

Net carbon uptake has increased through warming-induced changes in temperate forest phenology

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The timing of phenological events exerts a strong control over ecosystem function and leads to multiple feedbacks to the climate system¹. Phenology is inherently sensitive to temperature (although the exact sensitivity is disputed²) and recent warming is reported to have led to earlier spring, later autumn^{3,4} and increased vegetation activity^{5,6}. Such greening could be expected to enhance ecosystem carbon uptake^{7,8}, although reports also suggest decreased uptake for boreal forests^{4,9}. Here we assess changes in phenology of temperate forests over the eastern US during the past two decades, and quantify the resulting changes in forest carbon storage. We combine long-term ground observations of phenology, satellite indices, and ecosystem-scale carbon dioxide flux measurements, along with 18 terrestrial biosphere models. We observe a strong trend of earlier spring and later autumn. In contrast to previous suggestions^{4,9} we show that carbon uptake through photosynthesis increased considerably more than carbon release through respiration for both an earlier spring and later autumn. The terrestrial biosphere models tested misrepresent the temperature sensitivity of phenology, and thus the effect on carbon uptake. Our analysis of the temperature–phenology–carbon coupling suggests a current and possible future enhancement of forest carbon uptake due to changes in phenology. This constitutes a negative feedback to climate change, and is serving to slow the rate of warming.

Changes in phenology greatly affect the carbon balance of terrestrial ecosystems. Warmer springs, for example, stimulate an early emergence from winter dormancy, leading to an extension of an ecosystem's carbon uptake period¹⁰. Warmer autumns, on the other hand, are thought to lead to carbon losses from ecosystems due to a greater increase in respiration than photosynthesis^{4,9}. Global mean temperatures have risen over the past decades¹¹. It is therefore imperative to develop a robust understanding of both the temperature sensitivity of phenology², and the associated changes in carbon cycling¹.

Given the importance of phenology to the earth system, and the recent changes in global temperatures, much attention has been focused on the detection of climate-induced trends in phenology.

Long-term ground observations of phenology have shown an increase in growing season length^{12–15}. Independent studies based on satellite reflectance corroborate this evidence, showing an earlier spring and later autumn in temperate and boreal forests^{5,16–19}. However, the long-term impacts of changes in phenology on temperate forest carbon uptake and storage have yet to be quantified at the regional scale.

Here we report multi-decadal phenological trends in temperate forests in the eastern US, and quantify the subsequent impact on regional carbon cycling. We combine three different remote sensing greenness indices (daily MODIS enhanced vegetation index (EVI), normalized difference vegetation index (NDVI), and green chromatic coordinate (GCC)), two date extraction techniques, and the MODIS land cover dynamics product²⁰, with two decades of ground observations of individual tree phenology, and measurements of CO₂ exchange between forests and the atmosphere at seven long-term research sites. Across all scales (organism, ecosystem, landscape) we detect a consistent trend of earlier spring and later autumn over the past two decades. We derive the temperature sensitivity of spring and autumn phenology, and show how it can be used to improve the representation of seasonality by land surface models. Using the observed ecosystem–atmosphere carbon exchange, we quantify the impact that both interannual variability and long-term changes in phenology are having on forest photosynthesis and respiration, and consequently CO₂ uptake.

Spatially coherent trends of earlier spring phenology were evident across the different remotely sensed measures of greenness we analysed (Fig. 1). Spring phenology advanced on average by 0.48 ± 0.2 d yr⁻¹ ($P < 0.01$; panel analysis) for the period 2001–2012. The detection of false but statistically significant phenological trends is possible using individual remote sensing metrics^{21,22}. The magnitude of the spring trends we detect is largely independent of the metric used (Fig. 1 and Supplementary Fig. 1), and matches changes recorded in ground observations (see below), thus enhancing our confidence in these results.

In contrast, autumn trends in the MODIS data were dependent on the index used (Supplementary Figs 3–5). A trend of later autumn senescence has recently been reported over the eastern US (ref. 19)

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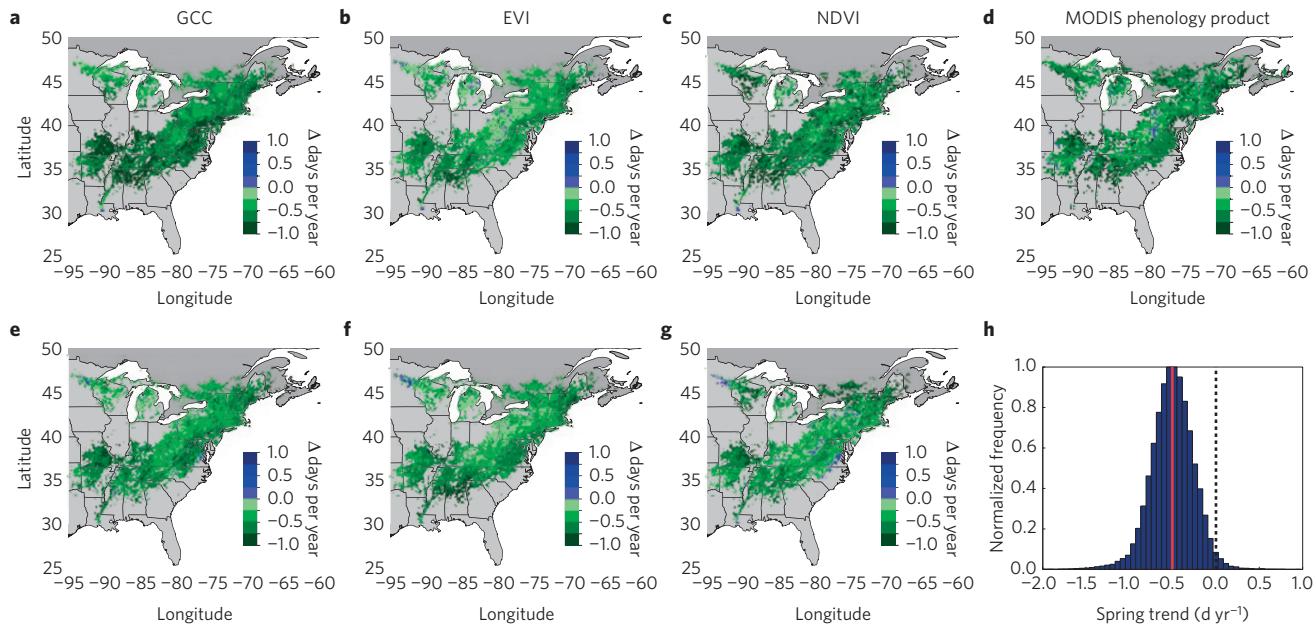


Figure 1 | Long-term changes in satellite-derived spring phenology. **a–h**, Regional changes in spring phenology for deciduous broadleaf forests in the Eastern US since the start of the century (2000–2012) based on remotely sensed daily greenness indices: green chromatic coordinate (**a,e**), enhanced vegetation index (**b,f**), normalized difference vegetation index (**c,g**) and the 8-day MODIS phenology product (**d**). Daily indices were extracted using two date extraction techniques: a robust smoothing-spline approach (**a–c**) and a dual logistic greendown curve fitting method (**e–g**). All trends shown (estimated using panel analysis) are significant at $P < 0.05$ (96.7% of all deciduous broadleaf forest pixels). **h**, Histogram of all trends from all methods. The vertical red lines illustrate the mean trend across all indices and date extraction methods. See Methods section for a description of the indices used.

using a longer time series of NDVI (1989–2008) from the Advanced Very High Resolution Radiometer (AVHRR), which is at a coarser spatial and temporal resolution. Although this was not consistently observed in the shorter MODIS data (Supplementary Fig. 3), we did detect a trend of later autumn in the long-term ground observations (see below).

Two decades of ground observations show consistent trends of earlier spring and later autumn. Ground observations of phenology for the dominant canopy species, red oak (*Quercus rubra*), at Harvard Forest (Massachusetts, USA; 1991–2013) corroborate the satellite observations, showing a similar trend of earlier spring budburst ($0.47 \pm 0.4 \text{ d yr}^{-1}$, 95% CI, $P = 0.05$) and later autumn senescence ($0.83 \pm 0.3 \text{ d yr}^{-1}$, 95% CI, $P < 0.01$; Fig. 2). The same pattern was also evident in two decades of ground observations of the dominant canopy species at Hubbard Brook Experimental Forest (New Hampshire, USA; 1991–2013, Fig. 2) and in the flux observations across all sites (Supplementary Fig. 9). For the Hubbard Brook ground observations, spring advanced by 0.28 d yr^{-1} ($P = 0.13$; Fisher combined probability (FCP) over multiple species), and autumn delayed by 0.25 d yr^{-1} ($P < 0.01$; FCP). The trends observed here in two decades of ground observations are consistent with decadal trends reported in studies that infer phenology from atmospheric CO₂ (ref. 4) or satellite remote sensing^{16,19}.

Coincident flux observations at Harvard Forest show a trend of an earlier start of both net ecosystem carbon uptake (F_c) and gross photosynthesis (F_p) of 0.67 d yr^{-1} ($P = 0.07$, Supplementary Fig. 9) since 1992, whilst over all sites the onset date of carbon uptake advanced by 1.3 d yr^{-1} ($P = 0.08$, FCP across multiple sites, Supplementary Fig. 9) for deciduous forest sites and 1.5 d yr^{-1} ($P = 0.5$, FCP, Supplementary Fig. 9) for evergreen forest sites. Similarly, a trend of a later end of carbon uptake was evident at most flux sites (Supplementary Fig. 9). The long-term ground and satellite observations therefore show a mean spring trend of similar magnitude and direction, whereas the autumn trend is regionally less consistent.

We quantified the impact of changes in phenology on carbon fluxes in spring and autumn using the long-term flux data. A one-day change in flux-derived spring onset translated to a change in F_p of 7.5 gC m^{-2} ($P < 0.01$, FCP across multiple sites) and 3.8 gC m^{-2} ($P < 0.01$, FCP) for deciduous and evergreen forests, respectively (Fig. 3). Owing to concurrent but smaller changes in ecosystem respiration (F_r), this translated to a net change in forest F_c of 4.5 gC m^{-2} ($P < 0.01$, FCP) and 3.0 gC m^{-2} ($P < 0.01$, FCP) per day change in flux-derived spring phenology, for deciduous and evergreen forests respectively. This indicates that photosynthesis increased by 60% and 79% more than respiration, per day earlier spring and later autumn, respectively.

Contrary to previous suggestions^{4,9} a later autumn invariably led to larger net carbon uptake, owing to larger increases in F_p than F_r . The mean increase in both F_p and F_c per day of later autumn was larger than that observed per day of earlier spring (Fig. 3), although more variable between sites and with lower statistical significance. This suggests that, if warming leads to a later autumn^{19,23}, future autumn warming may contribute to enhance net forest carbon uptake due to larger increases in photosynthesis than respiration.

A general trend of increasing gross primary photosynthesis and net carbon uptake during both spring and autumn was evident across sites (Fig. 4). The trend of increasing spring photosynthesis was larger in late spring than early spring. This reflects more fully developed leaf area during late spring, consistent with a trend of earlier canopy development reported in the ground observations (Fig. 2). Conversely, the trend of increased photosynthesis and net carbon uptake in autumn was more evident in early autumn (Fig. 4), which is consistent with foliage remaining photosynthetically active later in the season. The trend of increased carbon uptake during spring was evident at all sites, with the exception of Howland Forest (Ho1), the only boreal evergreen forest included. During autumn, the trend was most evident at the deciduous sites with the longest data records (UMB, MMS, Ha1; Fig. 4).

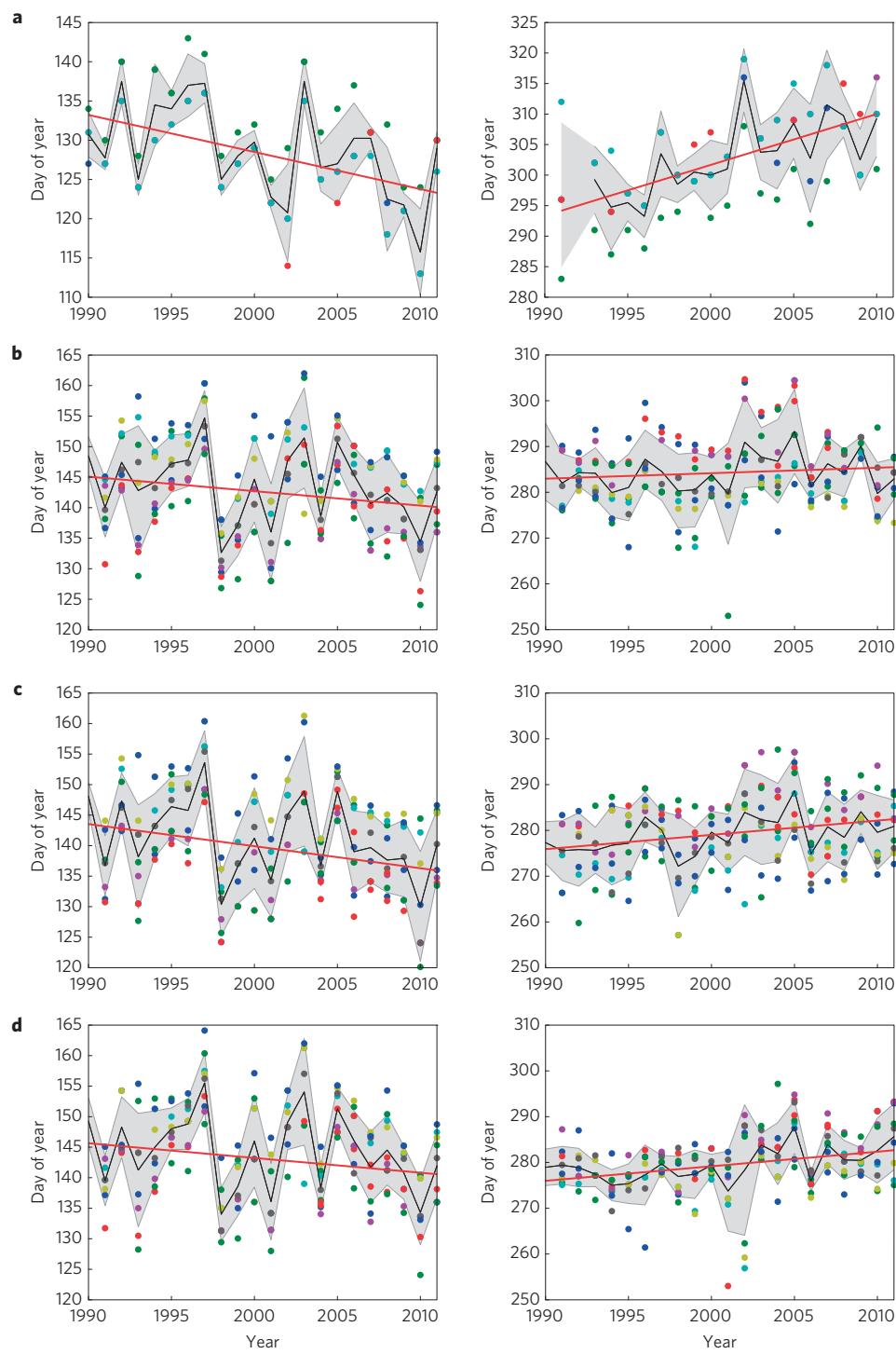


Figure 2 | Long-term changes in ground observations of spring phenology. **a-d**, Manual ground observations of spring (left column) and autumn (right column) phenology over two decades at Harvard Forest (Red oak (**a**)) and Hubbard Brook (American beech (**b**); Sugar maple (**c**); Yellow birch (**d**)). Coloured dots represent individual trees, with the mean and standard deviation of all trees given by the black line and shaded area. Red lines represent the long-term trend estimated using the non-parametric Mann-Kendall Tau-b with Sen's method (Supplementary Information Methods).

Interannual variability in spring phenology was highly correlated with temperature anomalies for both deciduous ($r^2 = 0.61$, $P < 0.01$, FCP, Fig. 5) and evergreen forests ($r^2 = 0.71$, $P = 0.04$, FCP, Fig. 5). The sensitivity of flux-derived spring phenology to spring temperature anomalies was highly consistent across sites, with a 1 °C difference from the mean temperature leading to a 2.8 day ($P < 0.01$, FCP) change in the spring phenology date for deciduous forests and a 4.8 day ($P < 0.01$, FCP) change for evergreen forests

(Fig. 5). Flux-derived autumn phenology was less well explained by temperature anomalies for both deciduous ($r^2 = 0.42$, $P < 0.01$, FCP) and evergreen ($r^2 = 0.55$, $P < 0.01$, FCP) forests, although warmer autumn temperatures invariably lead to later senescence (Fig. 5). The sensitivity of autumn phenology to a change from the mean temperature was similar across forest types, with a 1 °C difference from the mean temperature leading to a 1.8 day ($P = 0.09$, FCP) change in autumn senescence for deciduous

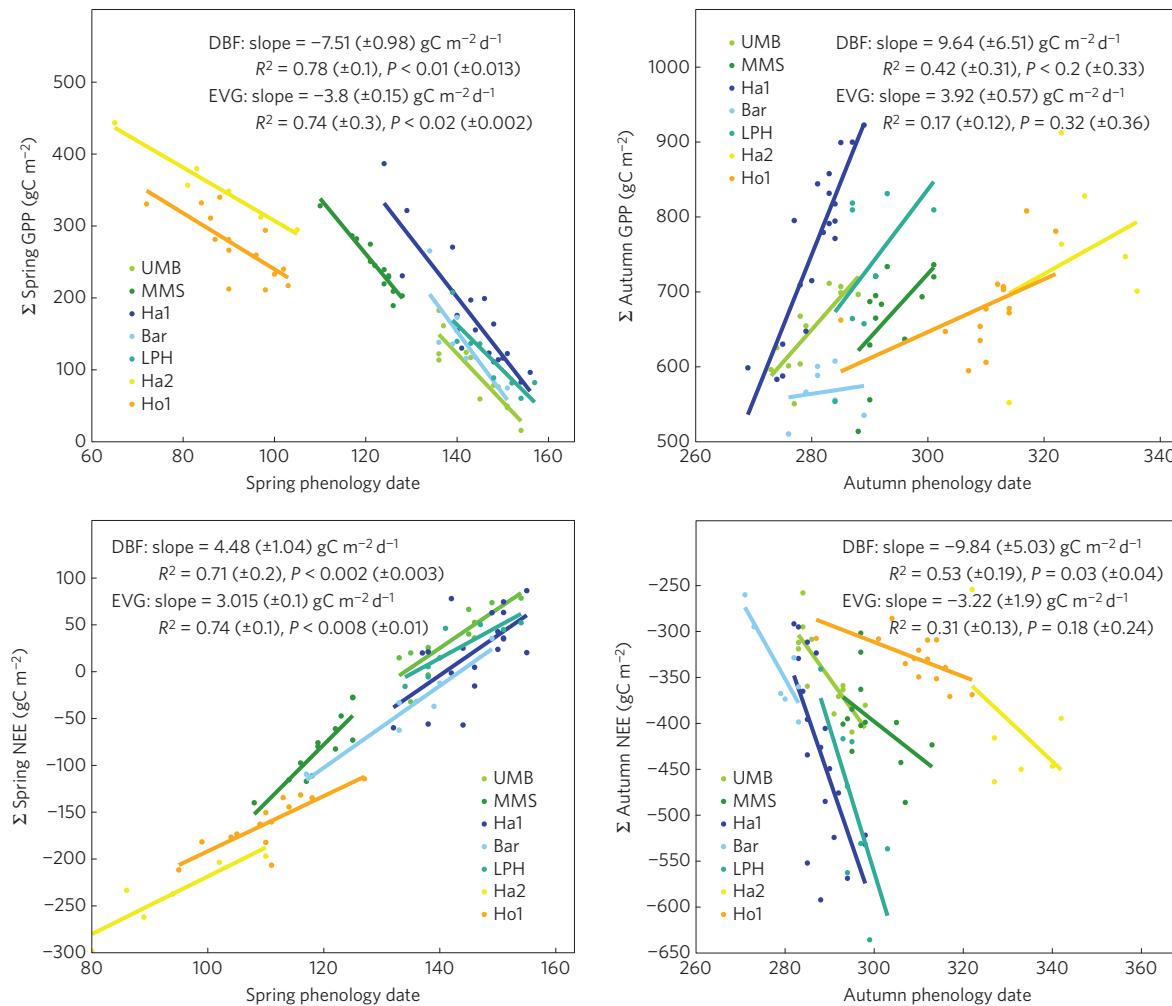


Figure 3 | The relationship between phenology and carbon fluxes. Effect of changes in phenology on gross ecosystem photosynthesis and net carbon uptake across seven forest sites in the northeastern US. Phenological transition dates are estimated from the flux data using the PhAsT framework: gross primary photosynthesis (GPP; top row) and net ecosystem carbon exchange (NEE; bottom row). Spring is defined as March–May (left column). Autumn is defined as September–November (right column). Σ NEE and Σ GPP values are season totals. Negative NEE indicates transfer of CO_2 from the atmosphere to the forest. Blue/green colours represent deciduous forest (DBF). Orange/yellow colours represent evergreen forests (EVG).

forests, and a 6.3 day ($P < 0.01$, FCP) change in evergreen forests. The highly linear nature of the derived temperature-phenology relationship (Fig. 5) suggests the potential for a large response of phenology to future climate warming, although photoperiod, chilling and dormancy constraints are likely to limit such a response²⁴.

To test whether the derived temperature sensitivity of phenology was well represented by current state-of-the-art terrestrial biosphere models, we examined 18 models (Supplementary Table 2) at a subset of the eddy-covariance flux sites. We found that, in contrast to the observed sensitivity of phenology to temperature anomalies, which was well constrained across sites, the models showed a wide spread in temperature sensitivities (Supplementary Fig. 11). The majority of models underpredicted the temperature sensitivity of spring phenology (Supplementary Fig. 11), with individual model responses ranging from -5 to $0 \text{ d } ^\circ\text{C}^{-1}$ warming, compared to the observed sensitivity of $-2.8 \text{ d } ^\circ\text{C}^{-1}$. For autumn phenology, the mean modelled response fell within the range of the observed sensitivity ($1.7 \pm 0.8 \text{ d } ^\circ\text{C}^{-1}$, Supplementary Fig. 11), but model responses ranged from 0 to $6 \text{ d } ^\circ\text{C}^{-1}$ warming. The models assessed here have been shown to poorly simulate phenological events^{25,26}, although the reason for poor model performance had not been identified. Our results suggest that the mischaracterization of the

temperature sensitivity of phenology contributes to the poor model performance. Given the ubiquitous control of temperature on phenology, accurately representing its temperature sensitivity is essential regardless of the approach taken to modelling phenological events (such as growing degree days, chilling requirements, photoperiodic control, temperature thresholds and so on). Model performance can therefore be improved by using the observed temperature sensitivity to guide model development.

By merging three different scales (organism, ecosystem, landscape) of long-term phenological observations, we show a consistent trend towards earlier spring and later autumn over the eastern US. Using forest carbon flux measurements, we show that photosynthesis is more responsive to phenology than respiration in both spring and autumn. The observed trend has therefore led to enhanced carbon uptake across the eastern US. We estimate that changes in spring phenology have led to an increase in gross photosynthesis of roughly $0.02 \pm 0.003 \text{ PgC}$ (Supplementary Information) and net carbon uptake of $0.01 \pm 0.002 \text{ PgC}$ over the study area during the past two decades. The larger response of photosynthesis than respiration to autumn phenology stands in contrast to previous studies^{4,9} (but see ref. 10). Those studies focused on northern boreal forests, which are primarily evergreen dominated, whilst here we examine temperate forests. This suggests

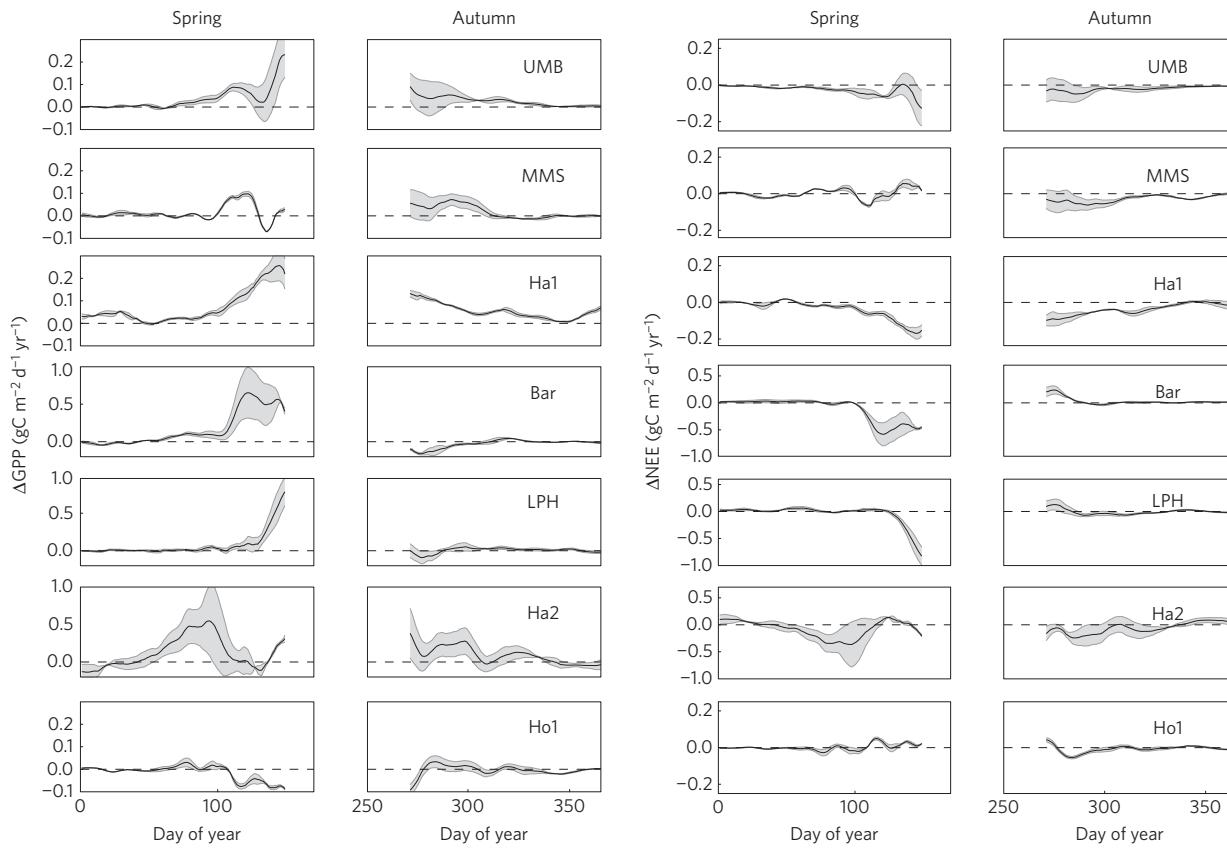


Figure 4 | Decadal trends in carbon cycling. Long-term trend in daily carbon fluxes ($\text{gC m}^{-2} \text{d}^{-1} \text{yr}^{-1}$) at each site for GPP (left) and NEE (right). Shaded areas represent 1 s.d. around the mean trend. The trend for a particular day of year is estimated using the data from that day in all years.

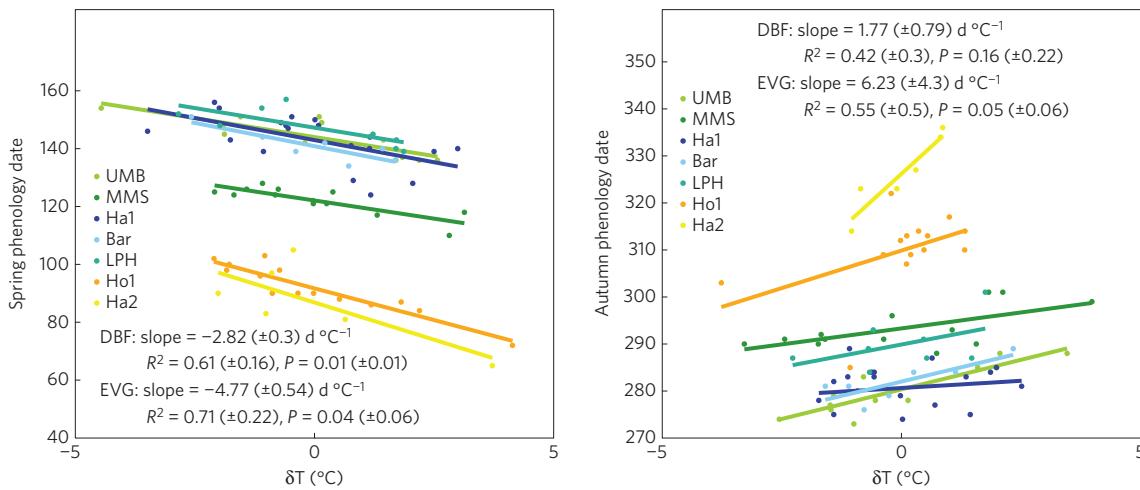


Figure 5 | The temperature sensitivity of spring and autumn phenology. Phenological dates for spring (left) and autumn (right) are estimated from flux data using the PhAsT framework. δT is calculated as the temperature anomaly of the month preceding the mean phenology date for each site. Blue/green colours represent deciduous forest (DBF). Orange/yellow colours represent evergreen forests (EVG).

a fundamental difference in the response of these two ecosystem types to changes in phenology.

Given the increase in global temperatures¹¹, phenology-driven increases in carbon uptake may be expected for temperate forests globally. This could partially explain the reported enhancement of global carbon sequestration²⁷. Secondary effects of the observed change include an increased risk of spring frost damage²⁸, changes in competitive interactions²⁹, and drought-induced declines in summer uptake³⁰ (but see ref. 10), along with multiple

feedbacks to the climate system¹. The observed phenology-induced enhancement of carbon uptake over the past few decades constitutes a negative feedback to climate, serving to reduce the growth rate of atmospheric CO₂ and slow future warming.

Methods

We analysed long-term changes in phenology, and subsequent changes in the carbon balance of forest ecosystems at three different scales (organism, ecosystem and landscape), using ground observations of phenology, eddy-covariance

estimates of ecosystem–atmosphere carbon exchange, and phenological metrics derived from satellite reflectance.

At the scale of individual trees, we used ground observations of phenology, from the Harvard Forest (1990–2012, dataset HF003 <http://harvardforest.fas.harvard.edu/data-archive>), and Hubbard Brook Experimental Forest (1989–2012, <http://hubbardbrook.org/data/dataset.php?id=51>). At both sites, individual trees were visited every three to five days throughout spring and autumn over the past two decades, and their phenological status recorded³¹. Further details of ground observations are given in the Supplementary Information.

At the ecosystem scale, we derived phenological transition dates from eddy-covariance data of ecosystem carbon flux measured at seven sites distributed across eastern and northeastern US forest ecosystems (Supplementary Table 1). Measurements used include half-hourly canopy-scale CO₂ flux, meteorological variables, and estimates of gross primary photosynthesis (GPP) derived from the CO₂ flux measurements. The data records ranged in length from 7 to 18 years. GPP represents the carboxylation rate minus photorespiration in this study. At night, net ecosystem carbon exchange (NEE) consists of all respiratory processes except photorespiration. There are a variety of approaches to derive GPP. Previous comparisons have shown good agreement between different approaches but recommend the consistent use of a particular approach across sites³². Carbon fluxes were processed using the standard FLUXNET on-line flux-partitioning tool (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/>).

We developed a framework, 'PhAsT' (Phenological Assessment of Trends), for detecting phenological transition dates from the high-frequency flux data and the terrestrial ecosystem models. The PhAsT framework derives phenological transition dates from time series based on singular spectrum analysis (SSA). The SSA concept exploits the idea that measured time series $Y(i)$, $i = 1, \dots, N$, result from superimposed modes of characteristic variability, X_f , where the index f indicates the frequency subsignal class. SSA can therefore distinguish rapid and slow system responses. The seasonal signal can be extracted from the CO₂ flux time series derived from specific (low-frequency) subsignals, independent of confounding factors that operate on other scales (for example, day-to-day variability). See Supplementary Methods for further information.

At the regional scale, we analysed four different phenology metrics at 500-m resolution, calculated from three different vegetation indices (VIs) derived from 13 years (2000–2012) of MODIS reflectance data. The first three metrics were calculated from the MODIS daily surface reflectance product (MOD09GA, v005) and based on the vegetation indices EVI, NDVI and GCC. The fourth metric used was the MODIS Land Cover Dynamics phenology product (MCD12Q2 Collection 5 (ref. 20), which is based on nadir BRDF-corrected MODIS surface reflectance data (MCD43A4) with 8-day temporal resolution and 500-m spatial resolution.

Phenological dates were extracted from each of the daily MODIS VIs (EVI, NDVI, GCC) using two different methods: a robust smoothing-spline approach (RSM) and a dual logistic greendown curve fitting method (GDM; ref. 33). For both methods, a conservative winter was defined ($330 < \text{Day of year} < 70$) for which values were replaced by the pixel-mean winter value. This improves the curve-fitting procedure by removing winter noise¹⁹. Spring and autumn phenological dates were extracted using the RSM by applying a threshold approach. For each pixel, spring and autumn thresholds were set at 30% of the mean amplitude for all years for that pixel. For example, the VI spring date was defined as the date at which the smoothed signal first crossed the threshold of mean winter VI +30% of the mean VI amplitude over all years. For the GDM approach, a greendown dual logistic curve³³ was fitted to each year of daily VI data. See Supplementary Methods for further details, an example application of both methods to the three daily VIs at Harvard Forest (Supplementary Fig. 12) and a comparison against ground observations of phenology (Supplementary Figs 7 and 8).

Trends were extracted from the MODIS-derived dates for all deciduous-dominated pixels in the eastern US, using a widely applied econometric modelling technique known as panel analysis³⁴. In panel analysis, a linear fixed-effects regression model is applied to all contiguous pixels in non-overlapping 1/8-degree windows (so-called panels). This approach provides an estimate of the common trend over the sample of pixels in each panel, where the larger sample size in each panel increases the degrees of freedom, thereby allowing stronger statistical inferences to be drawn. See Supplementary Methods for more information.

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Author contributions

T.F.K. and A.D.R. designed the study and are responsible for the integrity of the manuscript. A.D.R. planned the flux data analysis, with input from D.Y.H., J.W.M., G.B., H.P.S. and D.D. A.D.R., D.Y.H., J.W.M., G.B., H.P.S., B.Y., J.G., M.T. and J.O.K. contributed data. T.F.K. compiled the data sets, and detailed and performed the analysis. M.A.F., I.S.W. and J.G. performed the panel analysis. T.F.K. led the writing, with input from all other authors. All authors discussed and commented on the results and the manuscript.

Additional information

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Competing financial interests

The authors declare no competing financial interests.