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A tale of two springs: using recent climate anomalies to characterize the sensitivity of temperate forest phenology to climate change

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Abstract

By the end of this century, mean annual temperatures in the Northeastern United States are expected to warm by 3–5 °C, which will have significant impacts on the structure and function of temperate forests in this region. To improve understanding of these impacts, we exploited two recent climate anomalies to explore how the springtime phenology of Northeastern temperate deciduous forests will respond to future climate warming. Specifically, springtime temperatures in 2010 and 2012 were the warmest on record in the Northeastern United States, with temperatures that were roughly equivalent to the lower end of warming scenarios that are projected for this region decades from now. Climate conditions in these two years therefore provide a unique empirical basis, that complements model-based studies, for improving understanding of how northeastern temperate forest phenology will change in the future. To perform our investigation, we analyzed near surface air temperatures from the United States Historical Climatology Network, time series of satellite-derived vegetation indices from NASA's Moderate Resolution Imaging Spectroradiometer, and *in situ* phenological observations. Our study region encompassed the northern third of the eastern temperate forest ecoregion, extending from Pennsylvania to Canada. Springtime temperatures in 2010 and 2012 were nearly 3 °C warmer than long-term average temperatures from 1971–2000 over the region, leading to median anomalies of more than 100 growing degree days. In response, satellite and ground observations show that leaf emergence occurred up to two weeks earlier than normal, but with significant sensitivity to the specific timing of thermal forcing. These results are important for two reasons. First, they provide an empirical demonstration of the sensitivity of springtime phenology in northeastern temperate forests to future climate change that supports and complements model-based predictions. Second, our results show that subtle differences in the character of thermal

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forcing can substantially alter the timing of leaf emergence and canopy development. By explicitly comparing and contrasting the timing of thermal forcing and leaf phenology in 2010 and 2012, we show that even though temperatures were warmer in 2012 than in 2010, the nature and timing of thermal forcing in 2010 lead to leaf emergence that was almost a week earlier than 2012.

Keywords: climate change, temperate forests, phenology

1. Introduction

The effects of climate change on terrestrial ecosystems have been reported for over a decade (Hughes 2000, Walther *et al* 2002, Parmesan and Yohe 2003). Specific examples include changes in the timing and length of growing seasons (Menzel *et al* 2006, Schwartz *et al* 2006, Cleland *et al* 2007), disruptions to migration patterns (Sherry *et al* 2007, Visser 2008), changes in plant function and nutrient cycles (Groffman *et al* 2012, Keenan *et al* 2013, Davidson and Janssens 2006), and perturbations to trophic interactions and reproductive strategies (Bale *et al* 2002, Memmott *et al* 2007). While the long-term biological importance of climate change is undisputed, understanding of how ecosystems are likely to respond is incomplete (Wolkovich *et al* 2012). A need therefore exists to improve knowledge and models of how expected changes in the climate system will affect ecosystem properties and function in the coming decades.

Phenology, the seasonal progression of organisms through stages of dormancy, active growth, and senescence is a key regulator of ecosystem processes (Richardson *et al* 2013). In temperature and photoperiod-limited ecosystems, phenological events (e.g., spring leaf emergence and autumn senescence) are highly sensitive to climate change and variability (e.g., Hufkens *et al* 2012a). As a result, phenology has been identified as ‘perhaps the simplest process by which to track changes in the ecology of species in response to climate change’ (Parry *et al* 2007). Further, and equally importantly, phenology is an important pathway of climate-biosphere interactions (Penuelas *et al* 2009). However, despite the central role of phenology in ecosystem function and its importance as a diagnostic of ecosystem response to climate change, understanding of long-term climate-phenology interactions is incomplete (Richardson *et al* 2013). Specifically, the nature and magnitude of phenological responses to interannual and longterm changes in climate forcing is poorly understood. As a consequence, current generation land surface models do not capture the timing or magnitude of interannual variation in phenological responses to climate forcing, which in turn leads to significant errors in modeled fluxes of carbon, energy and water (Keenan *et al* 2012, Richardson *et al* 2012).

A key impediment to improving understanding of how the phenology of ecosystems will respond to future climate variation and change is that the available datasets are geographically sparse, and in most cases include relatively short time series. A number of studies have identified long-term trends in the timing of spring and fall phenology (e.g., Menzel *et al* 2006), but results from these studies do not generalize very well (e.g., Richardson *et al* 2006) and are based on retrospective analyses that are difficult to extrapolate to future climate conditions (Migliavacca *et al* 2012). Controlled experiments designed to characterize the sensitivity of plants to warming have also been attempted (e.g., Chapin *et al* 1996), but such studies are difficult to implement and conduct, and have yielded equivocal results (Wolkovich *et al* 2012). Because controlled experiments do not effectively capture the response of vegetation to warming, understanding of how plants will respond to future climate change is incomplete. In temperate forests, for example, Richardson *et al* (2013) surveyed the literature and found projected rates of change based on retrospective analyses that ranged from 1.8–7.8 d/decade. More generally, projecting changes based on as-of-yet unobserved conditions is extremely challenging because models are tuned to current conditions, and depending on their formulation, show variable sensitivity to temperature forcing.

A key goal of this paper is to address these challenges in a way that complements model-based studies, but which is explicitly empirical. To do this, we exploit natural experiments provided by recent anomalous springtime temperatures in the Northeastern United States to characterize the response and quantify the sensitivity of springtime temperate forest phenology to future warming. Specifically, North American temperatures in the springs of 2010 and 2012 were among the warmest on record (Blunden *et al* 2011, 2013). In the Northeastern United States, which is the focus of this study, the magnitudes of observed temperature anomalies were consistent with the low end of warming projections for this region by the end of the century (Hayhoe *et al* 2008). Springtime temperatures in 2010 and 2012 therefore provide a unique opportunity to characterize and quantify the sensitivity of temperate forest ecosystems to climate change, and more specifically, to improve understanding of how the springtime phenology of Northeastern forests will change in the future. To exploit this opportunity, we used data from ground-based meteorological stations distributed across the Northeastern United States, *in situ* phenological measurements available from two long-term research sites, and satellite-based measurements of phenology that provide information related to the timing of green leaf development at regional scale to

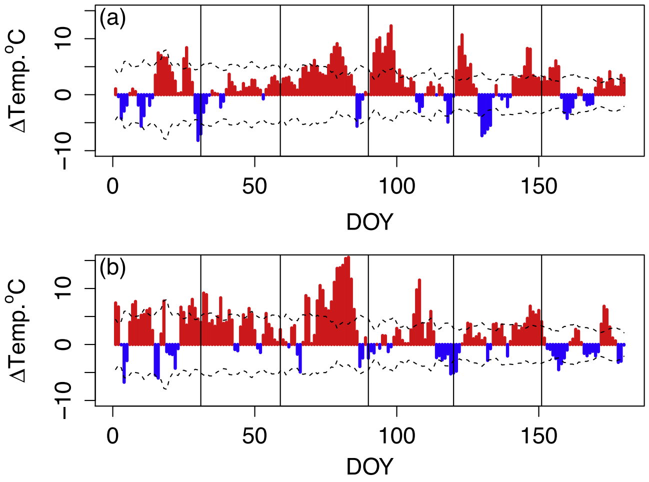

Figure 1. Anomalies in daily temperatures at 79 USHCN stations in 2010 (a), and in 2012 (b), relative to the long-term averages based on data from 1971–2000. Vertical lines indicate first day of month for February–June. The horizontal dashed lines show ±1 standard deviation in daily mean temperature based on USHCN stations in the study area from 1971–2000.

assess and quantify the sensitivity of northeastern temperate forest phenology to climate change. Our results reveal extensive early onset of spring leaf development throughout the study region in 2010 and 2012 that support results from model-based studies, but which also provide new insights regarding how subtle differences in future changes to the magnitude and timing of thermal forcing may influence the response of temperate forest phenology.

2. Study region and data

Our study region encompassed land areas between roughly 40° and 45° North and 70° and 80° West. This region includes the northern third of the Eastern Temperate Forest ecoregion, with substantial areas of higher elevation extending from Pennsylvania to Canada. Natural ecosystems in the study region are dominated by deciduous broadleaf species, with oak-hickory forests in the south and northern hardwood forests dominated by maple, birch and beech species in the north. The climate in this region is humid continental, with ample moisture throughout the year, but strong seasonality in temperatures and a frost-free growing season that ranges from about 100 days in the northern interior parts of the study area to about 160 days in southern coastal areas.

Surface meteorological data used for the analysis include daily mean near surface air temperatures for 1971–2012 measured at United States Historical Climatology Network (USHCN) stations distributed throughout the study region. Only sites with at least 90 percent of daily data were included in the analysis. Missing data in the retained sites were gap filled using inverse distance weighted interpolation based on the 15 nearest stations, adjusted for elevation. Daily mean temperatures were computed for each site based on the average of daily minimum and maximum temperatures, and daily temperature anomalies were computed relative to 30-year averages using data from 1971–2000. Based on these data, we computed the thermal forcing at each USHCN site in growing degree days (GDD) using a base temperature of 5 °C and 1 March as the day of year (DOY) on which GDD begins to accumulate. To select sites that were representative of forest ecosystems and isolated from perturbations caused by human land use and urban heat islands, we used the Collection 5 Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type product (Friedl *et al* 2010) to identify USHCN sites where the majority of MODIS pixels in 3×3 windows surrounding each site were forested. The total number of USHCN sites in our study region was 183. After screening for data quality and land cover, the final air temperature data sets included 42 years of data for 79 USHCN sites.

Ground-based observations of phenology were derived from data collected at the Harvard Forest and Hubbard Brook Long Term Experimental Forests, where *in situ* measurements have been collected for over 20 years using consistent (but different) protocols (for details, see O'Keefe 2000 and Bailey 2013). These data are among the only long-term records of woody plant phenology that have been collected in the United States, are well understood and have excellent quality assurance, and have been heavily used in previous studies (e.g., Richardson *et al* 2006, Migliavacca *et al* 2012). Both data sets include observations for multiple trees and multiple species. Here we use the median DOY when leaf emergence was observed across dominant species at each site. For the Harvard Forest data, we used the median date on which canopy budburst reached 50%, weighted according to the three dominant species at the site: Red Oak (*Quercus rubra*), Red Maple (*Acer rubrum*) and Yellow Birch (*Betula alleghaniensis*). At Hubbard Brook observations are collected for Yellow Birch, Sugar Maple (*Acer saccharum*) and American Beech (*Fagus grandifolia*), which are the dominant tree species at the site. To identify the DOY corresponding to the start of leaf emergence each year, we used the median date for observations where the spring phenology index was greater than 1 ('bud swelling noticeable') and less than 3 ('leaves ½ of final length') across all plots and species.

Satellite-based observations of phenology were derived from the MODIS Collection 5 Land Cover Dynamics Product, which provides estimates for the timing of key phenological transition dates at each 500 m MODIS pixel based on remotely sensed observations (Ganguly *et al* 2010). Specifically, the Land Cover Dynamics Product uses time series of MODIS Enhanced Vegetation Index (EVI; Huete *et al* 2002) measurements to estimate seven metrics that characterize the seasonal phenology of green leaf vegetation at each pixel. For this work we use the DOY corresponding to the onset of greenness increase, which is designed to identify the timing of leaf emergence on the ground. To account for known biases in this product, we applied two corrections to these data. First, to correct for an error in the date assigned to MODIS reflectances that are used to estimate EVI values and the onset of greenness increase, we shifted all greenup dates later by 8 days. Second, because the MODIS product tends to be biased

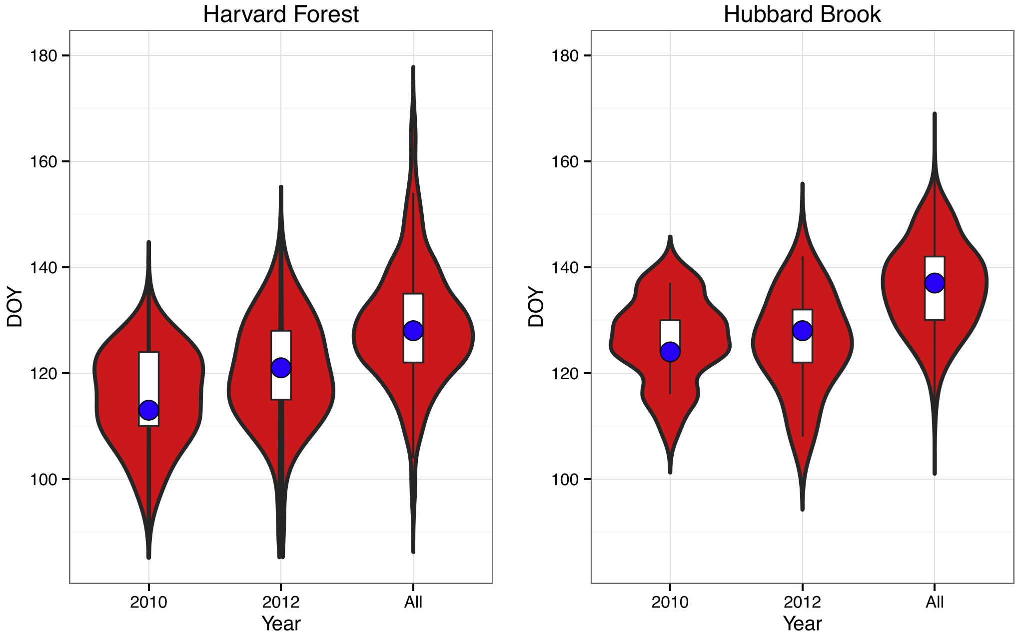

Figure 2. Violin plots showing the timing of tree canopy leaf emergence at Harvard Forest (left) and Hubbard Brook (right) based on 23 and 24 years of data, respectively. Each plot shows data from 2010, 2012, and data pooled across all other years at each site (i.e., 1990–2009 and 2011 at Harvard Forest; 1989–2009, and 2011 at Hubbard Brook). The width of the violin plots shows the density of observations as a function of day of year. Imbedded boxplots show the median (blue dots), inter-quartile range (clear boxes) and ±1.5 times the interquartile range (black lines) of the data in each case.

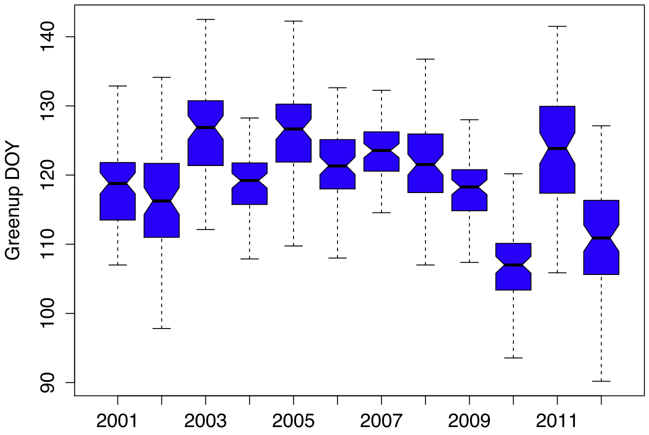

Figure 3. Boxplots showing the timing of spring greenup across 79 USHCN stations located in northeastern temperate forests for each year in the MODIS record.

early relative to forest canopies in the Northeastern United States (e.g., Hufkens *et al* 2012b), we used a threshold corresponding to 20% of the seasonal amplitude in EVI (instead of 10%, which is used in the standard product) to identify the DOY corresponding to greenup.

3. Results

Figure 1 shows anomalies in mean daily temperature in the Northeastern United States from DOY 1 to 180 (1 January–1 July) in 2010 and 2012 relative to 30-year mean values based on USHCN data from 1971 to 2000. On average, daily temperatures in the first half of 2010 and 2012 were 1.9 and 2.5 °C warmer (respectively) than long term daily mean temperatures for the study region. More importantly, during the critical period associated with bud swelling and leaf emergence and growth in March, April and May, temperatures were 2.8 and 2.9 °C warmer than average in 2010 and 2012, respectively. At the same time, important differences between 2010 and 2012 are also evident; in 2012, the largest anomalies (5–15 °C) occurred early in spring (DOY 60–90). Spring temperature anomalies in 2010, on the other hand, were somewhat lower in magnitude relative to 2012 (5–10 °C), but were strongest directly prior to and during the period of bud swelling and leaf emergence in April and May (DOY 90–150).

Ground-based measurements of leaf phenology at Harvard Forest and Hubbard Brook showed strong responses to the anomalously warm temperatures in 2010 and 2012 that also reflected differences in the timing of temperature anomalies in each year. To illustrate, figure 2 presents violin plots showing the timing of leaf emergence at each site in 2010 and 2012, along with the long-term timing based on 22 and 21 years of data collected at the Hubbard Brook and Harvard Forest LTER sites, respectively. The median dates of leaf emergence in 2010 were the earliest on record at each site, although 1998 is tied with 2010 for the earliest date at Hubbard Brook. At Harvard Forest, leaf emergence in 2010 was the earliest on record by eight days. Relative to long-term medians (excluding 2010 and 2012), the timing of leaf emergence was 15 and 7 days early at Harvard Forest and 13 and 9 days early at Hubbard Brook in 2010 and 2012, respectively. For context, the standard deviation in the median

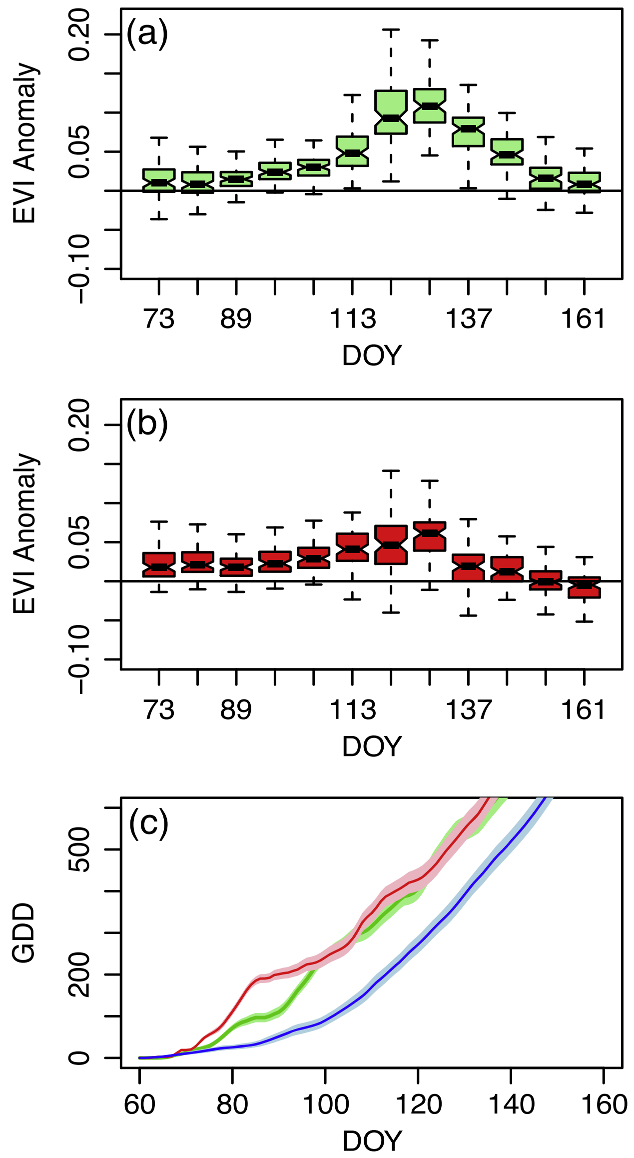

Figure 4. (a) Boxplots showing 2010 departures from average EVI at USHCN stations for eight-day time periods spanning spring greenup period in the Northeastern United States; (b) same as (a), but for 2012; (c) median daily growing degree days for 2010 (green), 2012 (red), and long-term average (blue) for DOY 65–150 across 79 USHCN stations ±95% confidence intervals.

timing of annual leaf emergence is 5.2 days at Harvard Forest and 6.5 days at Hubbard Brook, which are of roughly the same magnitude that recent studies have estimated for changes in the timing of spring phenology in temperate forests at decadal and longer time scales (1.8–7.8 d/decade; Richardson *et al* 2013). In other words, the average magnitude of interannual variation in springtime phenology is about the same as the magnitude of observed long-term trends, and in the case of extreme years such as 2010 and 2012, anomalies reflect conditions that long term trends suggest will become normal decades from now. Hence, year-to-year variations, and extreme years in particular, provide a powerful basis for improving understanding and quantifying the sensitivity of temperate forest phenology to climate change.

Patterns in spring phenology at regional scale derived from MODIS at USHCN sites are similar to those observed from *in situ* measurements (figure 3). Across the 79 USHCN sites included in our analysis, the median timing of spring greenup from MODIS was DOY 121 across 2001–2009 and 2011. More specifically, figure 3 clearly shows that 2010 and 2012 are large outliers in this relatively short record; according to MODIS, median greenup across the USHCN sites was 14 and 10 days early in 2010 and 2012, respectively, which are consistent with anomalies observed in ground observations at Harvard Forest and Hubbard Brook.

To illustrate covariance in the timing and magnitude of anomalies in thermal forcing and MODIS data, figure 4(c) plots GDD time series for 2010 and 2012 across the USHCN sites included in our analysis, along with time series of long term mean GDD for the same sites for 1971–2000 during the spring greenup period. The associated response of regional forest phenology observed from MODIS is shown in figures 4(a) and (b), which present boxplots of anomalies in MODIS EVI measurements at eight-day time steps at the same USHCN sites in 2010 and 2012. Data from 2010 and 2012 show large departures from average conditions in both GDD and EVI. However, because of differences in the timing of temperature anomalies in 2010 versus 2012 (cf, figure 1), EVI anomalies in 2010 are larger and occur earlier than in 2012. Specifically, positive temperature anomalies in April and May of 2010 provided the driver for rapid and early leaf development throughout the study region. Positive temperature anomalies in 2012, on the other hand, were largest in March, but with the exception of a one-week warm spell in mid-April, daily mean temperatures in the spring of 2012 were within about 2–3 °C of long-term average daily temperatures. As a consequence, even though springtime temperatures in 2012 were the warmest on record, observed patterns in the timing of leaf development (both on the ground and from MODIS) in 2012 lagged the timing observed in 2010.

To quantify the magnitude of anomalies in thermal forcing, we computed anomalies in GDD at each USHCN station in 2010 and 2012 on the DOY corresponding to the median timing of spring greenup from MODIS across 2001–2009 and 2011. Figure 5 shows the geographic pattern in these anomalies, along with density plots showing frequency distributions for anomalies in each year. The anomalies ranged from 51 to 230 GDD in 2010 and from 52 to 243 GDD in 2012, with median anomalies of 119 and 147 GDD, respectively. For context, the average thermal forcing across all years and all stations on the median date of spring greenup from MODIS was 217 GDD.

To illustrate the relationship between anomalies in thermal forcing and anomalies in the timing of spring greenup from MODIS, figure 6 plots annual anomalies in the timing of spring phenology against corresponding anomalies in GDD across all sites for each year of MODIS data. While the MODIS record only provides 12 years of data, the overall pattern is clear, with positive GDD anomalies (i.e., warmer temperatures) leading to negative timing anomalies (earlier springs), and vice versa; the magnitude of the anomalies in

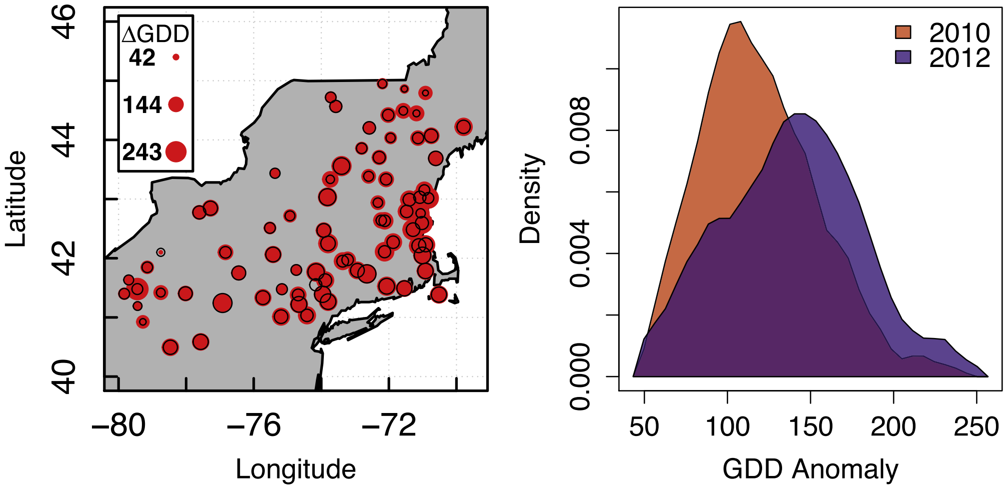

Figure 5. GDD anomalies in 2010 and 2012 relative to long term averages based on data from 1971–2000. The left-hand panel shows a map of USHCN sites included in the analysis, where the area of the circle at each station is proportional to magnitude of the GDD anomaly (solid red circles = 2012, open black circles = 2010). The right-hand panel shows density plots for the magnitude of anomalies in 2010 and 2012.

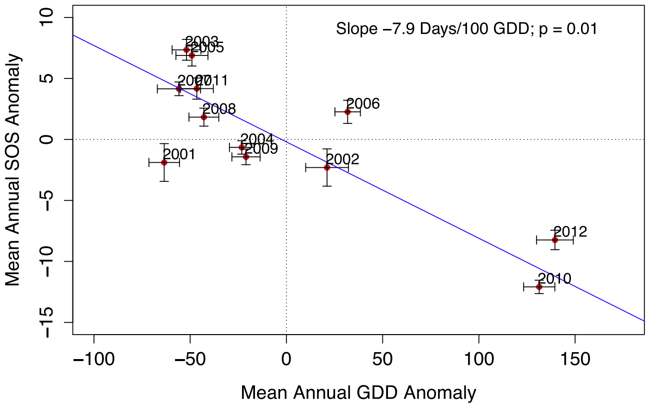

Figure 6. Mean annual anomalies (±95% confidence intervals) in greenup onset date from MODIS versus corresponding anomalies in growing degree days on the date of greenup identified by MODIS based on the 79 USHCN sites included in our analysis.

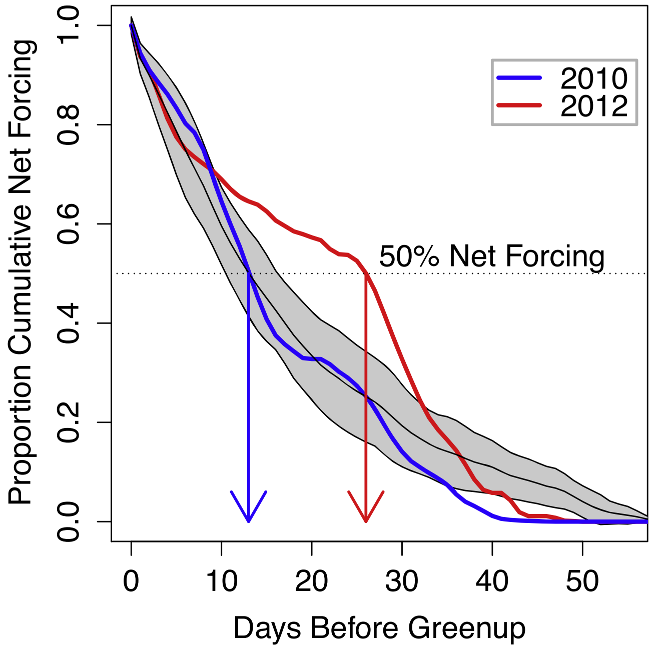

Figure 7. Proportion of cumulative net thermal forcing as a function of time before greenup at USHCN sites in the study region. The black line and gray area show the regional mean across years, ±1 standard deviation. The blue line shows the mean forcing across stations in 2010, and the red line shows the mean forcing in 2012. The blue arrow shows the timing at which 50% of net forcing occurred in 2010; the red arrow shows the timing of 50% net forcing in 2012.

2010 and 2012 is also evident. Over the 12-year record, the timing of median annual greenup onset varied by 20 days, with 2010 showing the earliest onset (median DOY = 107) and 2003 and 2005 showing the latest onset (median DOY = 127). A reduced major axis fit of average annual anomalies in spring onset to average annual anomalies in GDD indicates that the sensitivity of spring phenology to changes in temperature forcing is −7.9 days for every 100 GDD change in thermal forcing.

Consistent with patterns observed *in situ* at Harvard Forest and Hubbard Brook, figures 5 and 6 show that even though the spring of 2012 was warmer than 2010, the onset of leaf emergence from MODIS was earlier in 2010 than in 2012. To explore this, figure 7 plots the proportion of cumulative forcing as a function of time before greenup across the USHCN sites included in our study. This figure clearly shows that relative to the timing of leaf emergence, the timing of thermal forcing in 2010 was representative of long-term average patterns in the region, with 50% of thermal forcing occurring during the two weeks directly prior to greenup. In 2012, on the other hand, a substantial proportion of thermal forcing occurred earlier in the spring, with about 30% of forcing occurring in a one-week period 26–33 days prior to greenup, and the final 50% of thermal forcing distributed over nearly four weeks. In effect, this figure shows that despite the overall warmer conditions in 2012, much of the warmth occurred in the early spring, and that relatively cool temperatures in the period 1–4 weeks prior to greenup retarded leaf emergence relative to what would otherwise be expected based on the total anomaly in thermal forcing. In other words, both the timing and the magnitude of springtime thermal forcing influence the timing of leaf mergence over the study area.

4. Discussion and conclusions

Green leaf phenology is well known to be a sensitive indicator of climate change, and many papers have previously reported trends towards earlier leaf out over the last several decades (Parmesan and Yohe 2003, Cleland *et al* 2007, Richardson *et al* 2013). Results from this study, which used a combination of ground-based and remote sensing observations to characterize how climate variability affects springtime phenology in temperate forests of the Northeastern United States, are consistent with these previous studies. Specifically, we found that ground-based observations of springtime phenology at both Harvard Forest and Hubbard Brook showed strong sensitivity to interannual variability in springtime temperatures. At regional scale, observations of spring greenup from satellite observations showed corresponding sensitivity to variability in springtime temperatures.

The conclusion that springtime phenology in temperate forests is sensitive to temperature is clearly not new. Indeed, a number of previous studies have used models tuned to ground-based observations of phenology to forecast future changes to phenology in the northeastern temperate forests (e.g., Hayhoe *et al* 2007, Migliavacca *et al* 2012, Jeong *et al* 2013). However, the causal mechanisms that control phenology remain poorly understood, and warming experiments designed to simulate future climate conditions show equivocal results (Wolkovich *et al* 2012). A key factor that limits progress in this domain is the relatively short time span over which many phenological time series are available. In the Northeastern United States, the Harvard Forest and Hubbard Brook data sets provide the best available time series of phenology measurements to support this type of model development. At just over 20 years in length, however, these time series are quite short for model estimation purposes, and models developed from these time series are both site and species-specific (see, for example, Richardson *et al* 2006). Further, and perhaps more importantly, the available data sets upon which existing models are based do not typically include climate conditions that they are being used to forecast. In the case of this study, springtime temperatures in the Northeastern United States were the two warmest over the 100+ year period for which records are available. Development and evaluation of models that predict the response of phenology to climate change based on these records is therefore challenging, and potentially fraught with errors.

In this paper we pursue a somewhat different approach from previous studies that is explicitly empirical, and which attempts to use recent anomalous springtime conditions to characterize the sensitivity of temperate forest phenology to future climate change. Further, in addition to exploring patterns in phenology at a specific site, our analysis used satellite observations to characterize the nature and magnitude of phenological responses to anomalous springtime conditions at regional scale. An explicit assumption of this analysis was that springtime temperatures in 2010 and 2012 provide precursors of future springtime climate in this region, and that observed anomalies in both temperature and phenology can therefore be exploited to improve understanding of future changes to regional phenology. Within this framework, we show that springtime temperatures in 2010 and 2012 were about 3 °C warmer than long-term averages based on data from 1971–2000. Current projections suggest that mean annual temperatures in the Northeastern United States are likely to rise by 3–5 °C by the end of this century. Hence, springtime temperatures and phenology in 2010 and 2012 probably represent conservative scenarios for future climate conditions in the region.

Our results point to three main conclusions. First, both ground and satellite data reveal pronounced responses in green leaf phenology to the unusually warm conditions in 2010 and 2012. At Harvard Forest and Hubbard Brook, leaf emergence was 13–15 and 7–9 days early in 2010 and 2012, respectively, relative to long-term averages at each site. Observations from MODIS over 79 USHCN sites distributed throughout the Northeastern United States show parallel results: the median timing of greenup was 14 and 10 days early in 2010 and 2012, respectively. As we have stated previously, the fact that leaves emerged earlier than normal in 2010 and 2012 is not a surprise. However, the magnitude of the observed responses provide empirical evidence for what the future holds in this region with respect to changes in springtime phenology. Second, our results indicate that springtime green leaf phenology for temperate forests in our study region responds almost exclusively to temperature forcing. Figure 6, for example, suggests a linear response of phenology to changes in thermal forcing, even in 2010, which was the earliest spring leaf-out on record. Third, differences in springtime phenology in 2010 versus 2012 show that the timing (and not just the amount) of thermal forcing exerts substantial control on green leaf phenology in our study region. At the most general level, this conclusion is evidenced by the fact that leaf emergence occurred later in 2012 than in 2010, even though the spring of 2012 was warmer over the period from March through May. Figures 1 and 7, however, clearly show that the timing of thermal forcing in 2010 and 2012 was quite different. In 2010, thermal forcing was distributed more uniformly throughout the spring, whereas roughly half of the thermal forcing prior to leaf out occurred in March in 2012, roughly four weeks prior to leaf emergence. Stated another way, it would appear that thermal forcing that occurs more than two weeks prior to leaf emergence is significantly less effective than forcing that occurs in the two weeks directly prior to budburst (but see Clark *et al* 2013).

If the climate of the Northeastern United States continues to warm as expected over the coming decades, many properties and functional attributes of temperate forests that affect phenology in this region are likely to change. While changes in community composition will lag changes in climate, warmer temperatures will almost certainly lead to changes in the species composition of temperate forests by the end of the century. Similarly, life histories and trophic interactions for many species in temperate regions are tightly linked to climate, and increased frequency of extreme climate events will likely have important impacts on temperate forest ecosystems (Augspurger 2013, Hufkens *et al* 2012a). All of these properties and processes are intimately linked to phenology (e.g., Chuine 2010), and understanding how phenology will respond to future warming is therefore critical to predicting how ecosystems are likely to change in the future. By treating the unusually warm springtime conditions in the springs of 2010 and 2012 as precursors of future conditions, the results from this work provide an empirical demonstration that pronounced changes in the growing season of northeastern temperate forests are likely in the coming decades. However, as this and other studies have demonstrated, understanding of functional relationships and interactions among climate, phenology, and ecosystem properties is still quite rudimentary. Hence, to more fully understand how ecosystems will respond to both long-term warming and an increasingly variable climate system, continued efforts focused on both empirical and model-based studies that link climate change to ecosystem properties and processes are required.

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