LETTER

Phenological mismatch with trees reduces wildflower carbon budgets

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Abstract

Interacting species can respond differently to climate change, causing unexpected consequences. Many understorey wildflowers in deciduous forests leaf out and flower in the spring when light availability is the highest before overstorey canopy closure. Therefore, different phenological responses by understorey and overstorey species to increased spring temperature could have significant ecological implications. Pairing contemporary data with historical observations initiated by Henry David Thoreau (1850s), we found that overstorey tree leaf out is more responsive to increased spring temperature than understorey wildflower phenology, resulting in shorter periods of high light in the understorey before wildflowers are shaded by tree canopies. Because of this overstorey–understorey mismatch, we estimate that wildflower spring carbon budgets in the northeastern United States were 12–26% larger during Thoreau's era and project a 10–48% reduction during this century. This underappreciated phenomenon may have already reduced wildflower fitness and could lead to future population declines in these ecologically important species.

Keywords

climate change, carbon gain, forest understorey, herbaceous layer, light environment, phenology, spring wildflowers, Thoreau.

INTRODUCTION

Climate change is causing shifts in the timing of species interactions (Kharouba *et al.* 2018; Renner & Zohner 2018), a complex phenomenon that can lead to ecological mismatches and the restructuring of ecosystems. Phenological mismatch (also called trophic asynchrony) occurs when interacting species shift the timing of recurring life history events at different rates in response to environmental change (Visser & Both 2005; Renner & Zohner 2018). Renner & Zohner (2018) explicitly define phenological mismatch based on two criteria. First, in true phenological mismatch, interacting species' phenology must shift at uneven rates through time. Second, this pattern must be attributed to differing responses to climate.

Unequivocally discerning long-term, anthropogenically induced phenological mismatch from stochastic annual fluctuations in species interactions can be difficult. An increasing number of studies have explored phenological mismatch, with examples of asynchronous responses to climate change between birds (Marra *et al.* 2005; Mayor *et al.* 2017), pollinators (Kharouba & Vellend 2015), mammalian herbivores (Post & Forchhammer 2008) and their food sources. A recent global meta-analysis confirms widespread shifts in phenological synchrony among interacting species (Kharouba *et al.* 2018), with most examples involving interactions between animal species or between animals and plants.

Potential causes and predicted impacts to communities depend upon the type of ecological interaction (Renner & Zohner 2018). In antagonistic trophic interactions (e.g. plant–herbivore), instances of phenological mismatch are predicted to benefit one group of species to the detriment of another, while in mutualistic interactions (e.g. plant–pollinator), the fitness of both partner species is negatively affected. Though they are often overlooked, disruptions in non-trophic competitive interactions among plant species may also have significant impacts on ecosystem functioning. For example, in deciduous forests, where plant growth in the understorey is strongly limited by light availability, phenological mismatch between overstorey and understorey species could alter the understorey light regimes that are integral to many understorey species' life history strategies.

The herbaceous layer contains the most plant biodiversity in deciduous forests worldwide (Gilliam 2007), and these species have evolved diverse strategies in response to the timing of overstorey tree canopy closure (Neufeld & Young 2014). Plant growth in deciduous forest understories is controlled by this dramatic and predictable seasonal event, with full sunlight in the spring followed by low light levels soon after trees leaf out (Hutchison & Matt 1977). Many forest herbs (hereafter 'wildflowers') emerge and flower in the early spring to exploit this critical period of high light (Lapointe 2001; Kudo *et al.* 2008; Augspurger & Salk 2017), reaching maximum photosynthetic rates that abruptly decline as the

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overstorey trees leaf out and the canopy closes (Rothstein & Zak 2001; Kudo *et al.* 2008; Heberling *et al.* 2019) – a common shade avoidance strategy known as 'phenological escape' (Jacques *et al.* 2015). This phenomenon is most dramatic among spring ephemerals, which go dormant after overstorey leaves appear. But even for wildflower species that retain leaves into summer, this early period of high photosynthesis before canopy closure is critical for fruit development, plant growth and survival (Routhier & Lapointe 2002; Ida & Kudo 2008).

Leaf budburst in overstorey trees has been suggested to be more responsive to climatic variation than emergence in understorey wildflowers (Neufeld & Young 2014), creating the possibility of an ecological mismatch, with trees shading spring wildflowers earlier in the season under warming conditions. Spring wildflower emergence in northern latitudes is determined by snowmelt and soil temperature, while the timing of tree leaf out is driven by interactions among winter chilling, spring warming and photoperiod (Zohner & Renner 2014; Zohner *et al.* 2016, 2017). Due to yearly fluctuations in temperature and snowfall, the high irradiance period from wildflower emergence until overstorey canopy closure can vary by weeks (Kudo *et al.* 2008), but consistently earlier warm spring temperatures might shorten the shade-free time for wildflowers. How will fewer high light days in the spring impact seasonal carbon gain, reproduction and long-term survival of ecologically and culturally important wildflower species?

Here, to test whether phenological mismatch between overstorey and understorey species has occurred with anthropogenic climate change, we report results from a novel analysis of phenological observations from the past 160 + years. We took advantage of a unique, long-term dataset from Concord, Massachusetts initiated by Henry David Thoreau, the famous environmental philosopher and author of *Walden* (Primack & Miller-Rushing 2012). We combine these results with seasonal photosynthetic measurements of understorey spring wildflowers to estimate the impact of this overlooked, but potentially pervasive, component of environmental change.

MATERIALS AND METHODS

Tree and wildflower phenological observations

First flowering (FFD; wildflowers) and first leaf out (FLD; trees) dates were recorded by Henry David Thoreau (1852–1860), Alfred Hosmer (1878, 1888-1902) and Primack laboratory members (2004–2018) in Concord, Massachusetts (42.46°N, 71.35°W). FFD reflects dates when the first open flowers were observed for each species in Concord, and FLD refers to when young leaves with the recognisable shape of the adult leaves were visible on three overstorey branches in Concord. While we do not know the precise criteria that Thoreau and Hosmer used to determine FLD, the variation of one or few days that might be caused by different definitions is minor in comparison with the variation of 2–3 weeks in leafing out dates caused by yearly variation in climate. The strong correlations of FLD with temperature observed in this study and by Polgar *et al.* (2014) also strongly suggest that the

definitions of the different time periods are comparable. The data set included 14 herbaceous understorey wildflower species and 15 overstorey tree species, for a total of 685 phenological observations across 37 years between 1852 and 2018 (see Table S1).

We interpreted a change in FLD of common overstorey trees as a proxy of change in the onset of overstorey canopy closure. Similarly, we interpreted a change in FFD as a proxy for change in spring leaf out of wildflowers. Change in FFD is a robust proxy for changes in wildflowers' leaf emergence because these events are highly correlated, developmentally linked and responsive to spring temperature (Ettinger *et al.* 2018). However, depending on the species, these understorey species leaf out 0–3 weeks before FFD and both are tightly linked to spring temperature. Because historical leaf out data for understorey wildflower species were not available, we estimated FLD for these species based on FFD and contemporary observations on leaf out and flowering phenology in these species. Dates of first spring leaf expansion and FFD were observed for each wildflower species in 2018. Since FLD was not historically recorded (only FFD), we predicted FLD for each species and year by subtracting the interval from first leaf production to FFD in 2018 from FFD. Although a recent study with trees suggests the timing of leaf out to flowering is tightly correlated across species (Ettinger *et al.* 2018), it is unclear if these phenophases respond differently to spring temperature in wildflowers. It is important to note that three of the fourteen spring wildflowers have overwintering leaf tissue that may remain photosynthetically active in the spring (*Houstonia caerulea*, *Micranthes virginiensis*, *Viola pedata*). However, it is unlikely these leaves significantly contribute to their whole plant spring carbon budgets, due to their relatively small area and the generally cold conditions earlier in the season. Therefore, we defined FLD for all wildflower species as the date of the leaf expansion of the first leaves produced in the spring.

We modelled the relationship between spring temperature (March and April monthly means) and FLD separately for trees and wildflowers, including random intercepts for species and year. Monthly temperature data were from nearby Blue Hill Meteorological Observatory in East Milton, Massachusetts (NOAA National Centers for Environmental Information 2018). Daily temperature records were not available for the entire study period. Temperature responses were also tested separately for each species (including year random effects; Figs S1, S2). We used mean spring temperature rather than other metrics due to its clear correlation with phenology and to allow direct comparisons to previous phenological studies (e.g. Ellwood *et al.* 2013). Analyses were also done to confirm our conclusions were robust to different time periods. The inclusion of May temperatures did not qualitatively change our results (Fig. S3). Bayesian linear regression was performed in JAGS (Plummer 2003) using *r2jags* (Su & Yajima 2015) in R (R Core Team 2017). All prior distributions were non-informative. Normal distribution priors with mean zero and variance 10^5 were used for fixed effect parameters; and random effect standard deviations were sampled from a uniform prior (0,100). Final models were run with three parallel Markov chain Monte Carlo (MCMC) chains for

50,000 iterations, discarding the initial 10,000 for burn-in. Trace plots and the Gelman–Rubin diagnostic (< 1.1) were used to confirm convergence (Gelman & Hill 2007).

Wildflower carbon gain measurements

To model the effects of phenological mismatch on spring carbon gain in the understorey, we used detailed data in an ecologically similar set of herbaceous species from a separate companion study (see Heberling *et al.* (2019) for complete data set and results).

We established an *in situ* common garden of wildflowers common to the region in a closed canopy deciduous forest near Pittsburgh, Pennsylvania, USA (Trillium Trail Nature Reserve: 40.5201° N; 79.9010° W). Study species were selected to cover a range of phenological strategies exhibited by the native spring-blooming flora in this region (Table S2). Although these species studied in Pittsburgh were not the same as those monitored in Concord, both sets of species share important niche similarities (spring-blooming herbaceous perennials of the Eastern Deciduous Forest of North America) and span a similar range of phenological dynamics (Neufeld & Young 2014).

From leaf expansion to senescence in 2016, light response (A/q) and CO_2 response curves (A/C_i) curves were performed *in situ* on intact leaves using two LI-6400XT portable photosynthesis systems equipped with a CO_2 control module, 2×3 cm leaf cuvette and a red–blue LED light source (LI-COR, Lincoln, NE, USA). Photosynthetic response parameters were modelled in a hierarchical Bayesian framework (Feng & Dietze 2013), and species-level posteriors were used to estimate *in situ* daily carbon gain with understorey light data (Fridley 2012). See Methods S1 for additional details on common garden design, photosynthetic measurements and carbon gain models.

Wildflower carbon gain simulations under phenological mismatch

Simulations using seasonal carbon gain estimates were performed by adjusting the length of spring proportionally based on the change in the number of days before canopy closure (net effect of different rates of changes in overstorey tree leaf out and understorey wildflower emergence). We defined the spring carbon budget for each species from the date of median initial leaf expansion dates in 2016 (varies by species) until date of canopy closure (23 May; see Methods S1). The length of spring was adjusted proportionally by species, as described in Eqn 1–3 below:

$$\text{Spring Carbon Gain}_{sp}\left(\text{g m}^{-2}\right) = \sum_{i}^{\text{DOY}_{\text{emerge, sp}} \ to \ 142} \text{Daily C Gain}_i$$
$$+ \left(\frac{\Delta \text{ spring length}_{sp}}{143 - \text{DOY}_{\text{emerge,sp}}} \times \sum_{i}^{\text{DOY}_{\text{emerge, sp}} \ to \ 142} \text{Daily C Gain}_i \right)$$
$$(1)$$

where for each species, sp, Daily C gain is estimated from photosynthetic measurements (Methods S1; Heberling *et al.*

2019), $\text{DOY}_{\text{emerge}}$ is the median day of year for leaf emergence in 2016, 143 is the day of year of canopy closure in 2016 (first day of 'summer'), and Δ spring length is the net change between tree and wildflower phenology compared to 2016.

$$\text{Summer Carbon Gain}_{sp}\left(\text{gm}^{-2}\right) = \sum_{i}^{143 \ to \ \text{DOY}_{\text{senesce, sp}}} \text{Daily C Gain}_i$$
$$- \left(\frac{\Delta \text{ spring length}_{sp}}{\text{DOY}_{\text{senesce,sp}} - 142} \times \sum_{i}^{143 \ to \ \text{DOY}_{\text{senesce, sp}}} \text{Daily C Gain}_i \right)$$
$$(2)$$

where $\text{DOY}_{\text{senesce}}$ is the median day of year in 2016 for aboveground senescence. Summer carbon gain (Eqn 2) was calculated by subtracting the effect of a shifted spring phenology such that summer carbon gain actually *increases* when Δ spring length is negative (shorter spring) and *decreases* when Δ spring length is positive (longer spring).

$$\text{Annual Carbon Gain}_{sp}\left(\text{gm}^{-2}\right) = \text{Spring Carbon Gain}_{sp}$$
$$+ \text{Summer Carbon Gain}_{sp}$$
$$(3)$$

To place carbon gain simulations in specific past and future contexts, we predicted proportional change in carbon budgets (relative to 2016) during the Thoreau period (1850s) in Concord (−3°C compared to today; Ellwood *et al.* 2013) and Pittsburgh (−1°C; Shortle *et al.* 2015). We similarly forecasted future changes in carbon budgets based on CO_2 emission scenarios for the northeastern US (Horton *et al.* 2014). We used the posterior distributions from the models describing the overall tree and wildflower temperature response (described above) to estimate the relationship between spring length (i.e. time from wildflower leaf out until tree overstorey leaf out) and temperature.

We made several assumptions in our phenological analyses and seasonal carbon budget simulations (see Table S3). First, we assumed the overall mean responses across 14 wildflower and 15 tree species in Concord was similar to those wildflower species with gas exchange measurements in Pittsburgh. Unfortunately, none of the species monitored by Thoreau, Hosmer and the Primack laboratory in Concord are shared with than those measured in Pittsburgh. However, because these species are broadly similar in terms of habitat and phenology and our simulations are based on community-level responses rather than species-specific responses, differences between species and regions are unlikely to bias our conclusions. Second, we assumed that a reduction in spring carbon gain does not affect subsequent abilities for carbon acquisition or translocation after canopy closure. However, observational and experimental studies in ecologically similar species suggest earlier canopy shading alters subsequent carbon allocation patterns (Routhier & Lapointe 2002; Ida & Kudo 2008). Therefore, it is likely that reduced spring carbon budgets have additional indirect effects on summer carbon gain. Third, we assumed that total growing season length (days with aboveground photosynthetic tissue) was unaffected by changes in time from

wildflower leaf out to canopy closure, which may also be conservative, as time from canopy closure to senescence was found to be relatively constant in a prior study (Augspurger & Salk 2017). However, aboveground senescence in species capable of shade acclimation is affected by many factors, including whether fruits are produced. Fourth, our simulations cannot directly account for daily variation in carbon gain (e.g. due to temperature and radiation), but rather manipulate seasonal carbon budgets proportionally. Last, we did not consider possible photoperiodic effects due to seasonal changes in solar angle, or interactive effects of increasing atmospheric CO_2 and direct effects of leaf temperature on carbon gain in these species. We outline these assumptions, potential biases and future research needed in Table S3.

RESULTS

Overstorey trees are more phenologically responsive than understorey wildflowers

In Concord, where spring temperatures have increased by 3 °C over the past century (Ellwood *et al.* 2013), FLD for tree species have shifted significantly since the 1850s—overstorey tree species now leaf out nearly 2 weeks earlier (mean ± standard error across 15 species: 12.9 ± 0.7 days). As a group, trees leafed out an average of 4.4 days earlier per 1 °C increase in mean spring temperature (Fig. 1 inset, β_{FLD} 95% CI: (−5.5, −3.3); see Fig. S1 for species-level regressions). In contrast, estimated FLD for spring wildflowers were much less responsive to temperature change, shifting by less than a week during this time period (mean ± standard error across 14 species: 5.9 ± 2.2 days), or 2.2 days earlier per 1°C increase (β_{FFD} 95% CI: (−3.7, −0.76); Fig. S2).

Mean responses showed some variation by species (Fig. 2). The species-specific posterior distributions of slope parameters for all 15 tree species did not overlap zero (Fig. 2, Fig. S1), while 95% credible intervals phenological sensitivities for 3 of 14 wildflower species overlapped zero (Fig. 2, Fig. S2). Although the 95% credible intervals around the overall fixed effects for temperature responses overlap (Fig. 1 inset), overstorey trees on average were significantly more responsive to temperature than understorey wildflowers (test of difference between tree and wildflower β_{FLD} based on random sampling from posterior distributions: 95% CI (−3.97, −0.40)).

Effect of phenological mismatch on wildflowers

To quantify the potential impacts of this observed mismatch between tree and wildflower species on wildflower seasonal carbon budgets, we combined these results with contemporary carbon gain measurements from a separate study (Heberling *et al.* 2019) in six spring wildflower species growing in a forest near Pittsburgh, Pennsylvania. Regular *in situ* gas exchange measurements throughout 2016 allowed us to model the dependency of wildflower carbon budgets on light interception as driven by canopy phenology. Based on carbon gain simulations in which we adjusted the timing of overstorey canopy closure, we estimated that mean annual carbon budgets were 2.1–2.7% higher depending on species
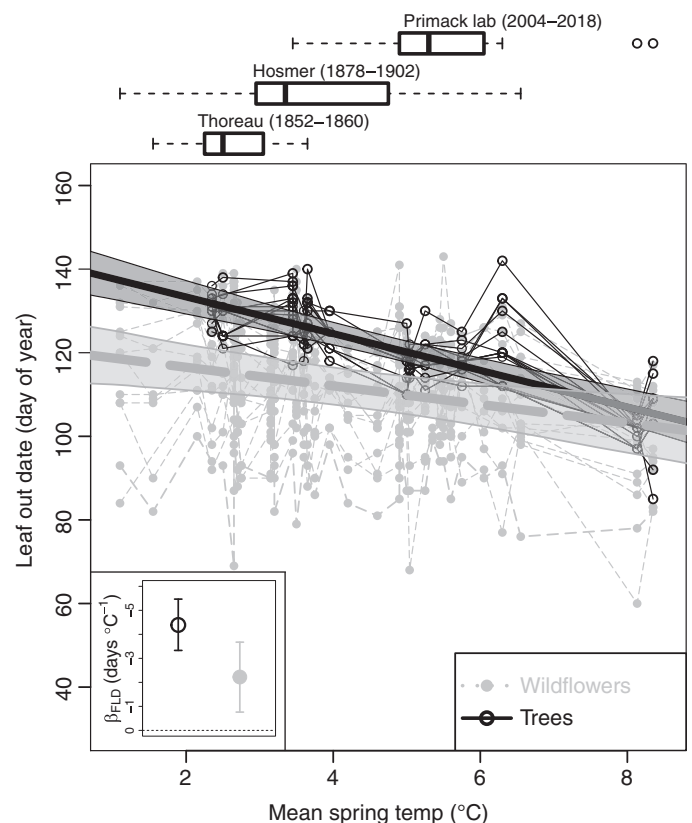

Fig. 1 Phenological responses to spring temperatures for tree (black) and herbaceous wildflower (grey) species in Concord, Massachusetts. Boxplots summarise spring temperatures (March, April means) for each time period that correspond to phenology observations; note the two outlier warm years from the Primack laboratory. Thick lines indicate overall regression fits of spring temperature and first leaf out date (FLD) for trees (solid) and wildflowers (dashed). Connected points show empirical values for each tree (*n* = 15; black solid line, open points) and wildflower (*n* = 14; gray dashed line, closed points) species. Inset figure shows overall slope estimates (with 95% credible intervals) for FLD (β_{FLD}) for trees and wildflowers.

(estimate based on species average response: −2.3%; 95% CI: (−4.2, −0.4); Fig. 3a) a century ago when spring temperatures were approximately 1 °C colder in Pennsylvania (Shortle *et al.* 2015), corresponding to two more days between wildflower leaf out and canopy closure [based on cross-species mixed models; mean: 2.17 days °C^{-1}; 95% CI: (−3.97, −0.40)]. Expressed in terms of carbon assimilation in the spring, carbon budgets were 4.0–8.7% [mean species response: 5.7%; 95% CI: (1.0, 10.5)] higher a century ago than today in Pittsburgh (Fig. 3b). Changes were greater when translated to phenology trends in Concord, where temperatures were 3 °C cooler during Thoreau's era (due to anthropogenic greenhouse gas emissions and urban heat island effects; Ellwood *et al.* 2013). Wildflowers in Concord had an estimated 6.2–8.0% larger annual carbon budget in the 1850s [mean species response: 6.8; 95% CI: (1.3, 12.5)] when there were 6.5 more days between wildflower leaf out and canopy closure [95% CI: (1.2, 12.0)], which resulted in a 12.0–26.0% [mean species response: 17.2%; 95% CI: (3.2, 31.5)] increase in spring carbon acquisition (Fig. 3b).
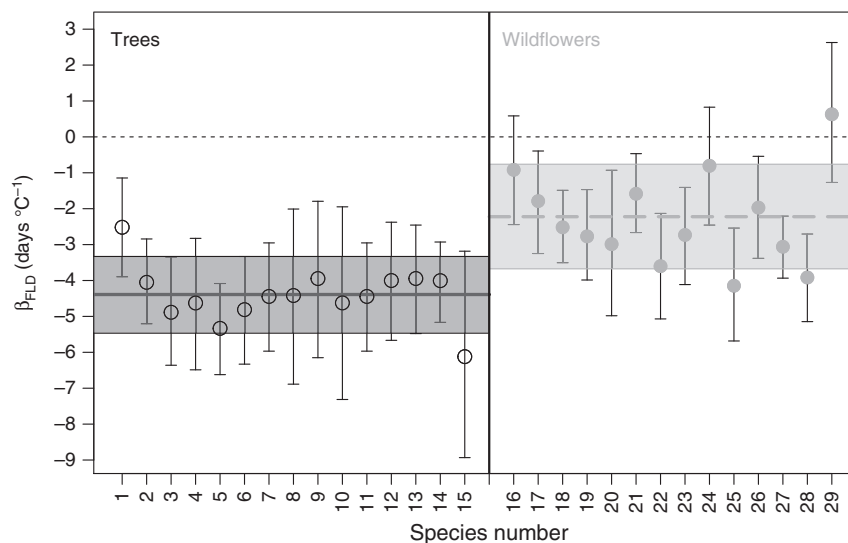
Fig. 2 Model slope estimates β_{FLD} ($\pm$95% credible intervals) for each tree and wildflower species in Concord. Separate regressions for phenology as function of spring temperature (March, April means) were run separately by species, including a year random effect. Overall group estimates ($\pm$95% credible intervals) from models with species and year included as random effects (Fig. 1) for trees and wildflowers are shown as horizontal lines, with grey region denoting 95% credible intervals. Species numbers: 1 = *Acer saccharinum*, 2 = *Acer saccharum*, 3 = *Acer rubrum*, 4 = *Betula lenta*, 5 = *Betula papyrifera*, 6 = *Betula populifolia*, 7 = *Carya glabra*, 8 = *Fagus grandifolia*, 9 = *Fraxinus americana*, 10 = *Nyssa sylvatica*, 11 = *Populus grandidentata*, 12 = *Populus tremuloides*, 13 = *Quercus alba*, 14 = *Quercus rubra*, 15 = *Ulmus americana*, 16 = *Aquilegia canadensis*, 17 = *Anenome quinquefolia*, 18 = *Aralia nudicaulis*, 19 = *Cypripedium acaule*, 20 = *Caltha palustris*, 21 = *Geranium maculatum*, 22 = *Houstonia caerulea*, 23 = *Hypoxis hirsuta*, 24 = *Micranthes virginiensis*, 25 = *Moehringia lateriflora*, 26 = *Packera aurea*, 27 = *Silene caroliniana*, 28 = *Trientalis borealis*, 29 = *Viola pedata*

Phenological mismatch and the future of forest understorey species

If the mean temperature projections of 2.5–4.5°C warming by 2080 in the northeastern United States are realised (Horton *et al.* 2014), a further decrease in the separation between wildflower emergence and tree leaf out in the future would be expected. Consequently, by 2080, mean annual carbon budgets of wildflowers will be 5.7–12.6% lower under two emissions scenarios (A2: 2.5–5.6°C; B1: 1.7–3.3°C) for the northeastern United States (Horton *et al.* 2014). Spring carbon budgets for these wildflowers will decrease substantially by 2080, ranging from 10% lower in the earlier-emerging *Sanguinaria* [Fig 3b; 95% CI: (−18.4, −1.8)] with a 2.5 °C increase (B1 low emissions scenario) to 48% lower in the later-emerging *Arisaema* [Fig 3b; 95% CI: (−88.3, −8.8)] with a 5.6 °C increase (A2 higher emissions scenario).

DISCUSSION

We combined results from the historical records initiated by Henry David Thoreau (1850s) and an experimental common garden study to explore the effects of climate change on an overlooked phenomenon of phenological asynchrony. Our novel approach reveals an underappreciated consequence of climate change in temperate deciduous forests. First, trees and herbaceous spring wildflowers respond to warming at strikingly different rates. The possibility of contrasting tree and wildflower phenological responses to temperature have been suggested in earlier studies (Lapointe 2001; Ida & Kudo 2008; Neufeld & Young 2014; Jacques *et al.* 2015; Augspurger & Salk 2017), but has not been demonstrated. Second, as a result of these differing phenological responsiveness between forest layers, the window of high light availability in the spring is decreasing with warmer spring temperatures. This seasonal period of high light availability before overstorey canopy closure has been shown to be critical for spring wildflowers (Ida & Kudo 2008; Heberling *et al.* 2019). We show this critical period has decreased by nearly 1 week in Concord since Thoreau initiated this study over 160 years ago. Lastly, due to phenological mismatches with the overstorey, we found substantial reductions in spring carbon budgets and project these shifts to become more pronounced in future decades based on regional climate trends.

Our findings highlight unexpected consequences of phenological mismatch under climate change. Soil warming experiments have predicted fitness increases in forest herbs due to earlier spring emergence in warmed plots (Jacques *et al.* 2015). Another study experimentally manipulated the emergence of spring ephemeral species, highlighting the physiological constraints of cold and shade on growth and reproduction for these species (Augspurger & Salk 2017). However, these two experiments and other climate change studies that include wildflowers (e.g. Miller-Rushing & Primack 2008; Willis *et al.* 2008) do not explicitly account for the contrasting phenological responses of overstorey species, which could drive significant changes in wildflower species carbon budgets, abundances and community composition in the future.

Our results highlight the importance of community-wide phenology studies that incorporate multiple phenological responses and growth habits within a single trophic level. Here, change in a key limiting resource, light, is influenced by the differing phenological responses of interacting plant
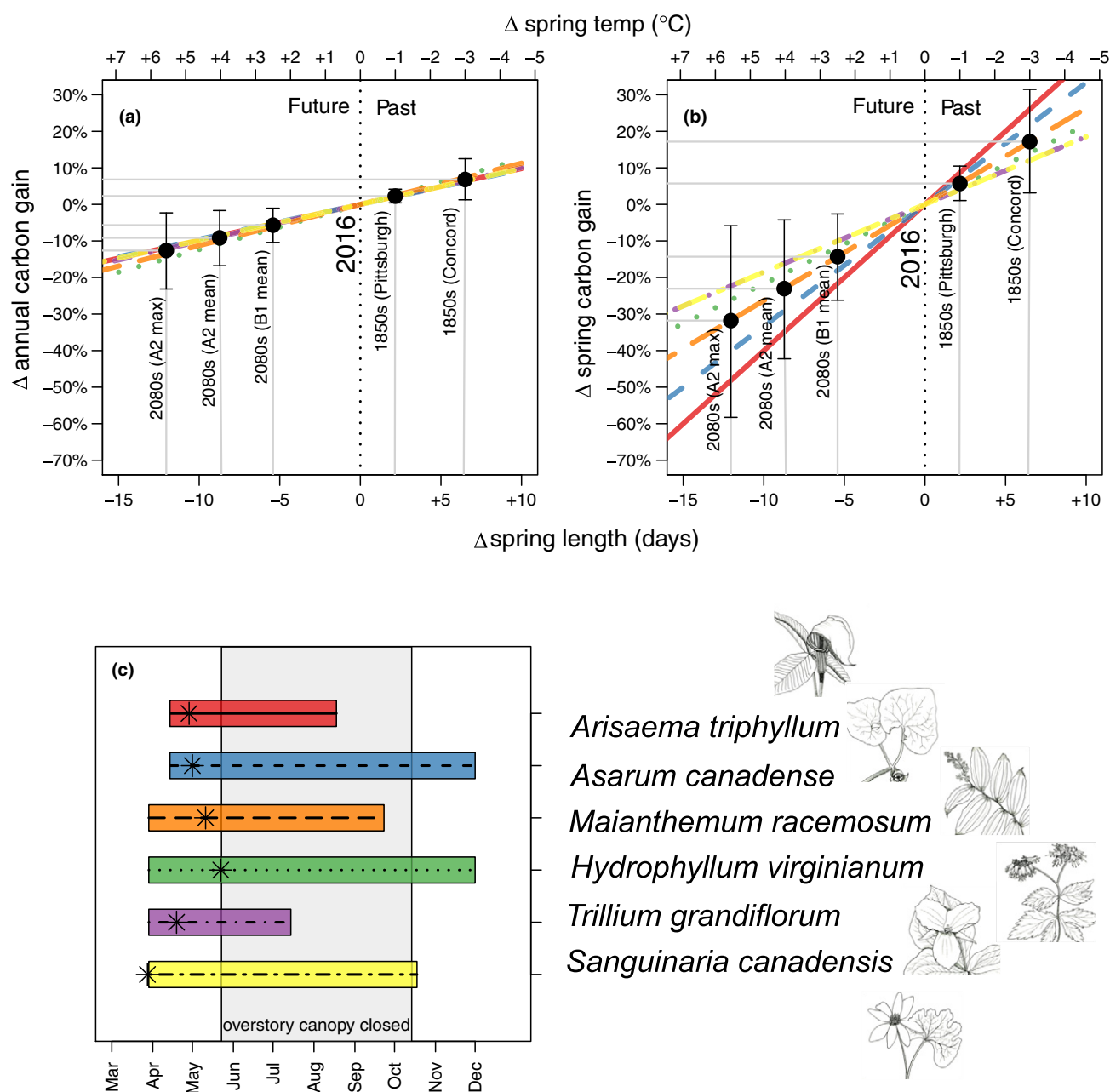
Fig. 3 Effects of phenological mismatch with trees on wildflower carbon budgets. Estimated impact of changes in future declines and past increases in the number of days from wildflower leaf out to canopy closure (spring length), as affected by changes in spring temperature on a) annual and b) spring carbon budgets for six common wildflower species measured in Pittsburgh, PA that vary in dates of emergence, flowering and senescence. Points (±95% credible intervals) in a) and b) highlight past (1850s) and future (2080s) predictions of carbon budgets relative to recent baseline measurements (2016). A2 and B1 refer to regional climate projections under high and low emission scenarios respectively (Horton *et al.* 2014). (c) Leaf phenology (time of active photosynthesis) of focal understorey wildflowers in 2016. Coloured boxes indicate median emergence and senescence dates for each species, asterisks denote median flowering date. Vertical lines denote dates of canopy closure in spring to canopy leaf drop in fall. Drawings by Allison Heberling.

species. Although the importance of light has been shown to be a limiting resource for many species in the herbaceous layer of deciduous forests (reviewed in Neufeld & Young 2014), few studies have considered the indirect effects of climate change on light availability via contrasting phenological responses between species and forest strata. The potential to understand these types of phenological changes and mismatches over larger geographical areas will be enhanced by the increasing amount of biodiversity data, especially herbarium records, that are georeferenced and digitised, remote sensing data and the growing enthusiasm for large-scale citizen science monitoring initiatives (Willis *et al.* 2017).

Impacts to spring carbon budgets from phenological mismatches were particularly strong in later-emerging wildflowers, while impacts on an annual basis were consistent across species due to the stabilising effect of carbon gain after

canopy closure (Fig. 3). Despite apparently modest changes in annual carbon gain, the large shifts we report for spring carbon budgets can have substantial consequences, as many life history events, including fruit maturation and seed set, critically depend upon spring carbon acquisition (Routhier & Lapointe 2002; Ida & Kudo 2008; Kudo *et al.* 2008). In particular, a decrease in spring carbon budgets will likely result in reductions or failures of fruit set (Ida & Kudo 2008), especially in years where other stressors (e.g. drought, high herbivory) further limit carbon gain. Also, phenological mismatches under climate change may result in higher perennial wildflower mortality rates and lower future flowering, as survival and reproduction in subsequent years depend on carbon stored in belowground organs (Routhier & Lapointe 2002; Augspurger & Salk 2017).

Our novel approach utilising historical and contemporary phenological observations, paired with recent carbon gain measurements, provides new insights into an important, potentially widespread phenomenon. However, our approach relies on several assumptions that merit further testing (Table S3). For example, we assumed the collective set of 15 tree species measured by Thoreau are representative of overstorey phenological dynamics across the larger deciduous forest biome. Canopy composition varies across space and time due to land use change, including within Concord (Primack *et al.* 2009) and across the Eastern US (Thompson *et al.* 2013). We were also limited by the available historical phenological data, which consists of earliest leaf out dates (FLD) for trees and earliest flowering dates (FFD) for an uneven subset of years. Recent evidence indicates temperature-related trends in the time from tree leaf budburst to leaf maturity (Klosterman *et al.* 2018), but lacking historical and experimental data, it remains largely unknown how changing spring temperatures affect the duration and timing of vegetative and reproductive phenophases in understorey wildflowers. In addition, although the general forest type was similar, our carbon gain simulations were based on data in a different site using a different set of species from the historical phenological data. Future work is needed to consider the potentially confounding effects of other variables that have changed over the past century on wildflower seasonal carbon budgets (e.g. leaf temperature, CO_2, N availability), alongside the changes in understorey light availability we report. It is also likely that some wildflower species will be impacted more than others by this phenomenon. Future studies are needed on species-specific and regional responses. Despite the limitations of this study, our results provide the first evidence for an overlooked, but potentially critical, component of global change.

CONCLUSIONS

Forest understorey species are subject to diverse, potentially interacting, anthropogenic stressors worldwide (Gilliam 2016), including succession and fragmentation, elevated atmospheric CO_2, nitrogen deposition, introduced species and changing herbivore populations. We combined historic data, current physiological metrics and modelling to indicate the potential for dramatic effects of phenological mismatches between trees

and wildflowers. Accordingly, our results should motivate future studies on the underlying mechanisms to test their generality. The use of data from historic records, like herbarium specimens, may provide evidence for climate-induced decreases in wildflower survival and reproduction. Metrics from these records, such as greater abundances of flowers per plant, higher flowering frequencies or greater percentage of fruit set in the past, may indicate changes in fitness related to the reduced spring light environment. Likewise, current demographic studies can be used to determine population decline or local extinction for particular species relative to prior data (e.g. Willis *et al.* 2008; McDonough MacKenzie *et al.* 2019). Most importantly, contemporary observations of phenology and reproductive success, seasonal measurements of carbon budgets (and concomitant direct effects of increased leaf temperatures and atmospheric CO_2) and artificial shading experiments are needed. These phenological measurements, coupled with local historical data, will shed further light on the consequences of tree–wildflower phenology mismatches across latitudes and forest types. Phenological mismatches between overstorey trees and understorey wildflower species may be a widespread phenomenon that will affect the future of temperate deciduous forests under climate change.

AUTHORSHIP STATEMENT

R.B.P., C.M.M. and J.M.H. conceived the study; J.M.H. performed the analyses with input from J.D.F.; All the authors contributed to manuscript writing.

DATA ACCESSIBILITY STATEMENT

Data analysed during this study are available in the supporting information and the references cited. Data supporting the results are also archived in Dryad (https://doi.org/10.5061/dryad.3h7951k).

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SUPPORTING INFORMATION

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