temperature in *T. discolor* ($r^2 = 0.32$, $P = 0.072$; Fig. 4). The flowering season length of the forest community (i.e. the time between first flowering in spring and last flowering in mid-summer) increased with warming by 16 days in 2011 and 10 days in 2013, relative to controls, due to community-level advances in first flowering date and delays in last flowering date.

Experimental vs. interannual phenological responses

An unusually cool spring in 2013 allowed us to test whether phenological shifts driven by experimental warming were equivalent to phenological shifts that

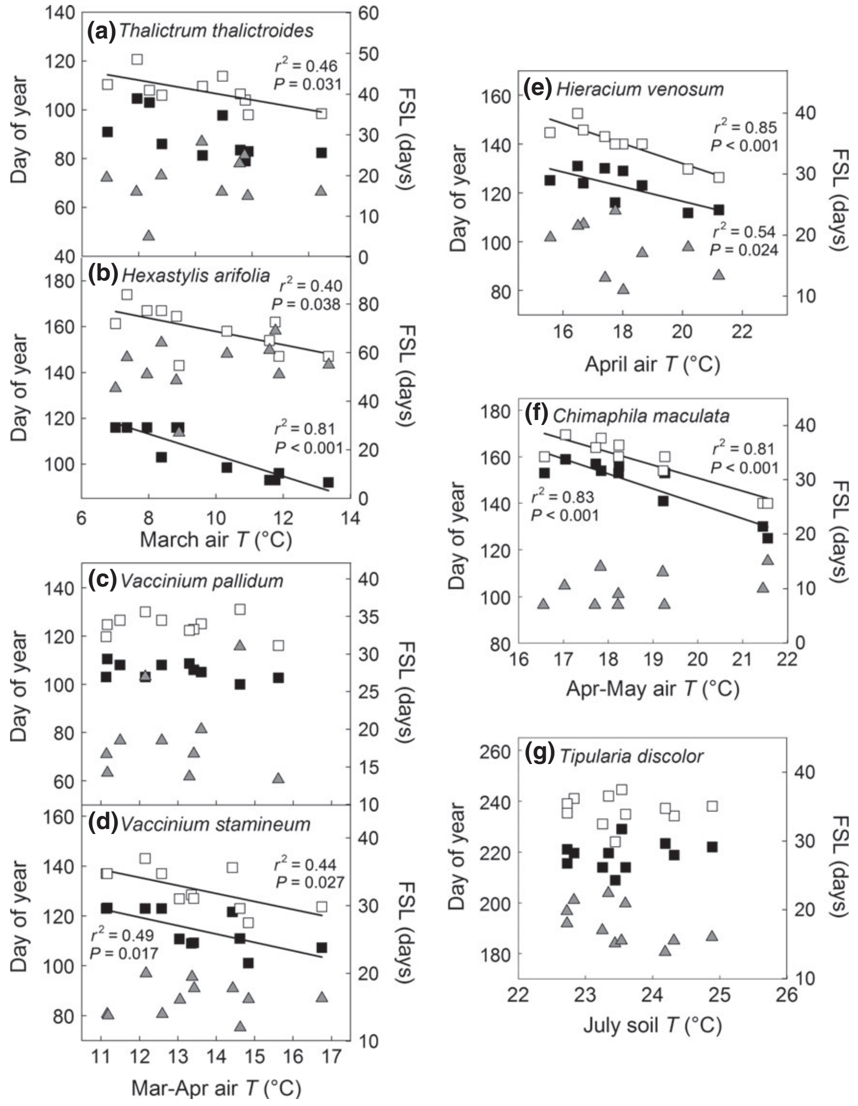

Fig. 4 The effect of air/soil temperature on day of first flowering (black squares), day of last flowering (white squares), and flowering season length (gray triangles) for all species in 2011 and 2013. Points represent individual chamber means, and significant temperature effects ($P < 0.05$) are depicted by a solid trendline.

occurred as a result of interannual temperature variability. Budburst was significantly earlier in 2011 than in 2013 by 9-13 days for most species ($t_{6–7} \geq 3.05$, $P \leq 0.028$); the response was not significant for *Q. rubra* ($t_5 = 2.56$, $P = 0.063$). Rates of advancement in budburst ranged from 1.8 to 2.9 days per °C (Table 4). Overall, mean shift in budburst dates across species did not differ between interannual observations and experimental warming in either study year ($t_5 \leq 1.805$, $P \geq 0.131$).

Compared to the colder year 2013, first flowering in 2011 was significantly advanced by 18 days in *H. arifolia* ($t_6 = 5.67$, $P = 0.003$) and by 14 days in *V. stamineum* ($t_3 = 141.00$, $P < 0.001$). For these two species, rates of advancement in flowering date ranged from 5.7 to 6.3 days per °C (Table 4). There was a trend for earlier flowering in 2011, relative to 2013, for *T. thalictroides* ($t_9 = 2.35$, $P = 0.057$). Despite the temperature difference between years, there was no significant interannual difference in flowering date for the other four species ($t_{3–8} \leq 3.00$, $P \geq 0.095$). Interannual observations overpredicted flowering responses of the spring-flowering species to experimental warming in 2013 ($t_6 = 2.731$, $P = 0.034$) and failed to accurately predict shifts in summer-flowering species (Table 4).

Discussion

Warming effects on budburst phenology

Experimental warming of 0.6–5.0 °C advanced date of budburst of six temperate deciduous species in this

Table 4 Temperature sensitivity of leafing and flowering phenology (change in days per °C) in a warming experiment to observations of interannual variability in phenology

	Experimental (Δ Days per °C)		Observational (Δ Days per °C)
Species	2011	2013	2011–2013
Leafing			
C. tomentosa	+1.4	−2.0***	−2.0*
Q. alba	−0.2	−2.0**	−1.8**
Q. rubra	−4.2	+0.2	−0.8
A. rubrum	−1.2	−2.1	−2.8***
V. pallidum	−0.9*	+2.6	−2.4*
V. stamineum	−1.6	−0.9	−2.9***
Mean	−1.1	−0.7	−2.1
Flowering			
T. thalictroides	+0	+3.8	−2.9
H. arifolia	−3.9	−2.0	−5.7**
V. pallidum	−2.3	−0.5	−0.8
V. stamineum	−4.0	−3.6	−6.3***
H. venosum	−2.7*	+2.9	−1.1
C. maculata	−8.9***	−2.4	−0.8
T. discolor	+10.8	+2.8	−4.4
Mean	−1.6	+0.1	−3.1

Experimental budburst/flowering is the mean sensitivity of all heated chambers, and observational budburst/flowering is the difference in control plants between 2011 and 2013. Mean temperature from 15 February to 15 March was 4.6 °C higher in 2011 than in 2013. Asterisks denote significant differences between heated and control plants (experimental) or between years (observational): $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

study (Fig. S3), which is in agreement with nearly all observational and experimental studies in temperate ecosystems (Parmesan & Yohe, 2003; Root *et al.*, 2003; Menzel *et al.*, 2006; Wolkovich *et al.*, 2012; IPCC, 2014b). Temperature accumulation in the spring is strongly correlated with budburst date (Fig. 1), but temperature alone cannot explain the diverse budburst responses observed among plant functional types. Budburst of the three diffuse-porous species was best predicted by a model that did not include temperature and only included year, and there was a nonlinear effect of warming on *Q. alba* where advances in budburst became more modest as the extent of warming increased (Table 2; Fig. S3). Few studies include strong warming treatments (≥3 °C) which extend beyond recent climate variability. In those rare studies, nonlinear budburst responses to temperature have been found for some species (Morin *et al.*, 2010; Gunderson *et al.*, 2012). These studies and the response of *Q. alba* in our study suggest that even if estimates of budburst advancement based on historic variation are correct, rates of advancement may decrease with warming in the coming century. Although *Q. alba* was the only species with a significant quadratic term, most species did not show linear budburst responses to temperature, but rather had complex phenological responses with strong interannual differences not explained by a simple temperature response framework (Table 2).

Nonlinear phenology responses could be explained by a constraining interaction of warmth with chilling exposure, photoperiod, or both (Cannell & Smith, 1983; Morin *et al.*, 2009, 2010; Gunderson *et al.*, 2012; Iler *et al.*, 2013). Chilling and photoperiod cues could promote safety of sensitive, newly emerged plant tissues by reducing the risk of premature budburst during warm winter spells, but may limit the potential for species to advance budburst as climate warms in the future and these cues become out of sync with thermal cues (Salk, 2011). It is commonly believed that budburst of ring-porous tree species such as *Quercus* is photoperiod-sensitive (Körner & Basler, 2010). Our results are consistent with this view and are the first to clearly demonstrate a divergence of budburst phenology between diffuse- and ring-porous species in response to warming (Fig. 1; Fig. S3). There was no difference in $\mathrm{GDD}_{\mathrm{BB}}$ across years for ring-porous species (Fig. 1), suggesting these trees are influenced by factors that are invariant from year to year (such as photoperiod). Budburst of diffuse-porous species grown at similar spring temperatures occurred at lower $\mathrm{GDD}_{\mathrm{BB}}$ in 2011 (i.e. earlier in the warmer year), suggesting that a process that varies from year to year (such as winter chilling) is more important in regulating budburst (Fig. 1).

Future warming may cause budburst shifts to differ between these two plant functional types, as reductions in winter chilling will occur as climate warms, but photoperiod is not affected by changes in climate. If ring-porous species such as *Quercus* are indeed photoperiod dependent, budburst advances in ring-porous trees may be smaller than advances in diffuse-porous trees in the future. The more conservative response to spring temperature in ring-porous trees may represent an adaptive frost-avoidance strategy in trees with large-diameter xylem vessels that are prone to frost-induced dysfunction (Lopez *et al.*, 2008). As a result of their differential phenological responses to warming, competitive interactions between diffuse- and ring-porous species may change as forest communities warm in the future. However, which functional group will be most limited in the future depends on details of future global change such as relative temperature in winter and spring and the frequency of late frosts (Augspurger, 2013), issues that are beyond the scope of this paper.

Warming effects on leaf senescence and growing season length

Budburst timing is particularly critical for tree seedlings in the understory that intercept most of their annual light during a brief spring window before canopy closure (Augspurger, 2008; Lopez *et al.*, 2008). Yet, delays in autumn leaf coloring due to warming of 0.6–5.0 °C were even larger than advances in budburst in our experiment (18–21 days delay in leaf coloring vs. 5–15 days advance in budburst). Other artificial warming experiments found comparable delays of 4–22 days in leaf coloring/abscission with warming of 1.5–4.0 °C (Norby *et al.*, 2003; Morin *et al.*, 2010; Gunderson *et al.*, 2012). Ultimately, earlier leaf emergence in the spring has a greater influence on seasonal carbon uptake than an equivalent delay of fall senescence. Potential carbon gains in autumn can be offset by increased respiration (Piao *et al.*, 2008), which are exacerbated by lower solar radiation and late-season declines in photosynthetic capacity of old leaves (Salk, 2011; Gunderson *et al.*, 2012).

Experimental warming in our study extended the growing season of four deciduous woody species by 20–29 days in the warmest treatments, as hypothesized. Field observations and model simulations indicate that an extended growing season can increase productivity in forest ecosystems (Goulden *et al.*, 1996; Rötzer *et al.*, 2004; Richardson *et al.*, 2010; Keenan *et al.*, 2014). Net productivity of forest ecosystems has increased by 1–1.6% per day added to the growing season over the past century (White *et al.*, 1999; Dragoni *et al.*, 2011). If budburst shifts of canopy trees are similar in magnitude to responses of seedlings in our study, productivity could potentially increase by 20–32% with a 20-day extension of the growing season in the future. The nonlinearity of budburst responses to warming suggests that increases in productivity will not continue indefinitely at ever higher temperatures (see *Q. alba*, Fig. S3). In years with late spring frosts, early budburst can damage leaf tissues and erase any carbon gains due to longer growing seasons (Augspurger, 2009, 2013). Many other factors can potentially interact with phenology to limit increases in carbon sequestration of forests in the future, such as drought, herbivory, heat stress, or disease (Taylor & Whitelaw, 2001; Burt *et al.*, 2014).

Warming effects on reproduction

Warming caused a phenological divergence in flowering times of species in the temperate forest understory, a phenomenon that has been reported previously for a temperate grassland (Sherry *et al.*, 2007) and a subalpine meadow (Aldridge *et al.*, 2011). Spring and summer-blooming plants advanced flowering or had no significant response to warming, while warming delayed flowering of one species that blooms after the peak summer temperature (Figs 3 and 4; Marchin *et al.*, 2014). Divergence in flowering times among species resulted in a longer flowering season by 10-16 days in the forest community, in agreement with our hypothesis and previous studies (Aldridge *et al.*, 2011; CaraDonna *et al.*, 2014). It is worth noting that the increase in flowering season length occurred for the forest community, but not for individual species. The majority of forest understory species tracked changes in spring temperature with linear and parallel advances in first and last flowering dates, resulting in no change in the length of the flowering season (Fig. 4). Temperature explained 40-85% of the variation in timing of flowering for four of seven species studied here, but was not a good predictor of flowering for three species (Fig. 4). There is little known about how cues for flowering vary throughout the flowering season (Pau *et al.*, 2011), but clearly cues besides temperature (e.g. photoperiod) can control flowering time and may prevent large shifts in reproduction in the future (Iler *et al.*, 2013).

Most studies report that early blooming species are more responsive to warming (Rathcke & Lacey, 1985; Bradley *et al.*, 1999; Cook *et al.*, 2012; Wolkovich *et al.*, 2012; but see Menzel, 2003; Sherry *et al.*, 2007). Strong sensitivity to temperature in early blooming plants, whose reproduction is susceptible to late spring frosts, would be advantageous for avoiding fitness costs should reproduction fail (Pau *et al.*, 2011). Contrary to our hypothesis, however, we found greater sensitivities to experimental warming in species that flower in late spring or mid-summer, relative to those that flower in early spring, in Duke Forest (6-23 days vs. 3-5 days, respectively; Table 4). Chilling or photoperiod requirements may have restricted advances in flowering time with experimental warming in spring-blooming plants, such as *H. arifolia* and *V. stamineum*. Indeed, shifts in flowering were larger in these species between study years than in response to experimental warming (Table 4). Nonresponding species such as *V. pallidum* may have opposite responses to fall/winter vs. spring warming that can prevent shifts in flowering (Cook *et al.*, 2012). In other words, spring warming advances flowering, but reductions in winter chilling delay flowering (Cook *et al.*, 2012). It is not yet clear which environmental cues are used by spring- and summer-blooming plants to time their reproduction (Pau *et al.*, 2011).

Increased bimodality in community-level flowering patterns could be caused by differential responses of plant development to temperature (Sherry *et al.*, 2007), where warming in mid-summer exceeds optimal temperatures for reproduction and suspends reproductive development. Warming resulted in failed reproduction for two species that flower in mid-summer, *C. maculata* and *T. discolor* (data not shown) whose fruit are capsules that persist for months as seeds are slowly wind-dispersed. Premature fruit abortion occurred in all individuals of *C. maculata* whenever mean June temperature exceeded 26 °C, and all scapes of *T. discolor* failed to develop whenever mean July temperature exceeded 29°C (Marchin *et al.*, 2014). Future temperature increases of 2.5 °C above ambient temperature will likely result in reproductive failure for both species and potentially shift their southern range boundary to higher latitudes (Chuine, 2010). Current species distributions range as far south as Florida, but both species are rare in that state (USDA, 2013).

Can experiments forecast future phenological shifts?

In a recent study, Wolkovich *et al.* (2012) concluded that warming experiments underpredicted advances in budburst and flowering phenology by 4-fold and 8.5-fold, respectively, relative to long-term historical observations. Although this result could arise because temperature is necessarily quantified differently in experimental and observational studies (Clark *et al.*, 2014a), it may also reveal that plant responses to future warming will not match historic long-term responses to climate change. Smaller shifts seen in warming experiments may not be ‘underprediction’ *per se*, but rather an expected phenomenon if phenology responds nonlinearly to larger degrees of warming (e.g. *Q. alba*, Fig. S3). Budburst responses to experimental warming in our study were not significantly different from interannual historical variation (Table 4). Our observations based on interannual temperature variability, however, overpredicted shifts in first flowering of spring-blooming forest species relative to responses to experimental warming (Table 4). Disagreement between the two methods in our experiment cannot be attributed to experimental artifacts such as lower irradiance or drier soils (Wolkovich *et al.*, 2012), which did not vary systematically with warming (Fig. S2). Nor could it be caused by different temperature quantification methods (Clark *et al.*, 2014a), because we calculated temperatures over the same period for both types of analysis.

Predictions of flowering responses by warming experiments, rather than by observations under current temperatures, are likely to be more realistic in regard to future plant responses. Warming experiments simulate novel future climatic conditions, whereas observations based on interannual temperature variability fall within historical temperature ranges. For example, March temperature inside experimental chambers reached 15.4 °C in 2011, which is higher than maximum March temperature in the last 60 years (14.7 °C). The higher rates of phenological change in long-term observations may therefore decline with future warming as phenological thresholds are reached (Iler *et al.*, 2013). Species that have advanced flowering with warming to date may even reverse their trends and delay flowering in the future (e.g. *T. discolor*, Table 4). These results indicate that historical observations of recent flowering shifts may be insufficient for predicting how flowering will change with future warming (Table 4).

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References

Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716–723.

Aldridge G, Inouye DW, Forrest JRK *et al.* (2011) Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *Journal of Ecology*, **99**, 905–913.

Arft AM, Walker MD, Gurevitch J *et al.* (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491–511.

Augspurger CK (2008) Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia*, **156**, 281–286.

Augspurger CK (2009) Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. *Functional Ecology*, **23**, 1031–1039.

Augspurger CK (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology*, **94**, 41–50.

Bradley NL, Leopold AC, Ross J *et al.* (1999) Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 9701–9704.

Burt MA, Dunn RR, Nichols LM *et al.* (2014) Interactions in a warmer world: effects of experimental warming, conspecific density, and herbivory on seedling dynamics. *Ecosphere*, **5**, 1–12.

Cannell MGR, Smith RI (1983) Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *Journal of Applied Ecology*, **20**, 951–963.

CaraDonna PJ, Iler AM, Inouye DW (2014) Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 4916–4921.

Chapin FS, Shaver GR (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology*, **77**, 822–840.

Chuine I (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3149–3160.

Chuine I, Cour P (1999) Climatic determinants of budburst seasonality in four temperate-zone tree species. *New Phytologist*, **143**, 339–349.

Clark JS, Melillo J, Mohan J *et al.* (2014a) The seasonal timing of warming that controls onset of the growing season. *Global Change Biology*, **20**, 1136–1145.

Clark JS, Salk C, Melillo J *et al.* (2014b) Tree phenology responses to winter chilling, spring warming, at north and south range limits. *Functional Ecology*, **28**, 1344–1355.

Cook BI, Wolkovich EM, Parmesan C (2012) Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 9000–9005.

Crawley MJ (2007) *The R Book*, 1st edn. Wiley Publishing, West Sussex, England.

Davies TJ, Wolkovich EM, Kraft NJB *et al.* (2013) Phylogenetic conservatism in plant phenology. *Journal of Ecology*, **101**, 1520–1530.

Davis CC, Willis CG, Primack RB *et al.* (2010) The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3201–3213.

Dorji T, Totland Ã, Moe SR *et al.* (2013) Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. *Global Change Biology*, **19**, 459–472.

Dragoni D, Schmid HP, Wayson CA *et al.* (2011) Evidence of increased net ecosystem productivity associated with a longer vegetated season in a deciduous forest in south-central Indiana, USA. *Global Change Biology*, **17**, 886–897.

Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689–1691.

Fitter AH, Fitter RSR, Harris ITB *et al.* (1995) Relationships between first flowering date and temperature in the flora of a locality in central England. *Functional Ecology*, **9**, 55–60.

Goulden ML, Munger JW, Fan SM *et al.* (1996) Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science*, **271**, 1576–1578.

Gunderson CA, Edwards NT, Walker AV *et al.* (2012) Forest phenology and a warmer climate – growing season extension in relation to climatic provenance. *Global Change Biology*, **18**, 2008–2025.

Harte J, Shaw R (1995) Shifting dominance within a montane vegetation community – Results of a climate-warming experiment. *Science*, **267**, 876–880.

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. *Biometrika*, **76**, 297–307.

Iler AM, Hoye TT, Inouye DW *et al.* (2013) Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **368**, 20120489.

IPCC (2014a) Summary for policymakers. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea S, White LL), pp. 1–32. Cambridge University Press, Cambridge, UK and New York, NY, USA.

IPCC (2014b) 2014: North America. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL), pp. 1439–1498. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Jeong SJ, Ho CH, Gim HJ *et al.* (2011) Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982–2008. *Global Change Biology*, **17**, 2385–2399.

Kang H, Jang J (2004) Flowering patterns among angiosperm species in Korea: diversity and constraints. *Journal of Plant Biology*, **47**, 348–355.

Keenan TF, Gray J, Freidl MA *et al.* (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, **4**, 598–604.

Kennedy AD (1995) Simulated climate change: are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations? *Global Change Biology*, **1**, 29–42.

Kochmer JP, Handel SN (1986) Constraints and competition in the evolution of flowering phenology. *Ecological Monographs*, **56**, 303–325.

Körner C, Basler D (2010) Phenology under global warming. *Science*, **327**, 1461–1462.

Laube J, Sparks TH, Estrella N, Menzel A (2014) Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. *New Phytologist*, **202**, 350–355.

Lopez OR, Farris-Lopez K, Montgomery RA *et al.* (2008) Leaf phenology in relation to canopy closure in southern Appalachian trees. *American Journal of Botany*, **95**, 1395–1407.

Lynch IP (2006) *The Duke Forest at 75: A Resource for All Seasons*. Office of the Duke Forest, Durham, NC.

Marchin RM, Dunn RR, Hoffmann WA (2014) Are winter-active species vulnerable to climate warming? A case study with the wintergreen terrestrial orchid, *Tipularia discolor*. *Oecologia*, **176**, 1161–1172.

Menzel A (2003) Plant phenological anomalies in Germany and their relation to air temperature and NAO. *Climatic Change*, **57**, 243–263.

Menzel A, Sparks TH, Estrella N *et al.* (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976.

Menzel A, Estrella N, Heitland W *et al.* (2008) Bayesian analysis of the species-specific lengthening of the growing season in two European countries and the influence of an insect pest. *International Journal of Biometeorology*, **52**, 209–218.

Morin X, Lechowicz MJ, Augspurger CK *et al.* (2009) Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology*, **15**, 961–975.

Morin X, Roy J, Sonie L *et al.* (2010) Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist*, **186**, 900–910.

Norby RJ, Hartz-Rubin JS, Verbrugge MJ (2003) Phenological responses in maple to experimental atmospheric warming and CO_2 enrichment. *Global Change Biology*, **9**, 1792–1801.

Panchen ZA, Primack RB, Nordt B *et al.* (2014) Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytologist*, **203**, 1208–1219.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pau S, Wolkovich EM, Cook BI *et al.* (2011) Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, **17**, 3633–3643.

Pelini SL, Bowles FP, Ellison AM *et al.* (2011) Heating up the forest: open-top chamber warming manipulation of arthropod communities at Harvard and Duke Forests. *Methods in Ecology and Evolution*, **2**, 534–540.

Piao SL, Ciais P, Friedlingstein P *et al.* (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature*, **451**, 49–52.

Primack D, Imbres C, Primack RB *et al.* (2004) Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany*, **91**, 1260–1264.

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

Richardson AD, Black TA, Ciais P *et al.* (2010) Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3227–3246.

Root TL, Price JT, Hall KR *et al.* (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Rötzer T, Grote R, Pretzsch H (2004) The timing of bud burst and its effect on tree growth. *International Journal of Biometeorology*, **48**, 109–118.

Salk CF (2011) Will the timing of temperate deciduous trees' budburst and leaf senescence keep up with a warming climate? PhD Dissertation, Duke University, Durham, NC.

Sanz-Perez V, Castro-Diez P, Valladares F (2009) Differential and interactive effects of temperature and photoperiod on budburst and carbon reserves in two co-occurring Mediterranean oaks. *Plant Biology*, **11**, 142–151.

Saxe H, Cannell MGR, Johnsen B *et al.* (2001) Tree and forest functioning in response to global warming. *New Phytologist*, **149**, 369–399.

Sherry RA, Zhou XH, Gu SL *et al.* (2007) Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 198–202.

Sparks TH, Jeffree EP, Jeffree CE (2000) An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology*, **44**, 82–87.

Taylor JE, Whitelaw CA (2001) Signals in abscission. *New Phytologist*, **151**, 323–339.

USDA (2013) *The PLANTS Database*. NRCS, National Plant Data Center, Baton Rouge, LA.

Wang J, Ives NE, Lechowicz MJ (1992) The relation of foliar phenology to xylem embolism in trees. *Functional Ecology*, **6**, 469–475.

Way DA, Montgomery RA (2014) Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell and Environment*. doi: 10.1111/pce.12431.

White MA, Thornton PE, Running SW (1997) A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochemical Cycles*, **11**, 217–234.

White MA, Running SW, Thornton PE (1999) The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology*, **42**, 139–145.

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.

Willis CG, Ruhfel B, Primack RB *et al.* (2008) Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17029–17033.

Wolkovich EM, Cook BI, Allen JM *et al.* (2012) Warming experiments underpredict plant phenological responses to climate change. *Nature*, **485**, 494–497.

Yu HY, Luedeling E, Xu JC (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 22151–22156.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of individuals sampled for all study species in the chamberless control plots, control chambers, and heated chambers in 2011 and 2013. Chambers with individuals present that did not flower are denoted with "0". Species codes: ACRU, *Acer rubrum*; CATO, *Carya tomentosa*; QUAL, *Quercus alba*; QURU, *Quercus rubra*; VAPA, *Vaccinium pallidum*; VAST, *Vaccinium stamineum*, CHMA, *Chimaphila maculata*; HEAR, *Hexastylis arifolia*; HIVE, *Hieracium venosum*; THTH, *Thalictrum thalictroides*; TIDI, *Tipularia discolor*.

Table S2. Mean phenological sensitivity to air temperature (change in budburst date per °C, ±SE) for six species in Duke Forest, NC in both study years. Chamber temperature is mean air temperature (15 February−15 March) in °C above ambient. Positive sensitivities indicate that budburst is delayed with warming, whereas negative sensitivities indicate that budburst is advanced with warming. Sample sizes ranged from 1–12 plants per chamber. Asterisks denote significant mean differences between heated plants and control plants: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Figure S1. The relationship between target temperature and mean 15 February–15 March air temperature (°C above ambient) for the twelve experimental chambers in Duke Forest, NC in 2011 (black circles) and 2013 (gray circles). Mean 15 February–15 March air temperature of control chambers was about 0.5–0.9 °C above ambient temperature, so all warming treatments were calculated relative to control chambers to account for this small chamber effect.

Figure S2. The relationship between mean air temperature (15 February–15 March) and mean (a) soil temperature (°C), (b) relative extractable soil water content (REW), (c) relative humidity (%), and (d) daytime PAR (from 10 to 15 h, μmol m^{-2} s^{-1}) inside the twelve experimental chambers in 2011 (black circles) and 2013 (gray circles). The RH sensor for the hottest chamber malfunctioned in 2013 and was omitted from panel (c). Warming effects on chamber microenvironment were tested using linear regression for all parameters.

Figure S3. The effect of air temperature (15 February–15 March) on day of budburst in 2011 (black circles) and 2013 (gray circles) for (a–c) ring-porous and (d–f) diffuse-porous species. Points represent individual chamber means. The best-fitting model as determined by AIC (see Table 2) was used to determine trendlines for each species. For diffuse-porous species (d–f), the best-fit model had only year as a predictor, so horizontal lines represent mean flowering date in 2011 (solid line) and 2013 (dashed line).