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# A longer vernal window: the role of winter coldness and snowpack in driving spring transitions and lags

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#### **Abstract**

Climate change is altering the timing and duration of the vernal window, a period that marks the end of winter and the start of the growing season when rapid transitions in ecosystem energy, water, nutrient, and carbon dynamics take place. Research on this period typically captures only a portion of the ecosystem in transition and focuses largely on the dates by which the system wakes up. Previous work has not addressed lags between transitions that represent delays in energy, water, nutrient, and carbon flows. The objectives of this study were to establish the sequence of physical and biogeochemical transitions and lags during the vernal window period and to understand how climate change may alter them. We synthesized observations from a statewide sensor network in New Hampshire, USA, that concurrently monitored climate, snow, soils, and streams over a three-year period and supplemented these observations with climate reanalysis data, snow data assimilation model output, and satellite spectral data. We found that some of the transitions that occurred within the vernal window were sequential, with air temperatures warming prior to snow melt, which preceded forest canopy closure. Other transitions were simultaneous with one another and had zero-length lags, such as snowpack disappearance, rapid soil warming, and peak stream discharge. We modeled lags as a function of both winter coldness and snow depth, both of which are expected to decline with climate change. Warmer winters with less snow resulted in longer lags and a more protracted vernal window. This lengthening of individual lags and of the entire vernal window carries important consequences for the thermodynamics and biogeochemistry of ecosystems, both during the winter-to-spring transition and throughout the rest of the year.

Keywords: climate change, energy balance, lag, snow, soil, spring, stream, temperature, transition

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#### Introduction

The shortening of winter and the lengthening of the growing season are well-documented effects of climate change, both in the northeastern United States and across similar temperate latitudes that experience seasonal snow cover (Hodgkins *et al.*, 2002; Hodgkins & Dudley, 2006; Schwartz *et al.*, 2006; Hayhoe *et al.*, 2007; Burakowski *et al.*, 2008). As the end of winter and beginning of the growing season both move earlier in the year, the duration of the spring season between them is also likely to change, with implications for ecosystem function.

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Previous work examining changes in the timing of the spring wake-up period has typically focused on only part of the ecosystem in transition. Examples include studies addressing the timing of peak river discharge relative to winter precipitation (Hodgkins *et al.*, 2003; Stewart *et al.*, 2005, Adam *et al.*, 2009) or the greening of forest canopies as related to temperature (Jenkins *et al.*, 2002; Richardson *et al.*, 2006; Piao *et al.*, 2015). Such efforts have demonstrated the role that the onset of spring plays in critical ecosystem functions such as annual carbon uptake (Baldocchi *et al.*, 2005; Richardson *et al.*, 2009) and seasonal water availability (Barnett *et al.*, 2005; Harpold & Molotch, 2015). However, examining multiple aspects of the ecosystem as it transitions from winter to spring can provide new

insights into how climate change may affect the cascade of energy, water, nutrients, solutes, and carbon through terrestrial and aquatic ecosystems (Cayan et al., 2000; Molotch et al., 2009; White et al., 2009), both during the spring season and throughout the rest of the year (Schwartz & Crawford, 2001; Hodgkins et al., 2003; Aurela et al., 2004; Richardson et al., 2010).

Many studies examining the onset of spring focus on the date(s) on which system components 'wake up', but not on temporal delays, or lags, between these transitions. In phenology, lags are generally portrayed as intervals between changes in abiotic drivers and biological responses (e.g., Willis et al., 2008) or in the timing of the activities of two species in a community (Winder & Schindler, 2004; van Asch & Visser, 2007; Singer & Parmesan, 2010). While these asynchronies are relevant to ecosystem function, they do not fully describe the delays in energy, nutrient, carbon, and water flows that occur during the start of spring. For example, the lag between transitions such as soil warming and leaf emergence may be significant for ecosystem C balance because soil respiration increases during this period prior to vegetation C uptake (Groffman et al., 2012). Likewise, the interval between transitions such as the onset of snow melt and the closing of the forest canopy is important for ecosystem water balance because river discharge predominates over evapotranspiration during this time as the primary hydrologic process (Willmott & Rowe, 1985). The period between when air temperature warms and the snowpack disappears is critical for ecosystem energy balance as the high albedo of snow has a net cooling effect on the atmosphere (Betts et al., 2014). These and other lags represent periods during which crucial biogeochemical and thermodynamic processes occur. Yet they are rarely, if ever, explicitly considered in research on climate change and the earlier onset of spring.

In contrast to previous work, we conceptualize the shift from winter to spring in seasonally snow-covered systems as a 'vernal window' (sensu Groffman et al., 2012) that 'opens' with a change in ecosystem energy balance and the onset of snow melt and 'closes' as forests leaf out and pastures, croplands, and lawns green up. A series of dramatic and lagged transitions occurs within this window as the system sequentially crosses rapid thermodynamic and biogeochemical thresholds that drive energy, water, nutrient, and carbon flows (Fig. 1a). For example, a low albedo soil quickly replaces a high albedo snowpack as the system becomes snow free (Groisman et al., 1994). Soil temperatures then respond quickly to snow melt, warming as much as 5 °C during a single day (Molotch et al., 2009; Groffman et al., 2012). Snow melt commonly delivers a large volume of water to aquatic systems over a

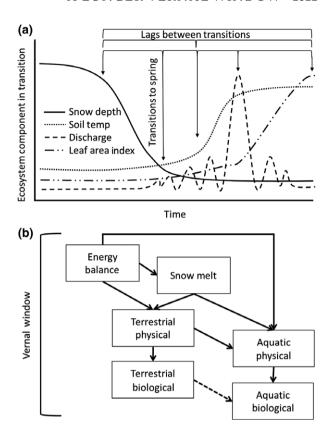


Fig. 1 (a) Stylized representation of the vernal window in which rapid transitions in energy, water, nutrients, and carbon take place as indicated by changes in ecosystem variables such as snow depth, soil temperature, stream discharge, and leaf area index. Lags are periods between pairs of individual transitions, and the entire vernal window is the lag from the first to the last transition. (b) Conceptual model of the vernal window which opens with a transition in the ecosystem energy balance and closes with transitions in terrestrial and aquatic biological phenomena. Each transition along the vernal window flow path lags behind the one that preceded it. The timing, magnitude, and duration of each transition can impact the one that follows it. In this model, transitions within ecosystem components are boxes, while lags between transitions are represented by arrows. The dotted line from terrestrial biological to aquatic biological systems indicates the lagged relationship between forest canopy green-up and in-stream productivity. The longest lag in the system is the entire vernal window, which starts with a change in energy balance and ends with forest canopy closure. Climate change will likely lengthen the vernal window, thereby elongating the arrows connecting lagged transitions in different parts of the ecosystem.

relatively short period of time, such that streams and rivers can exhibit the highest flows carrying higher mass fluxes of N and dissolved organic matter (DOM) than at any other time of the year (Pellerin et al., 2011). Figure 1b illustrates our conceptual model of the vernal window, in which transitions in each ecosystem component lag behind the ones that preceded them.

Although transitions that mark the beginning of the vernal window – warming air temperatures and disappearing snowpacks – are changing rapidly with the pace of climate change, the leafing-out of forest canopies that indicates the close of this window is responding much more slowly (Groffman *et al.*, 2012). The net result is a lengthening of the vernal window, during which lags between important thermodynamic and biogeochemical transitions may also become longer, with unclear ecosystem implications. More comprehensive measurements across ecosystem components are needed to better understand these ongoing and projected changes.

The objectives of this study were to determine the sequence of physical and biogeochemical transitions across multiple forest watershed systems during the vernal window and to understand how climate change might alter lags between these transitions. We hypothesized that the transitions followed a predictable sequence (H1), that there were lags between transitions (H2), and that the duration of these lags varied as a function of antecedent winter severity and snowpack characteristics (H3). Our third hypothesis emerged from patterns we observed in evaluating H1 and H2, and was not developed a priori. To our knowledge, this is the first study to evaluate how climate change might alter the duration of the vernal window as well as the lags between transitions that occur within the vernal window period.

#### Materials and methods

#### Study location

We used the upland forested ecosystem of New Hampshire, USA, as our model system for examining the effects of climate change on the vernal window. The range in winter air temperatures and snowpack depth and duration in New Hampshire are typical of a humid continental climate where winter precipitation falls as snow during a number of storms, resulting in a highly layered snowpack that accumulates throughout the winter to reach peak snow water equivalent depth in late winter/early spring. Rainfall can and usually does occur at least once during the winter, at which time liquid water channels through the snowpack, resulting in sporadic midwinter water runoff events. During the weeks of the spring snow melt period, the snowpack becomes isothermal with near-continual melt outflow. In New Hampshire, as in other areas of North America, the spatial extent of spring snow cover has declined significantly over the period 1972-2006, with the retreat of the spring snow cover extent depending on latitude and elevation (Déry & Brown, 2007). The rate of decrease in snowcovered area has accelerated over the last 40 years (Brown & Robinson, 2011) and is likely to continue under current warming (Hayhoe et al., 2007; Wake et al., 2014a, 2014b).

#### Data compilation

Table 1 summarizes the data used for analyzing transitions and lags during the vernal window. Data were primarily compiled from the New Hampshire Experimental Program to Stimulate Competitive Research (EPSCoR) Ecosystems & Society Statewide Sensor Network and can be accessed at the New Hampshire EPSCoR Data Discovery Center Website (http:// ddc.sr.unh.edu/). These data include climate and snow data collected as part of citizen scientist observations from the Community Collaborative Rain, Albedo, Hail, and Snow (CoCoRAHS Albedo) network (Burakowski et al., 2013; hereafter called snow); in-stream data collected by an aquatic statewide initiative called the Lotic Volunteer network for sensing Temperature, Electrical Conductivity, and Stage (LoVoTECS, hereafter aquatic statewide); and coupled climate, soil, and aquatic data at four intensively monitored forested sites, called terrestrial intensive and aquatic intensive in this study (Mulukutla et al., 2015). Beyond the EPSCoR sensor network, other data consisted of Moderate Resolution Imaging Spectroradiometer (MODIS) satellite spectral data (Land Processes Distributed Active Archive Center, 2013–2015; hereafter called satellite spectral) products used to obtain leaf area index (LAI); United States Geological Survey (USGS) discharge data (U.S. Geological Survey, 2001; hereafter called discharge); reanalysis weather data from the National Oceanic and Atmospheric Administration (NOAA) North American Regional Reanalysis (NARR) model output (hereafter weather reanalysis); and gridded snow data from the National Operational Hydrologic Remote Sensing Center Snow Data Assimilation System (hereafter called gridded snow; National Operational Hydrologic Remote Sensing Center, 2004). Each data source contained multiple variables collected at a variety of temporal frequencies and spatial scales covering a broad range of topography and forest cover throughout the state (Fig. 2). Based on differences in the breadth and depth of data sources, data were assigned to statewide or site-level analyses (Table 1). Although the statewide analysis did not have the same detail of colocated measurements of multiple variables as the site level analysis, the large geographic coverage demonstrated how transitions and lags changed over broad spatial areas. Statewide analyses were performed on the snow, water temperature, water conductivity, discharge, satellite spectral, weather reanalysis, and gridded snow data. Statewide data consisted of both point observations (snow, water temperature and conductivity, discharge) and gridded sources (satellite spectral, weather reanalysis, and gridded snow). Gridded data were extracted where pixels overlapped with sampling points from the intensive terrestrial and aquatic networks, as well as the snow, aquatic statewide, and discharge networks. Site-level analyses were performed on point data from four coupled terrestrial and aquatic sensor sites, two in the White Mountains (northern sites) and two in the Seacoast region (southern sites). While these sites were limited in their spatial coverage, they included 21 simultaneous, continuous measurements of terrestrial and aquatic system properties and processes and afforded tremendous insight into the sequences of transitions and the lags between transitions that occurred during the vernal window period. Figure 2 shows the

Data source	Transition	Component	Extent	Туре	Years	Frequency	Resolution	Algorithm
Community Collaborative Rain,	Air Temp Zero	Energy balance	State	Point	2012–2014	Daily	NA	Air temperature >0 °C
Albedo, Hail, and Snow Network; (CoCoRAHS)	Snow Albedo	Energy balance	State	Point	2012–2014	Daily	NA	Piecewise regression; end date when ground is snow free
(Cocold IIIo)	Snow Depth	Snowpack	State	Point	2012–2014	Daily	NA	Day when snow depth = 0 cm and is not >0 cm for rest of season
	SWE	Snowpack	State	Point	2012–2014	Daily	NA	Piecewise regression; end date when ground is snow free
National Operational Hydrologic Remote Sensing Center	Snow Depth	Snowpack	State	Grid	2012–2014	Daily	30 arcsec	Day when snow depth = 0 cm and is not >0 cm for rest of season
(NOHRSC)	SWE	Snowpack	State	Grid	2012–2014	Daily	30 arcsec	Piecewise regression; end date when ground is snow free
North American Regional Reanalysis (NARR)	Air Temp Zero	Energy balance	State	Grid	2012–2014	Daily	0.3°	Air temperature >0 °C
Terrestrial Intensive	Air Temp Zero	Energy balance	Site	Point	2014	Hourly	NA	Air temperature >0 °C
	Soil Temp	Terrestrial physical	Site	Point	2014	Hourly	NA	Piecewise regression
	Soil Moist Initial, Peak	Terrestrial physical	Site	Point	2014	Hourly	NA	Local peaks
	Soil SC Initial, Peak	Terrestrial physical	Site	Point	2014	Hourly	NA	Local peaks
Aquatic Intensive	Aquatic Temp	Aquatic physical	Site	Point	2014	Subhourly	NA	Piecewise regression
	Discharge	Aquatic physical	Site	Point	2014	Subhourly	NA	Baseflow peak
	SC Peak, Trough	Aquatic physical	Site	Point	2014	Subhourly	NA	Local peak and trough
	Aquatic NO <sub>3</sub>	Aquatic biological	Site	Point	2014	Subhourly	NA	Baseflow peak
	Dissolved organic matter (fDOM)	Aquatic biological	Site	Point	2014	Subhourly	NA	Baseflow peak
	Aquatic DO	Aquatic biological	Site	Point	2014	Subhourly	NA	Piecewise regression diel variation of DO
Lotic Volunteer Network for Sensing	Aquatic Temp	Aquatic physical	State	Point	2013–2014	Subhourly	NA	Piecewise regression
Temperature, Electrical Conductivity, and Stage (LoVoTECS)	Aquatic SC Peak, Trough	Aquatic physical	State	Point	2013–2014	Subhourly	NA	Local peak and trough
United States Geological Survey (USGS)	Discharge	Aquatic physical	State	Point	2012–2014	Daily	NA	Baseflow peak
MODerate resolution Imaging Spectroradiometer (MODIS)	LAI	Terrestrial biological	Site	Grid	2012–2014	Weekly	1 km <sup>2</sup>	Date LAI is within 0.8 SDs of summer levels.

locations of all the sites where point-level measurements were made. Table S1 contains geolocation for each of these points.

#### Delineation of transitions and lags

We devised algorithms based on specific criteria to determine the date(s) at which each variable in the data set transitioned from winter to spring. These new algorithms were necessary as many existing methods for defining the winter-to-spring transition did not apply to variables in our data set. For example, cumulative growing degree days is a common metric for evaluating the date when terrestrial vegetation produces buds, flowers, and/or leaves (Richardson *et al.*, 2006). However, these degree day calculations may not be relevant for soil and stream temperatures that do not consistently fall below 0 °C.

In addition, identifying a single degree day threshold for the entire ecosystem is problematic as autotrophic and heterotrophic organisms in terrestrial and aquatic environments each respond differently to temperature cues (Bonhomme, 2000). Similarly, the onset of spring for stream and river discharge has been defined as the center of volume date (Hodgkins *et al.*, 2003). While the center of volume date can be used to identify discharge thresholds, it does not necessarily delineate spring 'trigger' dates for other hydrologic variables with a different annual cycle, such as soil moisture. Thus, we developed a set of metrics for determining the timing of the onset of spring, which allowed us to analyze similar variables across the ecosystem with similar methods.

The algorithms we devised to delineate the date(s) at which each variable in the data set transitioned from winter to spring

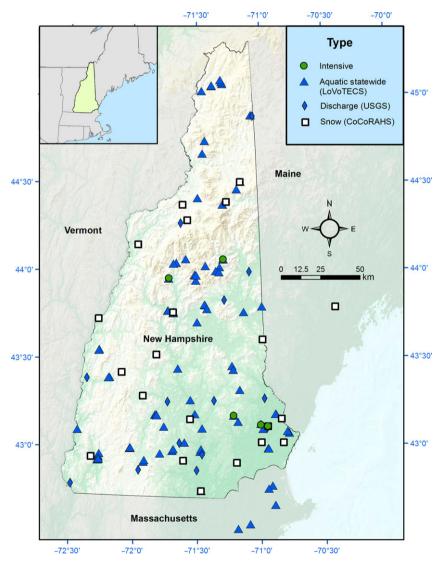


Fig. 2 Map of the study area showing location of point data collection, including the snow Community Collaborative Rain, Albedo, Hail, and Snow (CoCoRaHS) network, aquatic statewide Lotic Volunteer network for sensing Temperature, Electrical Conductivity, and Stage (LoVoTECS) network, discharge from United States Geological Survey (USGS) stream gages, and intensive coupled terrestrial–aquatic sensor locations. [Colour figure can be viewed at wileyonlinelibrary.com]

are summarized in Table 1. Scripts developed to apply these algorithms to the data can be downloaded via the GitHub digital repository (http://contosta.github.io/vernal-windows/). In some cases, algorithms were relatively simple; for example, snowpack disappearance was defined as the day of year when the snow depth measured 0 cm and did not rise above 0 cm until the following winter season. In most instances, the algorithms were more complex and involved data filtering and regression techniques. Regardless of the specific algorithm applied, data processing generally involved a Monte Carlo analysis where two factors were randomly varied over 1000 iterations. First, data were filtered using a rolling median to remove noise associated with short-term phenomena such as weather systems, storms, midwinter thaw events, and diel fluctuations. The number of days in the rolling median was allowed to randomly vary, usually between 5 and 120 days. Second, a start date and end date for the analysis window was determined, within which a wake-up date would be delineated. These start and end dates were allowed to randomly vary  $\pm$  15 days between February 15 and May 15. Having filtered the data and selected an analysis window, the date at which a variable transitioned, that is, the wake-up date, from winter to spring was determined. In many cases, this wake-up date was detected with piecewise regression (Toms & Lesperance, 2003; Tomé & Miranda, 2004) using the 'SEGMENTED' package in R (Muggeo, 2008). These three steps, (i) smoothing the data, (ii) determining the start and end date of the analysis window, and (iii) applying the algorithm to determine the wake-up date, were repeated using 1000 different combinations of numbers of days in the smoother and length of the analysis window. The wake-up date was identified as the mode of the 1000 estimated transition dates, with 95% confidence intervals (CIs) around that mode calculated as lower and upper 2.5% and 97.5% quartiles. Figure S1 shows an example time series for each variable included in the analysis with calculated transition dates plotted onto that time series, as well as a histogram showing the frequencies of wake-up dates selected over 1000 iterations. All variables are from the same paired terrestrial-aquatic intensive site to illustrate the flow of energy, water, nutrients, and solutes within the vernal window as different ecosystem components woke up.

Once transition dates were defined, lags were calculated as the number of days between pairs of transition dates in the same location. The possible combination of pairs for the statewide analysis was variable and depended on the number of simultaneous point-level or point-from-gridded-level transitions defined within a given area. For the site-level analysis, there were 210 individual lags determined at each location from 21 calculated transition dates.

#### Statistical analysis

The first task in testing H1 (transitions within the vernal window followed a predictable sequence) was to order the expected progression of transitions that occur during the spring wake-up period. Table 2 shows this progression, which was based on our conceptual model (Fig. 1) and the collective expertise of the coauthors. Once this hypothesized sequence

Table 2 Hypothesized sequence of transitions during the vernal window period. Rankings with the same number were predicted to occur simultaneously. Variables with more than one transition (indicated in parentheses) are ordered only once as each variable was originally hypothesized to show only one inflection point as it transitioned from winter to the growing season

Variable name	Ranking
Air temperature	1
Snow water equivalent	2
Snow depth	3
Albedo	4
Soil moisture at the surface(initial and peak)	5
Soil moisture at midprofile (initial and peak)	6
Soil specific conductance (initial and peak)	7
Soil moisture deep in profile (initial and peak)	8
Soil temperature at the surface	9
Stream nitrate concentration	10
Stream specific conductance (peak and trough)	11
Soil temperature at midprofile	12
Discharge	12
Aquatic temperature	13
Soil temperature deep in profile	14
Aquatic dissolved organic matter concentration	15
Aquatic dissolved oxygen concentration	16
(diel variation)	
Canopy closure	17

was established, we evaluated differences in the timing of each transition against every other transition. We used three different point-level data sets containing transition dates for the statewide statistical evaluation of H1: snow, aquatic statewide, and discharge data. Point-level field observations were supplemented with data extracted from gridded weather, snow, and satellite spectral sources to determine differences in spring wake-up dates across the ecosystem.

Differences in the timing of each wake-up date were compared to every other wake-up date using pairwise, paired Wilcoxon tests, with Bonferroni corrections for multiple comparisons. Here, 'pairwise' indicates that the date of each transition within the data set was compared with the date of every other transition, and 'paired' indicates the coupling of transition dates estimated from data collected within a given site. The site-level analysis did not contain enough replicates (n = 4 transition dates per variable) for statistical determination of these differences. As a result, H1 was tested at the site level by qualitatively examining variation in the timing of spring wake-up across variables within and among sites using box and whisker plots.

To statistically test whether there were quantifiable lags between transitions (H2), we performed Wilcoxon tests on each lag calculated within the snow, aquatic statewide, and discharge data sets for each year of data collection. These tests determined if lags between the wake-up dates of two variables were significantly different from zero. As with testing of H1, the lags calculated within the snow, aquatic statewide, and

discharge data sets contained data from gridded data sources to place lags within a broader biophysical context. Similar to the evaluation of H1, there were not enough replicates in the intensive terrestrial and aquatic networks for statistical testing of H2, and consequently, H2 was qualitatively evaluated by examining box and whisker plots of lags between variables within and among the intensive sites.

We used correlation analysis to test H3, which hypothesized that the timing of transitions and the duration of lags varied as a function of the size of the snowpack at the onset of melt (using SWE as the measurement) and winter severity (using freezing degree days (FDD) as the measurement). Cumulative freezing degrees were calculated each year for the period from December 1 to March 31 to capture the coldness of the entire winter season that preceded spring, using both the snow and the reanalysis weather data. Likewise, we determined the amount of SWE at the onset of melt using both point and gridded data sources. Our data indicate interannual and spatial variation in cumulative FDD and the amount of SWE at the onset of melt during our study period (Table 3). The southern half of New Hampshire (south of 43.90°N latitude; Wake et al., 2014b) was generally warmer and had less snow than the northern half of the state (north of 43.90°N latitude; Wake et al., 2014a). Within each region, 2012 was the mildest winter with the shallowest snowpack at the onset of melt, while 2014 was the coldest winter with the deepest snowpacks at melt onset. Thus, we experienced a range of winter coldness and snowpack conditions both in space and over time with which to test hypotheses about how changing winter conditions might impact lags within the vernal window. This pattern holds even when placed within a longer temporal context. Thirty-year climate normals from 1981 to 2010 (Anthony et al., 2010) show that 2012 was anomalously warm, 2014 anomalously cold, and 2013 close to average for both the northern and southern tiers of New Hampshire. Geographic differences in these climate normals also illustrate how our three-year sampling period captured a variety of winter climates; average winter temperatures in the northern part of New Hampshire in 2012 (the warmest sampling year) were comparable to the 30-year average for the southern half of the state.

Table 3 Snow water equivalent (SWE) at the onset of melt and cumulative freezing degree days (FDD) from the preceding winter across three study years and between the southern and northern areas of New Hampshire, USA. Values are medians of gridded snow and weather reanalysis data products for each year and area, and numbers in parentheses are the interquartile range around the medians

Area	Year	SWE (mm)	FDD
South	2012	36 (26, 46)	158 (114, 216)
	2013	63 (41, 82)	269 (197, 368)
	2014	119 (81, 142)	532 (408, 408)
North	2012	107 (100, 139)	481 (468, 522)
	2013	133 (99, 175)	687 (660, 735)
	2014	215 (157, 231)	992 (992, 1038)

We used the Kendall rank correlation test to assess the significance of relationships between certain time lags (see below) and our two independent variables (SWE at onset of melt and FDD). The Kendall analysis was applied to data from each year (2012, 2013, and 2014) and data from all three years together. The linear slope and intercept of these relationships, which are not available with Kendall analysis, were estimated using the Sen slope estimation (Sen, 1968).

We identified ten time lags for correlation analysis based on their expected or documented importance to ecosystem energy, water, solute, nutrient, and carbon flows, as well as terrestrial and aquatic biological activity (Tables 4 and 5). Lags relevant to energy flows included the time between air temperature and onset of melt transitions (lag 1) and air temperature to snow-free transition dates (lag 2), as these are indicators of shifting surface energy balance and snow melt dynamics (Betts et al., 2014). For water flows, the lag between melt onset and full canopy LAI (lag 3) was considered an indicator of the period when snow melt is the dominant hydrologic process because evapotranspiration fluxes dramatically increase when forest canopies close (Willmott & Rowe, 1985). The periods between the onset of melt and peak stream discharge (lag 4) and onset of melt and stream specific conductance (lag 5) were included as indicators of both the rate of snow melt and water flushing (water flows) and solute flux (Godsey et al., 2009). For nutrients, the lag between the onset of melt and stream temperature increase (lag 6) represented the period when soil water flow paths become more active and stream metabolism is very low, allowing nutrients to move more easily without a strong uptake demand (Pellerin et al., 2011). For carbon, the lag between the last day of snow and full canopy LAI (lag 7) was included as an indicator of the period when soil biogeochemical activity, particularly soil respiration, is active prior to vegetation C uptake (Groffman et al., 2012). Another period important for aquatic ecosystem C balance was the lag between the rise of stream temperature and full canopy LAI (lag 8), as this illustrates the period when stream metabolism is more active and stream shading is minimal (Hill et al., 2001). The lag between air temperature and stream temperature wake-up (lag 9) represented a potential asynchrony between terrestrial and aquatic biological activity, in which terrestrial organisms might become active prior or subsequent to aquatic organisms, depending on ecosystem energy flows. Finally, the lag between the rise of air temperature wake-up and full canopy LAI (lag 10) was included as an indicator of the entire vernal window period.

## Results

#### Statewide analysis

For the statewide analysis, the order of the transitions generally followed our hypothesized sequence for H1 (Fig. 3, Table S2), with the air temperature wake up occurring prior to onset of melt, and canopy closure following changes in the aquatic system. However, transitions within the aquatic system did not always follow the predicted order, with stream temperatures waking

up significantly earlier than anticipated. In addition, we observed an unexpected phenomenon in the stream specific conductance data. Although, as predicted, stream conductivity showed a large dilution that occurred subsequent to snowpack disappearance, we also observed a peak in stream specific conductance that preceded this dilution and was roughly concurrent with the onset of melt (Fig. S1 shows an example time series with a stream conductivity peak succeeded by rapid dilution).

In accordance with our second hypothesis, we observed significant lags between transitions (Table S3). However, there were some cases within each data set (snow, aquatic statewide, and discharge) in which lags did not significantly differ from zero, indicating that the timing of the transitions was essentially simultaneous. As an example, Fig. 4 shows the lags between the timing of stream temperature wake-up and relevant aquatic transitions in two study years, 2013 and 2014. These lags did not consistently exhibit the behavior that we anticipated. In 2013, onset of melt and air temperature preceded the increase in stream temperature, which was the hypothesized order; however, in 2014, the onset of melt, increase in air temperature, and increase in stream temperature happened concurrently. In addition, lags that did differ from zero were generally shortest in 2014 and longest in 2012. For example, the median lag between transitions in air temperature and forest canopy closure (i.e., the entire vernal window) was 75 days in 2012, 68 days in 2013, and 56 days in 2014 (Table S3a). Likewise, the median lags between the onset of melt and peak discharge, which are relevant for ecosystem water and solute fluxes, were 63, 24, and 17 days for 2012, 2013, and 2014, respectively (Table S3c).

### Intensive sites

Data from a southern (Fig. 5a) and a northern (Fig. 5b) intensive site suggest that neither soils nor streams always woke up in the sequence we anticipated (Table S4). As with the statewide analysis, stream conductivity showed an initial increase before reaching maximum dilution at peak discharge. In addition, many transitions within the stream occurred at the same time as transitions within the soil, which was not what we anticipated. For example, on the same day that the system became snow free, soils rapidly warmed, and soil moisture, soil specific conductance, and stream discharge reached their maximum.

Several other transitions took place out of our hypothesized order, but their relative position along the vernal window flow path was not consistent across sites. Stream temperature generally, but not always, transitioned before soil temperature (refutes H1). Instream dissolved organic matter (DOM) woke up before dissolved oxygen (DO) at the two northern sites (supports H1) but after DO at one of the southern sites (refutes H1; the other southern site had a data gap during the vernal window). This latitudinal disparity may have been related to heavy rainfall at the southern site following snow melt that flushed additional DOM into the stream and raised concentrations higher than the initial pulse from snow melt.

Because many of the transitions delineated from the intensive terrestrial-aquatic sites were simultaneous, many of the lags between transitions did not differ visually from zero. However, the period between pairs of transitions such as initial to maximum soil moisture and stream discharge to the flushing of DOM was longer in the warmer, more southern site as compared to the colder, more northern sites (Fig. 5).

Taking the statewide and intensive site analysis together, we observed synchronicity, or zero lags, between snow melt and many other transitions within the vernal window. We also saw that years with a greater snowpack, as in the statewide analysis, or sites with colder conditions, as in the intensive site data, showed a pattern of shorter lags between transitions and more transitions mapping onto the timing of snow melt. These emergent patterns suggest that the duration of lags within the vernal window may depend on antecedent snow and temperature conditions, with colder and snowier conditions leading to shorter lags.

Duration of lags as a function of winter severity and snowpack

Many of the lags relevant to ecosystem function were found to be negatively correlated to winter severity (FDD) and the amount of snow on the ground in late winter (SWE at the onset of melt) (Tables 4 and 5). Seven of ten lags were significantly, negatively related to SWE, and nine of ten lags were significantly, negatively related to FDD. The relationships sometimes varied from year-to-year, but this interannual variation was largely limited to relationships with fewer data points. For example, the lag between the onset of melt and peak discharge vs. the amount of SWE present at the onset of melt was not always significantly correlated in any given year, but a significant negative correlation emerged when years were combined.

The Kendall correlation analysis showed differences in FDD and onset SWE in explaining lag variability (Tables 4 and 5). Lags important to energy balance, aquatic biological activity, and aquatic carbon cycling were more related to FDD than SWE. Conversely, the amount of SWE at the onset of melt was generally a better predictor of lags related nutrient and solute flows.

Lags for onset of melt to canopy closure (water cycling), snow free to canopy closure (terrestrial carbon cycling), and air temperature to canopy closure (whole vernal window) were strongly related to both coldness and snowpack measures.

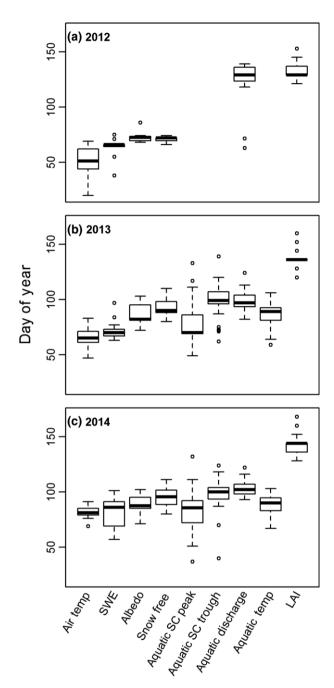
We examined Sen slope estimates to identify lags that were most sensitive to winter coldness and snowpack depth. Relationships with the steepest slopes were all strongly negative, indicating that the major time lags in the system shorten with colder and snowier winters (Fig. 6). For SWE, some of the most sensitive lags included indicators of ecosystem water flows, such as the onset of melt to peak discharge lag and the snow free to canopy closure lag. For FDD, some of the most negative lags were between air and stream temperature (impacting nutrient and carbon flows) and air temperature to the onset of melt (relevant to energy balance). The lag for the entire vernal window, as indicated by the air temperature to canopy closure lag, was very sensitive to both winter coldness and snowpack, with the lag shortening the more severe the winter.

#### Discussion

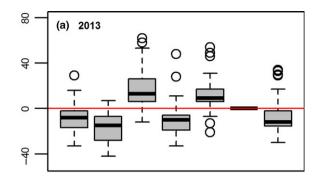
Sequence of transitions within the vernal window

Dates at which vernal transitions occurred generally agreed with our hypothesized sequence based on current understanding of spring phenology in seasonally snow covered, temperate ecosystems. Changes in the energy balance of the biophysical system, such as increases in air temperature over zero degrees, preceded the onset of melt and the disappearance of the snow-pack in accordance with fundamental snow melt physics (Wilson, 1941; Zuzel & Cox, 1975; Colbeck, 1980). Likewise, the relative dates at which air temperatures and LAI transitioned in our data set correspond with previous work showing that air and soil temperatures must warm over time before vegetation can leaf out (Baldocchi et al., 2005; Wu et al., 2013; Piao et al., 2015).

Despite this general agreement, we observed several unexpected results in the relative timing of transitions within the vernal window that did not follow our hypothesized order. One of these was the synchronicity of transitions throughout the ecosystem, which resulted in many zero lags (discussed below). We also found that transitions within the aquatic system, such as stream temperature and conductivity, did not take place subsequent to those in the snowpack and/or soils, suggesting that conditions above and directly adjacent to streams influenced aquatic systems during the vernal window as much as or more than interactions with the surrounding upland matrix.



**Fig. 3** Transition dates for the shift from winter to spring across New Hampshire for (a) 2012, (b) 2013, and (c) 2014. The order of transitions along the x-axis is set by the hypothesized sequence shown in Fig. 1 and Table 2. A vernal window that follows the hypothesized sequence would have progressively later dates moving along the x-axis. Parameters include air temperature (Air temp), snow water equivalent (SWE), albedo, the snowfree date (Snow free), aquatic specific conductance peak (Aquatic SC peak), aquatic specific conductance trough (Aquatic SC trough), aquatic discharge, aquatic temperature (Aquatic Temp), and canopy closure as indicated by leaf area index (LAI).



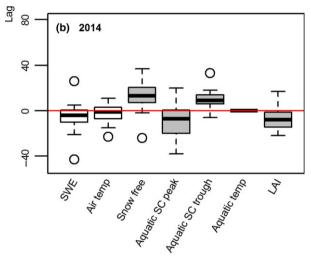


Fig. 4 Lags within the vernal window between stream temperatures and all other transitions derived from the aquatic statewide data set for (a) 2013 and (b) 2014. Data collection did not occur in 2012. The order of transitions along the x-axis is set by the hypothesized sequence shown in Fig. 1 and Table 2. Negative lags indicate that the transition for stream temperature occurred subsequent to the other transition in the lag calculation. Positive lags indicate that stream temperature transitioned prior to the other transition in the lag calculation. Lags that were not significantly different from zero appear white; those that did differ from zero are gray. Parameters include snow water equivalent (SWE), air temperature (Air temp), the snow-free date (Snow free), aquatic specific conductance peak (Aquatic SC peak), aquatic specific conductance trough (Aquatic SC trough), aquatic temperature (Aquatic temp), and canopy closure as indicated by leaf area index (LAI). [Colour figure can be viewed at wileyonlinelibrary.com]

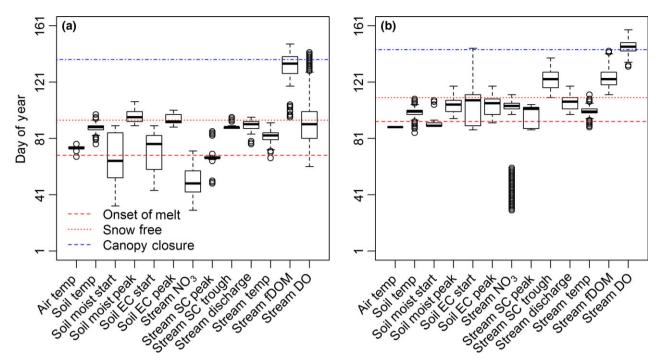
#### *Lags between transitions*

According to our conceptual model, lags between transitions represent delays in the movement of energy, water, carbon, nutrients, and solutes through an ecosystem. The synchrony we observed among several snow, soil, and stream transitions within the vernal window indicates that these transfers can be very fast. Some of these zero-length lags have been observed in other studies of spring wake-up. Molotch et al. (2009) demonstrated that initial increases in soil moisture coincided with onset of snow melt due to infiltration of meltwater into the soil matrix and Molotch et al. (2009) and Groffman et al. (2012) showed an almost instantaneous warming of soil temperatures following snowpack disappearance and the removal of the latent heat buffer that the snow provides.

In addition to zero-length lags, we also observed interannual variation in lags between pairs of transitions, both within and among ecosystem components. Many other researchers have documented year-to-year fluctuations in the timing of the onset of spring (Cayan et al., 2000; Molotch et al., 2009; White et al., 2009; Piao et al., 2015; Yue et al., 2015). However, changes in the direction of lags among onset of melt, air temperature wake-up, and stream temperature wake-up from positive to zero or vice versa were unexpected in forested ecosystems where vegetation and landscape features are relatively stable. Consequently, shifts in the magnitude and the direction of the interval between spring transitions are driven by exogenous climate controls that fluctuate across years, such as snow depth and winter coldness.

Lags between transitions vary with changes in winter coldness and snowpack

The negative relationship we observed between lag duration and antecedent snow depth and winter coldness highlights the role that ecosystem energy balance plays in driving the timing of the onset of spring. Colder winters with deep snowpacks may result in later springs due to thermal inertia in the system that must be overcome with larger energy inputs. The release of this accumulated energy accelerates transitions such as snow melt, soil warming, and the movement of water into aquatic ecosystems. When a snowpack is present, it provides a latent heat buffer between the atmosphere and terrestrial and aquatic ecosystems that absorbs and stores energy and water until the entire snowpack becomes isothermal (reaches 0 °C), ripens, and then melts rapidly. If snow is deep, then melt transfers large pulses of energy and releases water through the system that synchronizes the time at which other system variables transition. Because a deep snowpack also insulates soils and small streams against extremely cold temperatures and ice formation (Groffman et al., 2012), they require less energy to warm up and have increased hydrologic connectivity in spring, allowing for faster responses to melt. If the snowpack is shallow, it has much less thermal mass of water to contribute heat to the soil and stream, and consequently, the movement of energy and water through the system is much more incremental.



**Fig. 5** Transition dates for the shift from winter to spring within two of the intensive terrestrial—aquatic sensor sites, (a) a southern site at Thompson Farm located in southeastern, coastal New Hampshire and (b) a northern site at Hubbard Brook in the White Mountains of central New Hampshire. Horizontal lines indicating onset of melt, snow-free conditions, and canopy closure derived from gridded data sources. The order of the parameters along the *x*-axis is set by the hypothesized sequence shown in Fig. 1 and Table 2. Parameters include air temperature (Air temp), soil temperature (Soil temp), soil moisture, soil electrical conductivity (EC), stream nitrate (stream NO<sub>3</sub>), stream specific conductance (SC), stream temperature (Stream temp), stream fluorescent dissolved organic matter (fDOM), and stream dissolved oxygen (DO). [Colour figure can be viewed at wileyonlinelibrary.com]

The extent of winter coldness also plays a role in determining the duration of lags that occur within the vernal window. Winters with more freezing degree days are more likely to have precipitation fall as snow, and the resulting snowpack will require more thermal energy to bring the snow to the melting point. This creates a large latent heat buffer that tends to synchronize transitions within the vernal window. In a low-snow or snow-free year, colder temperatures result in deep freeze of the soils, which requires a larger amount of energy to warm as compared to unfrozen soils under deep snowpacks (e.g., NRCS, 2004). A more gradual wake-up ensues in response to increased energy inputs needed to warm the soil. When soils are frozen, both liquid precipitation and snow melt can run off via overland flow from upland to aquatic ecosystems (e.g., NRCS, 2004), resulting in smaller pulses of water than would occur with melting of a substantial snowpack. In warm years with no snow, the system lacks a latent heat buffer that either a snowpack or a frozen soil provides, resulting in lower thermal inertia and more gradual changes in the ecosystem as it transitions from winter to spring.

The strong roles that winter coldness and snowpack played in driving the duration of lags within the vernal window suggest a new conceptual model (Fig. 7) that replaces our original depiction of the spring wake-up period (Fig. 1). This new conceptual model highlights ecosystem energy balance as the dominant control on the timing of transitions at the start of spring, such that changes in the energy balance result in simultaneous snowpack, terrestrial physical, and aquatic physical transitions, which are followed by biological transitions in soils and streams. The model emphasizes the synchronicity of system transitions at the start of spring that result from a strong latent heat buffer and greater thermal inertia that a deep snowpack and/or a cold winter provides.

The results of our correlation analysis also demonstrated the roles that winter coldness and snowpack played in driving the lags between pairs of transitions that are important to ecosystem function. We show that the vertical flux of energy was dominant in initiating the springtime response, where the coldness of the winter is a strong predictor of the lags early in the system and of direct warming of the aquatic component. In contrast, the lateral flux of water, as indicated by snowpack volume, was more significantly correlated with later responses to springtime warming. Other studies have shown the importance of either cold temperatures

Ecosystem function	Dependent lag	Tau and <i>P</i> value 2012	Tau and <i>P</i> value 2013	Tau and <i>P</i> value 2014	Tau and <i>P</i> value all years	Sen slope estimate all years (days/SWE)	Sen intercept estimate all years (days)
1. Energy	Air Temperature (T) to Snow Water Equivalent (SWE)	0.200 (0.707)	-0.333 (0.251)	0.138 (0.848)	-0.184 (0.262)	-0.069	9.1
2. Energy	Air T to Snow Free	0.033 (0.452)	-0.222(0.466)	-1.000 (0.027)	0.053 (0.770)	0.042	11.1
3. Water	SWE to Leaf Area Index (LAI)	-0.185 (0.003)	-0.477 (<0.001)	-0.457 (<0.001)	-0.421 (<0.001)	-0.113	69.1
4. Water, solute	SWE to Discharge	-0.469 (0.024)	-0.260 (0.197)	-0.271 (0.180)	-0.332 (0.002)	-0.170	43.6
5. Water, solute	SWE to Stream Conductivity Peak	NA	-0.291 (0.003)	0.116 (0.278)	-0.157 (0.025)	-0.042	2.7
6. Nutrient	SWE to Stream T	NA	-0.308 (0.003)	-0.331 (0.013)	-0.372 (<0.001)	-0.100	18.2
7. Carbon	Snow Free to LAI	-0.359 (<0.001)	-0.492 (<0.001)	-0.144 (0.019)	-0.400 (<0.001)	-0.167	56.3
8. Carbon	Stream T to LAI	NA	-0.314 (0.003)	-0.191 (0.170)	-0.157 (0.053)	-0.040	53.7
9. Aquatic biology	Air T to Stream T	NA	-0.219 (0.031)	-0.148 (0.267)	-0.302 (<0.001)	-0.094	20.7
10. Vernal window	Air T to LAI	-0.272 (<0.001)	-0.344 (<0.001)	-0.409 (<0.001)	-0.474 (<0.001)	-0.197	85.7

**Table 5** Kendall correlation and Sen slope analyses between selected lags in the vernal window and winter freezing degree days (FDD). Significant results (P < 0.05) in bold

Ecosystem function	Dependent Lag	Tau and <i>P</i> value 2012	Tau and <i>P</i> value 2013	Tau and <i>P</i> value 2014	Tau and <i>P</i> value all years	Sen slope estimate all years (days/FDD)	Sen intercept estimate all years (days)
1. Energy	Air Temperature (T) to Snow Water Equivalent (SWE)	-0.592 (0.036)	-0.556 (0.048)	0.296 (0.279)	-0.366 (0.007)	-0.035	18.6
2. Energy	Air T to Snow Free	-0.556 (0.048)	-0.667 (0.016)	0.071 (0.902)	-0.346 (0.014)	-0.028	35.4
3. Water	SWE to Leaf Area Index (LAI)	0.141 (0.027)	-0.353 (<0.001)	-0.414 (<0.001)	-0.386 (<0.001)	-0.026	69.9
4. Water, solute	SWE to Discharge	-0.034 (0.912)	-0.010 (1.000)	0.010 (1.000)	-0.260 (0.014)	-0.042	45.1
5. Water, solute	SWE to Stream Conductivity Peak	NA	-0.218 (0.028)	0.161 (0.145)	-0.101 (0.157)	-0.009	2.2
6. Nutrient	SWE to Stream T	NA	-0.013 (0.907)	-0.314 (0.021)	-0.172 (0.030)	-0.011	12.2
7. Carbon	Snow Free to LAI	-0.349 (<0.001)	-0.572 (<0.001)	-0.216 (<0.001)	-0.475 (<0.001)	-0.051	62.3
8. Carbon	Stream T to LAI	NA	-0.428 (<0.001)	-0.233 (0.101)	-0.216 (0.009)	-0.015	56.9
9. Aquatic biology	Air T to Stream T	NA	-0.500 (<0.001)	-0.253 (0.061)	-0.474 (<0.001)	-0.039	31.9
10. Vernal window	Air T to LAI	-0.678 (<0.001)	-0.742 (<0.001)	-0.557 (<0.001)	-0.715 (<0.001)	-0.069	95.9

or snowpack as determinants of the onset of spring (Wang *et al.*, 2013; Fu *et al.*, 2014). Few, if any, have examined these drivers simultaneously as we have here. In addition, the strong role that the snowpack

played in driving lags in the vernal window period suggests that future research should more explicitly consider snowpack dynamics as a driver of vegetation phenology and the timing of spring (Wang *et al.*, 2013).

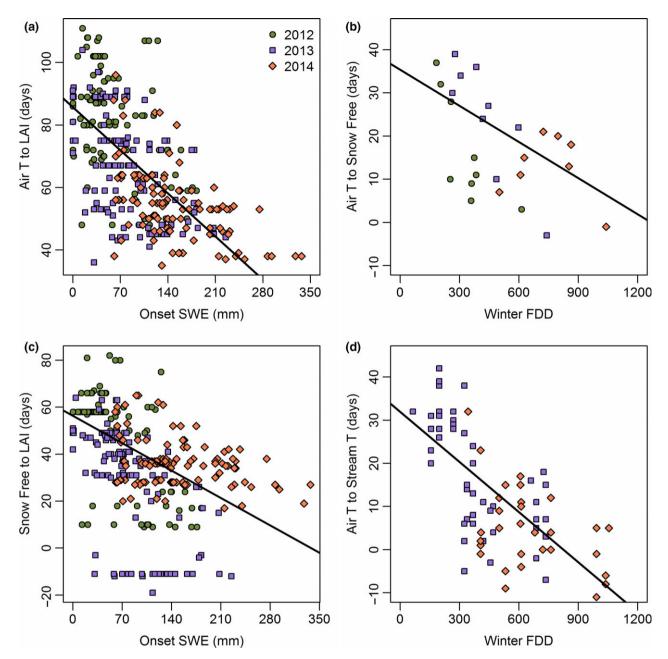


Fig. 6 Selected lags of transitions within the vernal window vs. size of snowpack (snow water equivalent, or SWE, at the onset of melt, left panels) and coldness of the winter (freezing degree days, or FDD, right panels). Symbols vary according to year. Black lines represent the model of the relationship for all years combined, calculated using the Sen slope algorithm. Selected lags include (a) air temperature (Air T) to canopy closure as indicated by leaf area index (LAI), (b) Air T to the snow-free date (Snow Free), (c) Snow Free to LAI, and (d) Air T to stream temperature (Stream T). [Colour figure can be viewed at wileyonlinelibrary.com]

Implications for ecosystem function with climate change

*Energy balance.* The high reflectivity of snow results in a net cooling effect at the surface relative to snow-free conditions. Our analysis indicated that snow melt as indicated by changes in SWE and depth were most sensitive to winter coldness. Moving toward warmer winters (Hayhoe *et al.*, 2007) and earlier spring onset (Labe

et al., 2016) in the future, we anticipate longer lags between when air temperature increases and the snow-pack responds, due in part to the fact that the transition in air temperature will happen earlier in the year when there is less incoming solar radiation. However, even though the lag between the increase in air temperature and the snow-free date may be longer, we will still expect snow-free days to occur earlier in the year,

exposing the underlying ground and resulting in more overall energy absorption into the system as compared to colder years.

Water availability. Our correlation analysis showed that lags relevant to ecosystem water cycling were significantly, negatively related to the amount of SWE present at the onset of melt. A longer lag between when the system becomes snow free and when the canopy closes could allow more water to flow more efficiently from soils to streams and rivers, due to minimal evapotranspiration until LAI reaches its maximum. Alternatively, excess soil moisture during a longer vernal window may enhance groundwater recharge (Rodhe, 1998), instead of producing more runoff.

Nitrogen cycling. We identified the lag between the onset of melt and stream temperature increase as the period when soil water flow paths become more active and stream metabolism is very low, allowing nutrients to move downstream more easily without a strong uptake demand. The strongly negative influence that the amount of SWE had on this lag suggests that in snowier winters, a large pulse of NO<sub>3</sub><sup>-</sup> might move from soils to streams when temperatures are too low and/or flows are too high to allow for biological uptake and transformation. Data from the intensive sites illustrate this potential dynamic, such that the transition date for NO<sub>3</sub><sup>-</sup> at the two northern sites coincided with peak discharge while the lags between the NO<sub>3</sub><sup>-</sup> and discharge transitions at the two southern sites was 50-70 days.

Ecosystem carbon balance. The duration of lags within the vernal window could alter net C balance by impacting the timing at which respiration and photosynthesis occur both in terrestrial and aquatic ecosystems. We identified the lag between snow-free date and canopy closure as indicating a period when soil respiration is active prior to net ecosystem productivity (Groffman et al., 2012). We observed rapid soil warming following snowpack disappearance that should promote both root and microbial respiration. Thus, a prolonged period between snow-free conditions and canopy leaf out that we expect to see more frequently in a future with shallower snowpacks (e.g., Hayhoe et al., 2007) and earlier spring onset (Labe et al., 2016) could increase terrestrial C loss in a mild spring. Paradoxically, longer lags between stream temperature and canopy closure transitions in the aquatic system, which we observed with fewer cumulative FDD, might result in increased C uptake because this period would allow aquatic primary producers to be active given relatively warm temperatures and minimal shading.

Climate forcing. The net result of changes in energy, water, nitrogen, and carbon balances may be a modification of the climate forcing by the vernal land surface. In terms of energy balance, earlier spring snow melt should increase soil heat storage due to a longer lag between the disappearance of a high albedo snowpack and the re-emergence of leaves that, through transpiration, drive latent heat fluxes. Increased soil moisture during a longer vernal window might amplify this dynamic by enhancing soil heat capacity, resulting in greater net soil energy storage and reduced energy flux to the atmosphere. Regarding carbon, earlier snow melt relative to the ramping up of photosynthesis also suggests that a longer vernal window will impact the extent to which terrestrial ecosystems take up or release CO<sub>2</sub> (Richardson et al., 2009, 2010; Galvagno et al., 2013; Keenan et al., 2014; Winchell et al., 2016). Emissions of non-CO2 greenhouse gases such as N2O might also change with a lengthening vernal window in which shifts in the timing of snow melt and photosynthesis alter conditions driving N2O flux, such as soil moisture and soil nitrogen availability (Blankenship & Hart, 2012; Morse et al., 2015). While net climate forcing was not one of the variables in our analysis, we propose that synergistic changes in energy, water, nutrient, and carbon flows during the vernal window could result in a perturbation to landscape-climate feedbacks, many of

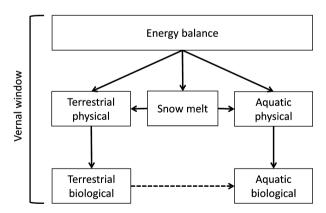


Fig. 7 Revised conceptual model of the system response to changing conditions from winter to the growing season. Compare with initial hypothesized model shown in Fig. 1. Rather than a cascading response that propagates across the ecosystem, increasing energy input from snow melt initiates a simultaneous response. That response occurs independently and concurrently across the snow, terrestrial, and aquatic systems, with some lags between physical and biological transitions. As in Fig. 1, transitions are the boxes, while lags between transitions are represented by arrows.

which are poorly understood and require additional research (Richardson *et al.*, 2013).

#### The vernal window

Our interpretation of the vernal window was based on three years of data collected across the forested ecosystems of New Hampshire, USA. This conceptual framework needs to be tested with long-term data sets and across a larger geographic scope. However, the three years we sampled represented a broad range of climatic conditions. Thus, our results highlight a realistic set of consequences that could accompany future changes in the timing of the transition from winter to spring. Our findings suggest that winter air temperatures and snowpack characteristics at the time of melt drive the duration of lags within the vernal window period. Our new conceptual model highlights the role that the snowpack plays as a latent heat buffer, as is evident in the synchrony of transitions when a substantial snowpack is present vs. the long lags between transitions when a snowpack is absent. This synchronicity is critical to ecosystem energy, water, nutrient, and carbon flows - all of which could be altered with climate change. Shifts in ecosystem processes and properties during the vernal window may also interact to alter the climate forcing of the vernal landscape, resulting in landscape-climate feedbacks that are unique to the spring wake-up period.

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#### **Supporting Information**

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

- **Table S1.** Latitude, longitude, and elevation for point data sources included in the vernal window analysis.
- **Table S2.** (a–c) Significant differences between transition dates in the statewide analysis of H1.
- **Table S3.** (a–c) Calculated lags and *p*-values of significant differences between lags within each statewide data set.
- **Table S4.** Estimated transition dates for 21 simultaneous, continuous measurements of biogeochemical variables in four coupled terrestrial-aquatic intensive sites.
- **Figure S1.** Example time series for each variable included in the analysis of the vernal window with calculated transition dates plotted onto that time series, as well as histograms showing the frequencies of wake-up dates selected over 1000 iterations.