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Long-Term Integrated Studies Show Complex and Surprising Effects of Climate Change in the Northern Hardwood Forest

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Evaluations of the local effects of global change are often confounded by the interactions of natural and anthropogenic factors that overshadow the effects of climate changes on ecosystems. Long-term watershed and natural elevation gradient studies at the Hubbard Brook Experimental Forest and in the surrounding region show surprising results demonstrating the effects of climate change on hydrologic variables (e.g., evapotranspiration, stream ow, soil moisture); the importance of changes in phenology on water, carbon, and nitrogen uxes during critical seasonal transition periods; winter climate change effects on plant and animal community composition and ecosystem services; and the effects of anthropogenic disturbances and land-use history on plant community composition. These studies highlight the value of long-term integrated research for assessments of the subtle effects of changing climate on complex ecosystems.

Keywords: climate change, forests, long-term studies, northeastern United States, winter

A dominant approach in climate change research has been to focus on the effects of changes in temperature and precipitation on broadscale ecosystem properties over large areas and long periods. This body of research suggests that climate change will substantially alter the distribution of species and the function of ecosystems (e.g., Iverson and Prasad 2001), with important effects on ecosystem services. These analyses are based on well-described effects of temperature and precipitation on the distribution and activity of organisms. However, climate change is playing out over the complex and dynamic hydrobiogeological structure of the landscape that is, the intertwined patterns of soils, vegetation, and hydrologic owpaths, with a spatially variable history of land use and a wide range of current human activities and concurrent environmental changes. The climate effects on ecosystem structure and function may be modi ed by interactions with these patterns and histories over a range of time scales. We assert that a key approach to

unraveling this daunting complexity is long-term studies, including those in which natural elevation gradients are exploited, as a foundation for detailed studies of critical and often unexpected climate-induced changes in forest structure and function.

In this article, results from the Hubbard Brook Experimental Forest (HBEF) and the surrounding region are used to illustrate how long-term studies can serve as a foundation for addressing the complex interactions that ultimately determine the effects of climate change on ecosystems. We combine data from long-term (50-year) measurements of multiple aspects of climate and ecosystem structure and function to highlight important but poorly studied interactions that could be critical determinants of the responses of plant and animal communities, uxes of water, element dynamics, and services in northern hardwood forest ecosystems. Our objective is to demonstrate how a combination of long-term and in-depth measurements facilitates

the understanding of the interplay between climate and forest ecosystem dynamics and how this interplay produces unanticipated and important new results.

In the sections below, we first present basic information on changing climate at the HBEF and show how this change acts on a hydrobiogeological template in ways that alter key hydrologic variables (e.g., evapotranspiration, stream flow, soil moisture) that influence multiple aspects of ecosystem structure and function. Climate change is also interacting with a variety of temporally dynamic ecosystem processes, and we describe how changes in the phenology of vegetation interact with climate change to affect fluxes of water, carbon, and nitrogen in the transitions between seasons. Temporal complexities in ecosystem processes are also highlighted by a discussion of unexpected effects of climate change in winter, which has long been considered to be a dormant season but has recently been shown to be functionally important and to have legacy effects during the growing season (Campbell et al. 2005). We end with a description of how the complex expression of climate change over landscape (approximately 3000 hectares [ha]) and regional (100,000 square kilometers) scales and over 50 300-year time frames influences plant community composition and likely future ecotone shifts in response to broad changes in climate zones (Iverson and Prasad 2001, Mohan et al. 2009).

The HBEF was established by the US Department of Agriculture Forest Service in 1955 as a center for hydrologic research in New England. The Hubbard Brook Ecosystem Study (HBES) originated in 1960, centered on the idea of the small-watershed approach to studying element fluxes and cycling (Likens and Bormann 1995). The site has been a component of the US National Science Foundation's Long Term Ecological Research (LTER) Network since 1988. The long-term studies in the HBES have maintained a balance between the original research interests (e.g., air pollution, land disturbance) and new foci, such as climate change, that have emerged in recent decades. Maintaining this balance is facilitated by ongoing scientific peer-review cycles, especially those associated with the LTER Network, and an open governance structure that encourages the participation of new investigators and the incorporation of new research ideas (Groffman et al. 2004).

The 3037-ha Hubbard Brook Valley is located in the White Mountain National Forest, in New Hampshire. The climate is humid continental, with short, cool summers and long, cold winters. The mean air temperature (measured between 1955 and 2000) is 19 degrees Celsius (oC) in July and 9oC in January (Campbell et al. 2007). The annual precipitation averages approximately 140 centimeters (cm), and a continuous snowpack usually develops early each winter to a depth of approximately 1.5 meters (Campbell et al. 2007). Vegetation is dominated by northern hardwood forests (e.g., American beech [Fagus grandifolia], sugar maple [Acer saccharum], yellow birch [Betula alleghaniensis]) that grade into red spruce (Picea rubens) and balsam fir

(Abies balsamea) along a dynamic ecotone at higher elevations (Schwarz et al. 2003). Soils are 75 100 cm deep, acidic (pH 4.0 in the surface organic horizons) typic and aquic haplorthods developed from unsorted basal tills. The HBEF was subjected to logging from 1880 to 1920 and then a salvage logging project following a hurricane in 1938. Grafton County, in which the HBEF is located, has a diverse history of agricultural activities beginning in the late eighteenth century, peaking in the 1860s, followed by almost complete abandonment of agricultural activities by the mid-twentieth century.

Climate change effects on the hydrobiogeological template that underlies the structure and function of the northern hardwood forest ecosystem

The climate of the HBEF has changed over the last half century. At the four weather stations with the longest records (43 52 years), the average annual air temperature has increased by 0.17oC 0.29oC per decade, with more marked warming in winter than in summer (Campbell et al. 2007, Hamburg et al. 2012). These local trends in air temperature are characteristic of the region and are expected to continue into the future, with projected increases of 2.1oC 5.3oC by 2100 (Hayhoe et al. 2007, Huntington et al. 2009). Precipitation volume has also increased at the HBEF and is indicative of regional trends. The long-term average annual precipitation ranges from 131 to 149 cm across the stations within the HBEF and has increased by 3.5 6.7 cm per decade, or 13% 28% over 50 years (Campbell et al. 2007). The trends in precipitation at the rain gauges with the longest records are stronger because of the influence of a protracted drought in the mid-1960s.

Winter precipitation has changed less than precipitation in other seasons, which, when it is combined with warmer winter air temperatures, has led to significant reductions in snowpack accumulation. Long-term (since 1959) weekly measurements of snow depth and snow water equivalent indicate that the maximum annual snowpack depth has declined by 4.8 cm per decade (1.4 cm snow water equivalent), and the number of days with snow cover has declined by 3.9 days per decade (Campbell et al. 2010). The annual and winter precipitation are projected to increase by 7% 14% and 12% 30%, respectively, by 2100, whereas summer precipitation is expected to show little change (Campbell et al. 2009). The climate projections for the northeastern United States are based on regionally downscaled, coupled atmosphere ocean general-circulation models that are driven by scenarios describing how population, technology, and energy use might develop in the future (Hayhoe et al. 2007).

Snowpack decline and precipitation increases have, in turn, influenced stream flow. Measurements of daily streamflow from the gauged reference watersheds at the HBEF since 1956 show that snowmelt-induced peak flows in spring have declined (Campbell et al. 2011) and have occurred earlier (Hamburg et al. 2012). In contrast, both winter and summer stream flow have increased. In winter, the increase is due to

reduced storage of precipitation in the snowpack, whereas in summer (typically a low-flow season), the increase is due to increases in precipitation and concomitant declines in evapotranspiration, as is described below. The increase in summer streamflow at the HBEF may be beneficial to some aquatic organisms, such as brook trout, whose upstream movement is limited by physical obstructions during low flows (Warren et al. 2008). The increase may have negative effects on nitrogen uptake or retention by streams, which is strongly flow dependent.

Interestingly, evapotranspiration, when measured indirectly as the difference between annual precipitation and annual streamflow, has shown slight but significant declines over the period of record beginning in 1959 (figure 1a; Campbell et al. 2011). The cause of the decline in evapotranspiration is not known but probably reflects decreases in transpirational water loss by vegetation that result from changes in vegetation composition, structure, or productivity or from possible reductions in stomatal conductance owing to increasing atmospheric carbon dioxide concentrations. Also probably influencing this trend are reductions in evaporative demand from the atmosphere driven by declines in solar radiation, vapor pressure deficit, and wind speed that are occurring at the HBEF as they are elsewhere (Roderick et al. 2009).

Changes in evapotranspiration and precipitation have effects on soil moisture. Although changes in soil moisture have clear consequences for ecological processes, the future direction of change is not well established. Although historical observations (since 1959) from the HBEF suggest that declines in evapotranspiration and increases in precipitation have led to increases in soil moisture (figure 1b), projections of future change from models indicate that soil moisture may decline because of increases in transpiration associated with enhanced net primary productivity in a warmer, wetter climate (Campbell et al. 2009, Huntington et al. 2009). These projected changes are highly uncertain, however, and indicate the need for continued monitoring and mechanistic studies (e.g., of carbon-dioxide-induced changes in stomatal conductance) in order to develop a better predictive capability for this key driver of climate change impacts on ecosystems. Moreover, soil moisture is not influenced by climate alone; its spatial variation is strongly controlled by the physical effects of geomorphology and soil texture. Therefore, changes in climate are superimposed on a geologic template that mediates the effects of climatic drivers on ecological processes.

Insights into the potential structural and functional ecosystem changes arising from changes in soil moisture and temperature can also be gained by exploiting the natural elevation gradient that creates a difference of approximately 2oC in mean annual temperatures between low- and high-elevation locations at the HBEF that show few differences in soil and vegetation types (Campbell et al. 2007). Observed differences in soil moisture along this gradient are large enough to affect the abundance, composition, spatial distribution, and dynamics of soil biota, including heterotrophs such as salamanders, insects, and snails (Rodenhouse et al. 2009). Hydrologic and gaseous nitrogen losses, as well as soil microbial processes (e.g., mineralization, nitrification) that increase nitrogen availability to plants have also been shown to be positively correlated with soil moisture at the HBEF (Groffman et al. 2009). Therefore, if drier soil conditions result from continued climatic warming, nitrogen availability to vegetation may decrease at the HBEF, which would exacerbate the nitrogen limitation of productivity but would decrease the potential for nitrogen saturation and losses to the environment. Greenhouse gas fluxes are also affected, with lower production of nitrous oxide and increased consumption of methane with lower levels of
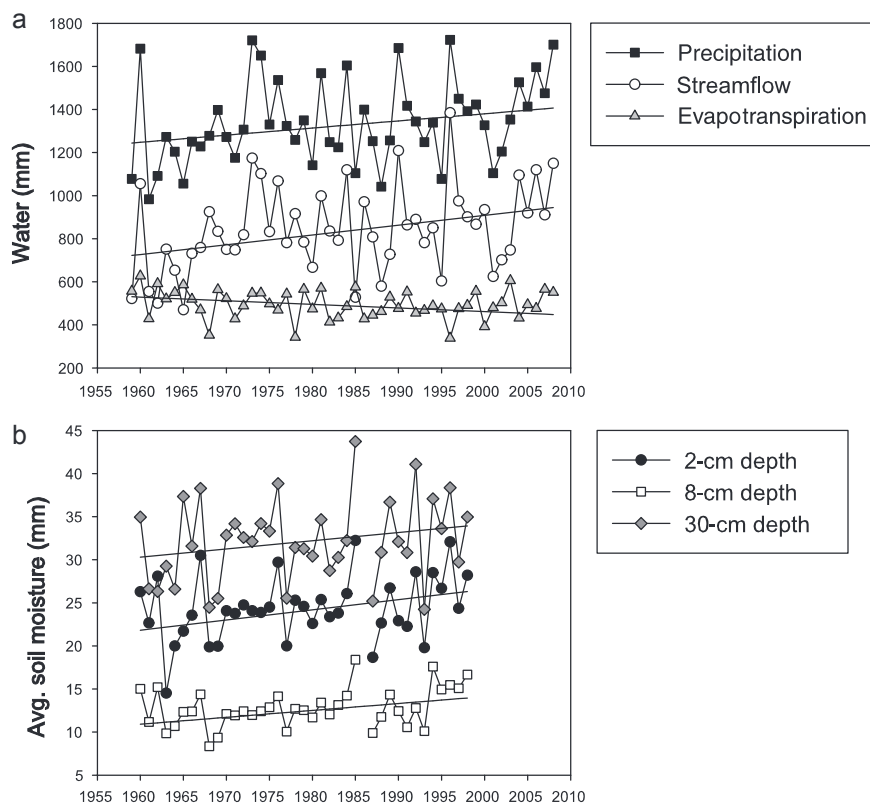

Figure 1. Changes in precipitation, streamflow, and evapotranspiration (a) and soil moisture at three depths (b) in the hydrologic reference watershed at the Hubbard Brook Experimental Forest, New Hampshire. Abbreviations: Avg., average; cm, centimeters; mm, millimeters.

soil moisture (Groffman et al. 2009). Soil moisture can also have a substantial effect on sulfur dynamics. For example, with decreasing atmospheric sulfur deposition, annual discrepancies in the watershed mass balances of sulfur are increasingly regulated by watershed moisture, because high-moisture soil conditions stimulate the net mineralization of soil sulfur pools (Mitchell and Likens 2011).

Life on the edges: Climate change amplifies temporal asynchronies between plant and soil microbial processes

A particularly intriguing aspect of climate change is the lengthening of growing seasons: Spring is advancing and fall is retreating (Huntington et al. 2009, Ibáñez et al. 2010). In the spring, the onset of the growing season in northern latitudes is heralded by a complex suite of environmental drivers, including a lengthening of the photoperiod; warming of the air and soil; shifts in precipitation from snow to rain; melting of the snowpack; thawing of surface soils; increases in available soil water; and, ultimately, budburst and leaf development (Jeong et al. 2012). The complete process of canopy expansion in spring may take several weeks in northern hardwood forest ecosystems.

Previous studies have addressed the asynchrony in the early spring when the amount of microbial mineralization of organic matter and solute transport through soil may be substantial but nutrient uptake by roots and movement to developing aboveground canopies may be minimal (Muller and Bormann 1976). Nutrient immobilization by microbes and uptake by spring ephemerals and understory vegetation can retard the loss of nutrients during this early spring period (Muller and Bormann 1976, Zak et al. 1990). Although it is now widely recognized that many belowground biological processes such as nutrient mineralization and immobilization continue under the snowpack and in soils with temperatures slightly above freezing, the rates of these processes are, in general, relatively low in winter (Brooks et al. 2011). Rapid biological activity is thought to commence when soil temperatures reach or exceed 4°C. The advance in spring snowmelt and warming air temperatures with climate change result in soil temperatures reaching biologically favorable conditions at earlier dates as well. It is not clear, however, whether the advance in soil warming is or will continue to be synchronous with advances in aboveground plant phenology (Polgar and Primack 2011). If changes in soil warming and plant phenology are not synchronous, there is the potential for greater decoupling of belowground microbial activity and the onset of rapid plant nutrient and water uptake that could lead to an increase in nutrient losses from the ecosystem.

At the HBEF, the snow-free period has increased by approximately 20 days over the last half century (Campbell et al. 2010). Green canopy duration has increased by approximately 10 days (Richardson et al. 2006), and the timing of the last measurable snowpack (around 13 days), the date of the last frost (about 8 days), and the timing of leaf expansion

(approximately 8 days) are earlier than they were in the mid-1950s (Richardson et al. 2006, Hamburg et al. 2012). In the fall, the dates of the first frost and the first measurable snowpack have been delayed by approximately 10 and 8 days, respectively (Hamburg et al. 2012). These observations illustrate the marked changes that have occurred in the physical environment in the spring and fall seasons, which may exacerbate existing seasonal asynchronies between microbial activity and plant uptake.

A closer examination of soil temperature data coupled with detailed phenological studies provides a new perspective on changes in spring asynchrony. Continuously recorded (hourly) soil temperature data are available at four northern hardwood Soil Climate Analysis Network sites—two in New Hampshire (including HBEF) and two in Vermont—for the period of 2002–2011. Data for all four sites and nine full years of record indicate a rapid increase of up to 8°C in surface soil temperature within 48 hours in early spring, usually occurring immediately after the snowpack melts completely (as is shown in figure 2 for a midelevation site measured in 2003). The likely cause of this sudden increase in soil temperature is the abrupt decrease in surface albedo in response to the loss of the reflective snowpack and exposure of dark soils to solar radiation unhindered by the forest canopy in these deciduous forest sites. This rapid and abrupt spike in soil temperature probably triggers immediate increases in biological activity (Campbell et al. 2005) and may serve as an index marking the onset of spring soil conditions under deciduous canopies, similar to the use of the timing of ice-out as an indicator of dramatic changes in the physical environment of lakes (Magnuson et al. 2000).

At the HBEF, discrete measurements of soil temperature and snowpack depth dating back to 1956 allow us to reconstruct the approximate timing of this soil temperature trigger in early spring (see figure 2b). For this analysis, time-series data were evaluated using the nonparametric Mann–Kendall test for trends. Prior to this analysis, the autocorrelation function test was used to ensure that the data met the assumption of serial independence. Trend lines were fitted by calculating the median slope of all the possible pairs in the data set. These records suggest that the date of snowmelt and the rapid increase in soil warming has advanced by 14.3 days over the period of record (1956–2010), or an average of 2.6 days per decade. Reconstructions of the concurrent trends in leaf phenology following Richardson and colleagues (2006) show that the timing of nearly complete canopy expansion for sugar maple, one of the dominant tree species at the site, advanced by only 6 days during the same period, or 1.1 days per decade. These data suggest that the period during which belowground temperatures are most conducive to biological activity (i.e., higher than 4°C) but the overstory vegetation is not maximally transpiring and taking up water and nutrients has increased by approximately 8 days over the past half century. This lengthening gap between belowground and canopy activity ought to elevate water and nutrient availability beyond plant uptake
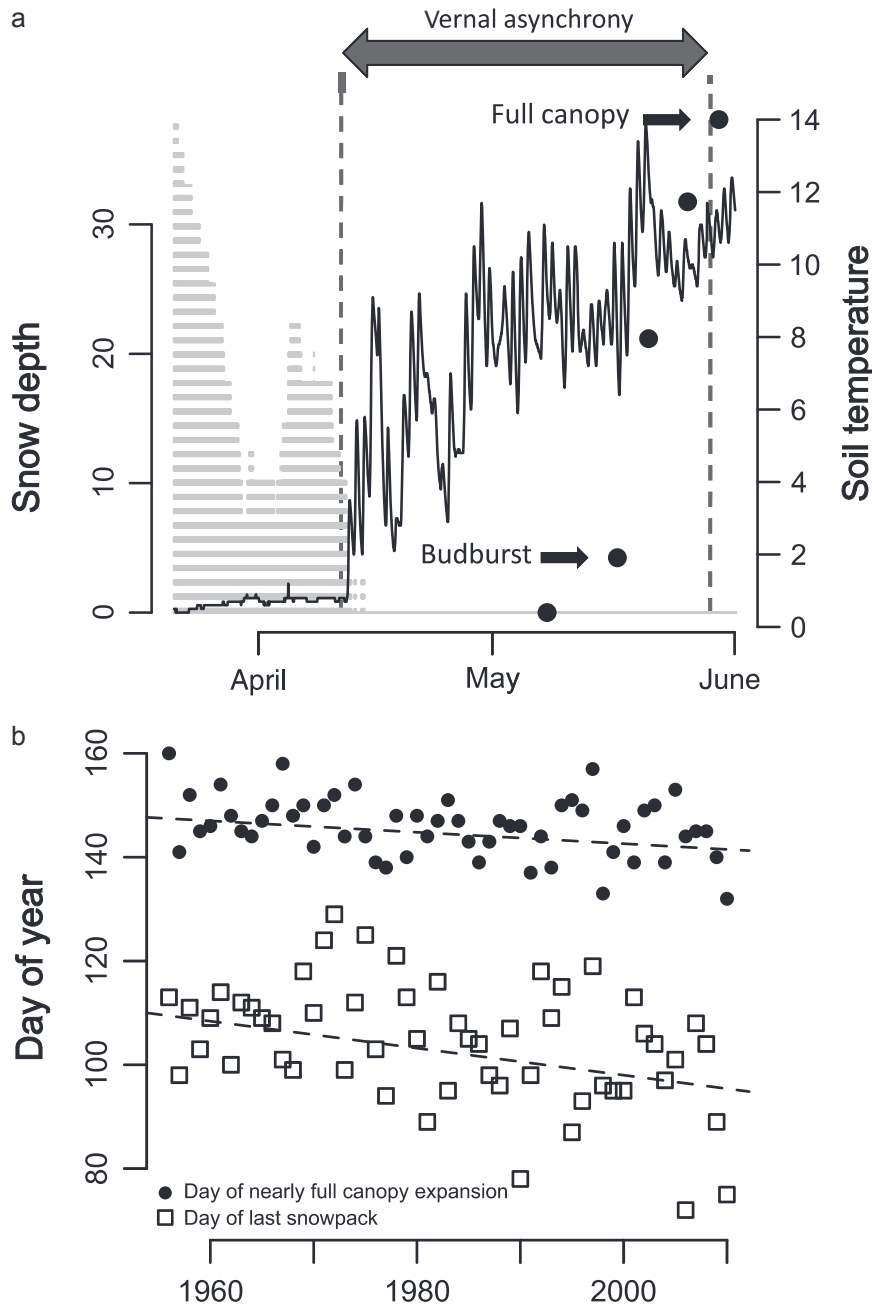
a

b

capacities and could exacerbate nutrient leaching. Further studies are needed to evaluate the impacts of this vernal asynchrony on above- and below-ground plant and microbial dynamics, carbon and nutrient retention, and plant growth in north temperate forest ecosystems.

These climate-change-driven seasonal asynchronies may be enhanced regionally if deciduous cover increases at the expense of conifer cover, as is expected with climate change in northeastern North America (Mohan et al 2009). For example, spring snowmelt is earlier in deciduous than in coniferous forests because of radiation absorption and re ection by the evergreen canopy; therefore, soil warming is delayed to a time when air temperature is generally higher. Moreover, the evergreen canopy, responding directly to increasing soil and air temperatures (Schwarz et al. 1997), demands water and nutrients earlier than the deciduous forest does, which thereby reduces the potential for asynchrony. Therefore, the spatial extent of the seasonal decoupling of water, carbon, and nitrogen cycles is likely to be larger if conifer abundance decreases across the region.

More surprises in winter

The well-documented past and projected changes in the duration and depth of the winter snowpack in northern forests (Hayhoe et al. 2007, Campbell et al. 2010) have stimulated recent interest in winter ecology, biogeochemistry, and trophic interactions in northern forest ecosystems (Campbell et al. 2005). There has, however, been less attention focused on potential changes in tree species composition caused by both limits in tolerance to winter climate change and shifts in competitive outcomes (Kreyling 2010) and on the impacts on human activities (e.g., logging, recreation, fall foliage viewing, maple syrup production, the potential lengthening of the spring mud season).

Winter biogeochemistry studies at the HBEF have built on the long-term snow cover record and have included analyses of the effects of soil-freezing events caused by low snow cover on

Figure 2. An example of (a) the relationship between the loss of snowpack (snow depth, in centimeters [cm]), soil temperature (in degrees Celsius), and spring leaf phenology and (b) changes in the modeled day of nearly complete canopy expansion and last snowpack at a middle elevation site in the Hubbard Brook Experimental Forest. In panel (a), data from 2003 show how the disappearance of snowpack (shown by the horizontal shading) coincides with an abrupt increase in soil temperature at 4 cm (the solid line). The closed circles represent spring leaf phenology, and the arrow denotes the period of vernal asynchrony (see the text) that has increased over time. Spring canopy expansion (the closed circles) is becoming earlier, at a rate of 1.1 days per decade (p = .02), whereas the day of last snowpack (the open squares) is becoming earlier at a rate of 2.6 days per decade (p = .004); therefore, the length of the period between snowmelt and full canopy development has increased by over 8 days in 55 years.

watershed nitrate exports (Mitchell et al. 1996, Fitzhugh et al. 2003), plot manipulation studies of snow cover and soil freezing (Groffman et al. 2001, 2010, Templer et al. 2012), and studies of winter processes along the natural elevation gradient at the site (Groffman et al. 2009). These studies have shown that soil-freezing events can lead to significant increases in nitrate, phosphate, and base cation losses (Fitzhugh et al. 2001) that appear to be driven by increases in the root mortality of some tree species, such as sugar maple (Tierney et al. 2001, Cleavitt et al. 2008). However, the response to soil-freezing events varies that is, there are not always marked increases in nitrate losses (Hentschel et al. 2009, Groffman et al. 2010). This variation in nitrate loss may be driven by variation in the response of dissolved organic carbon dynamics to soil freezing. In some cases, soil freezing mobilized dissolved organic carbon, which stimulates immobilization or denitrification, which, in turn, prevents a nitrogen response (Groffman et al. 2010). Moreover, the future trajectory of soil frost is also uncertain. Although a decrease in snow cover certainly increases the vulnerability of the ecosystem to soil-freezing events, at the same time, warming air temperatures decrease the potential for soil freezing (Campbell et al. 2010).

Evaluating the long-term effects of winter climate change on plant communities is particularly challenging. A reduction in the depth or duration of the winter snowpack could alter the reproduction and survivorship of some tree species, which could lead to changes in forest composition. As was mentioned above, sugar maple roots appear to be particularly susceptible to soil-freezing damage, which has contributed to episodes of sugar maple decline in northeastern North America (Auclair et al. 2010). Yellow birch benefits from enhanced seed dispersal on snow (Greene and Johnson 1997), and therefore, the regenerative success

of this species could also be diminished if the snowpack is reduced.

In addition to plants' physiological responses to climate shifts, animals may generate novel stresses on plant communities. For example, a decreased depth of snowpack can generate increased stress on young trees from foraging ungulates, such as moose (Alces alces; Faison et al. 2010). Either competitive outcomes or regeneration success could be affected by these compounded stresses (Crête et al. 2001), which would result in changes in forest composition that would not be predicted from simple climate vegetation relationships alone (Mohan et al. 2009, Iverson et al. 2011). Similarly, even though climate envelope models project an increasing abundance of eastern hemlock (Tsuga canadensis) throughout the eastern United States, this species is threatened by the hemlock woolly adelgid (Adelges tsugae). The distribution of the adelgid is currently limited in the north by winter temperatures, because it cannot tolerate temperatures below 25oC (Paradis et al. 2008). However, there has been a 40% decline in the number of days with a mean temperature of 25oC from the first to the last decade in the 50-year temperature record at the HBEF (Hamburg et al. 2012). With the combination of increasing temperatures and the potential selection for greater cold tolerance within hemlock woolly adelgid populations, eastern hemlock trees could be affected by this pest throughout their entire range within the next 30 years (Albani et al. 2010). This could lead to an increase in the abundance of hardwood tree species (Albani et al. 2010) and to increases in the rates of nutrient cycling, transpiration, and nutrient loss throughout this region (Campbell et al. 2009).

Shifts in winter climate will undoubtedly continue to influence wildlife in the HBEF region (Rodenhouse et al. 2009). As with vegetation, the impact of winter climate change on wildlife populations plays out in concert with other environmental and societal stressors, including historical and current land use, forest regeneration patterns, and hunting pressure on game species (Christenson et al. 2010). For example, as snow depth declines, a shift in the dominant ungulate herbivore could occur. Moose are currently the dominant herbivore at the HBEF (figure 3). They remove large volumes of browse material (approximately 25 kilograms dry weight per day) with preferential consumption of balsam fir during winter (Christenson et al. 2010). As snow depth declines below 45 cm, white-tailed deer (Odocoileus virginianus) will have greater access to these forests, because their movement is generally limited by deep snow (Morrison et al. 2003). We may be observing this transition currently;
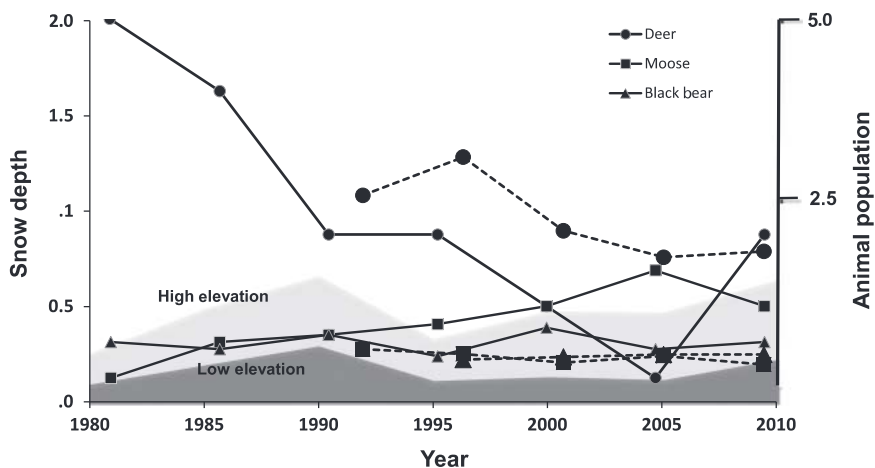

Figure 3. Average snow depth (in meters) at low (less than 1500 feet; the dark shading) and high (above 2500 feet; the light shading) elevations at the Hubbard Brook Experimental Forest (HBEF) and estimated deer, moose, and bear populations (in number of individuals per square kilometer) for the HBEF (the solid line) and for the state of New Hampshire (the dashed lines) from 1980 to 2010.

observations at the HBEF and by the State of New Hampshire indicate a slight decline in the number of moose and an increase in the number of white-tailed deer beginning in 2005, which coincides with less snow reported at the HBEF at lower elevations (figure 3). In addition to competing for resources, white-tailed deer have a negative influence on moose through the transport of a parasite lethal to moose (Parelaphostrongylus tenuis; Whitlaw and Lankester 1994). White-tailed deer preferentially browse a large number of woody species, including balsam fir, sugar maple, and oak, and avoid or positively affect striped maple, American beech, and black cherry (Crête et al. 2001). This change in browsing could profoundly influence tree species composition (e.g., the continued presence of spruce and beech and a reduction or elimination of selected hardwoods) in ways not predicted by models based on simple climate–vegetation relationships that suggest that forest composition in New Hampshire will transition to an oak-dominated forest.

Not all wildlife species will respond to changes in climate. Black bear (Ursus americanus) populations, for example, have remained relatively stable at the HBEF and across New Hampshire over the past two decades (figure 3). Bears are sometimes referred to as a landscape species (Samson and Huot 1998), because they can live in landscapes with a variety of vegetation; therefore, they are less susceptible to climate-induced changes in plant community composition. Bears also den during the winter season, so snow levels at this time of year do not have as much of an impact on them as on other animals, including deer. Together, these characteristics will allow bears to remain in the HBEF region, barring increased disturbance by humans.

Similar to aboveground plants and animals, belowground organisms are also vulnerable to shifts in winter climate. Soil frost decreases soil arthropod richness and diversity and reduces the abundance of many arthropod groups in northern hardwood forests (Templer et al. 2012). These responses may adversely affect other forest floor taxa and the entire forest food web. For example, reduced food availability could have negative consequences for the reproduction, winter survival, or migration of vertebrate insectivores that feed from the forest floor (e.g., salamanders [e.g., Plethodon cinereus], ovenbirds [Seiurus aurocapilla], or the multiple species of thrushes [Catharus spp.] that breed in the forest; Holmes and Sherry 2001). Conversely, some migratory birds (e.g., those feeding from foliage or on emerging aquatic insects) may benefit from advancing phenology. Warm spring conditions lengthen the breeding season and can allow facultative double brooders such at the black-throated blue warbler (Setophaga caerulescens) to increase fecundity by attempting a second brood later in the season, provided sufficient food is available (Holmes et al. 1992). Although food may become available earlier under warm spring conditions, the mismatch between the arrival or breeding of migratory songbirds and a peak in food abundance that occurs in European oak woodlands (Both 2006), where the larvae of a single species the winter moth (Operophtera
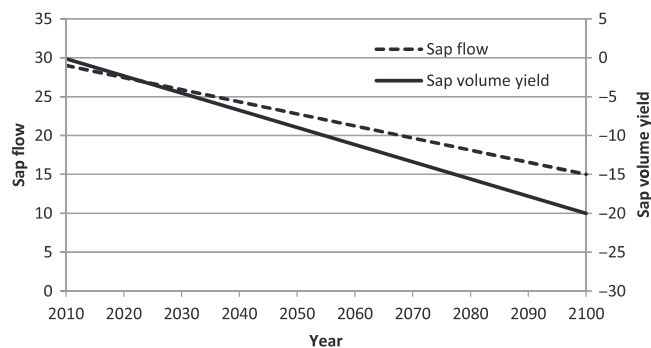

Figure 4. Possible changes in maple sap production as winter climates warm in the northeastern United States and adjacent Canada during this century. The projections are mean estimates based on modeled results for changes in the number of days of sap flow (Duchesne et al. 2009) and the overall yield of sap (Skinner et al. 2010) under various climate change scenarios.

brumata) dominates bird diets, is not expected at the HBEF. Similar to patterns found in deciduous European forests that are not dominated by oak (Quercus) species (Burger et al. 2012), foliage-gleaning birds in the northern hardwood forests at the HBEF feed on a diverse community of Lepidoptera larvae and adult insects of other species that develop during a wide window encompassing the entire avian breeding season. However, the early emergence of arthropods and earlier breeding by birds may put both at greater risk to losses associated with late-season frosts.

Climate change in winter could have a variety of substantial and potentially important human dimensions. For example, reduced snowpack and warmer winter temperatures are predicted to lead to a reduction of 20% or more in sugar maple sap yield (Duchesne et al. 2009) and to shorten the sap season by about half (Skinner et al. 2010) as the climate warms over the twenty-first century (figure 4), which will challenge the economic viability of the regional maple sugar industry. A decreased snowpack could also hasten the appearance of the mud season a time when unpaved roads and trails become unstable and impassable as snowpack melts and soils thaw. Winter timber extraction, which typically occurs on snow-covered soil to reduce soil compaction and erosion from skid trails, could also be adversely affected by decreased snowpack.

Changes to winter snowpack are also likely to affect winter recreation. Increased snowmaking at ski resorts over the last few decades has compensated for declines in natural snow accumulation. However, opportunities for snowmaking will decrease as winter temperatures continue to rise. At the HBEF, the number of days with temperatures producing good conditions for snowmaking (i.e., daily average temperatures of -2^oC or lower; Steiger and Mayer 2008) has declined significantly over the early-season period of November through January, with December showing the most significant change. Another immediate albeit complex concern is the possibility

that climate change is facilitating the northward spread of Lyme disease and the impact that this will have on mammals, including humans (Subak 2003). These examples point to the need for research on the emerging aspects of climate change that are most likely to resonate with the general public.

Climate change is just one of many factors driving vegetation change in the northern hardwood forest

Since the most recent glaciation, vegetation communities have undergone a series of shifts, responding to changes in climate and other disturbances, including disease, re, and human use of the landscape. Although many vegetation assemblages are clearly related to the soil parent material and hydrology characteristics of the hydrobiogeological template (Leak 1978), vegetation community interactions with animals and, most noticeably, the legacies of human use (e.g., timber removal and clearing for agriculture) have generated a complex mosaic of forest communities not necessarily at steady state with respect to current climate or habitat (Vadeboncoeur et al. 2012). Human land-use history has shaped unique vegetation associations (Cogbill 2000), each of which may respond differently to climate change. Therefore, it is important to consider climate change as one of multiple drivers of vegetation composition that interact on a template of hydrobiogeochemical variation and disturbance history. The great challenge is to understand how anthropogenic disturbances such as atmospheric deposition; the introduction of exotic species, pests, and pathogens; and forest fragmentation will modify the template on which climate change is acting and will contribute to future vegetation community shifts (Iverson et al. 2011).

Over the past two centuries, hardwoods have displaced conifers such as spruce at intermediate montane elevations in northern New England (Hamburg and Cogbill 1988, Vadeboncoeur et al. 2012), whereas more recent data show a range of species shifts, from further upward encroachment of the northern hardwood zone in the Green Mountains of Vermont (Beckage et al. 2008) to apparent increases in spruce and r at the HBEF. Hamburg and Cogbill (1988), using historical and modern data, suggested that climate change was the most likely driver of the loss of red spruce during the twentieth century as the dominant tree in midelevation forests of the HBEF region. However, climate change is not the only potential explanation for these shifts. For example, elevated acid deposition reduces cold tolerance in red spruce and has been linked to spruce decline at high altitudes (Schaberg et al. 2001) and to declines in sugar maple (Moore and Ouimet 2006) and montane paper birch (*Betula papyrifera*; Halman et al. 2011). Multiple stressors and changes in historical disturbance regimes in the coming century may lead to further declines of these species, whereas others, including beech and red oak, may increase (Mohan et al. 2009). Introduced pests and diseases, both already present (e.g., beech bark disease) and expected in the future (e.g., hemlock woolly adelgid, emerald ash borer), may alter the community dynamics or even remove species from the forest entirely. Climate change might hasten these invasions or might mediate their effects on forest structure. For example, beech bark disease appears to have increased the susceptibility of American beech to ice storm damage while also leading to high rates of regeneration, which allows the beech to respond rapidly to increased light in gaps (Weeks et al. 2009).

Our detailed monitoring and studies of vegetation at the HBEF have implications for other long-term monitoring programs. At the HBEF, complete inventories of the 13.2-ha reference watershed (watershed 6) that have been conducted every 5 years since 1977 show marked shifts in forest composition (Schwarz et al. 2003, Van Doorn et al. 2011). However, forest aging following logging and hurricane disturbance in the early twentiety century, along with elevated nitrogen and sulfur deposition, ecosystem acidi cation, and beech bark disease, make it impossible to ascribe the observed changes in forest composition to any one cause in particular. The complexity of vegetation change underscores the need for long-term monitoring in a focused spatial framework. In areas of rugged topography such as the HBEF, monitoring should be focused at or near current transitions between vegetation types (e.g., the ecotone between hardwood and boreal forest zones), and it should be designed to quantify stress responses and competitive interactions among species. Monitoring must also encompass the full range of disturbance histories in an area. Whereas the HBEF represents a relatively narrow range of disturbance histories, the surrounding landscape spans a range of disturbances, including abandoned small-scale agriculture at lower elevations, heavy commercial logging, extensive res in the more remote mountainous areas in the late nineteenth and early twentieth centuries, and modern exurban development along roads (gure 5; Vadeboncoeur et al. 2012). There should also be a focus on monitoring regeneration (including seedlings and saplings), because these size classes will be the rst to respond to change (Cleavitt et al. 2011). Monitoring should be keyed to disturbance regimes (e.g., forest gaps), which may provide opportunities for new species to colonize. Monitoring should also be sustained to distinguish stable sink populations of seedlings from advancing fronts of an invading species. The long-term monitoring of key variables must also be standardized in order to facilitate comparisons among sites to better distinguish similarities and differences in response to climate change across the landscape.

Conclusions

Whereas the scale and pervasive nature of climate change motivate macroscale approaches that can couple and depict atmospheric and ecosystem processes at regional and global scales, these methodologies may result in an incomplete or inaccurate assessment of climate change effects on ecosystem structure, function, and services at local scales. Because climate change plays out on a complex hydrobiogeochemical template (i.e., the intertwined patterns of soils, vegetation,
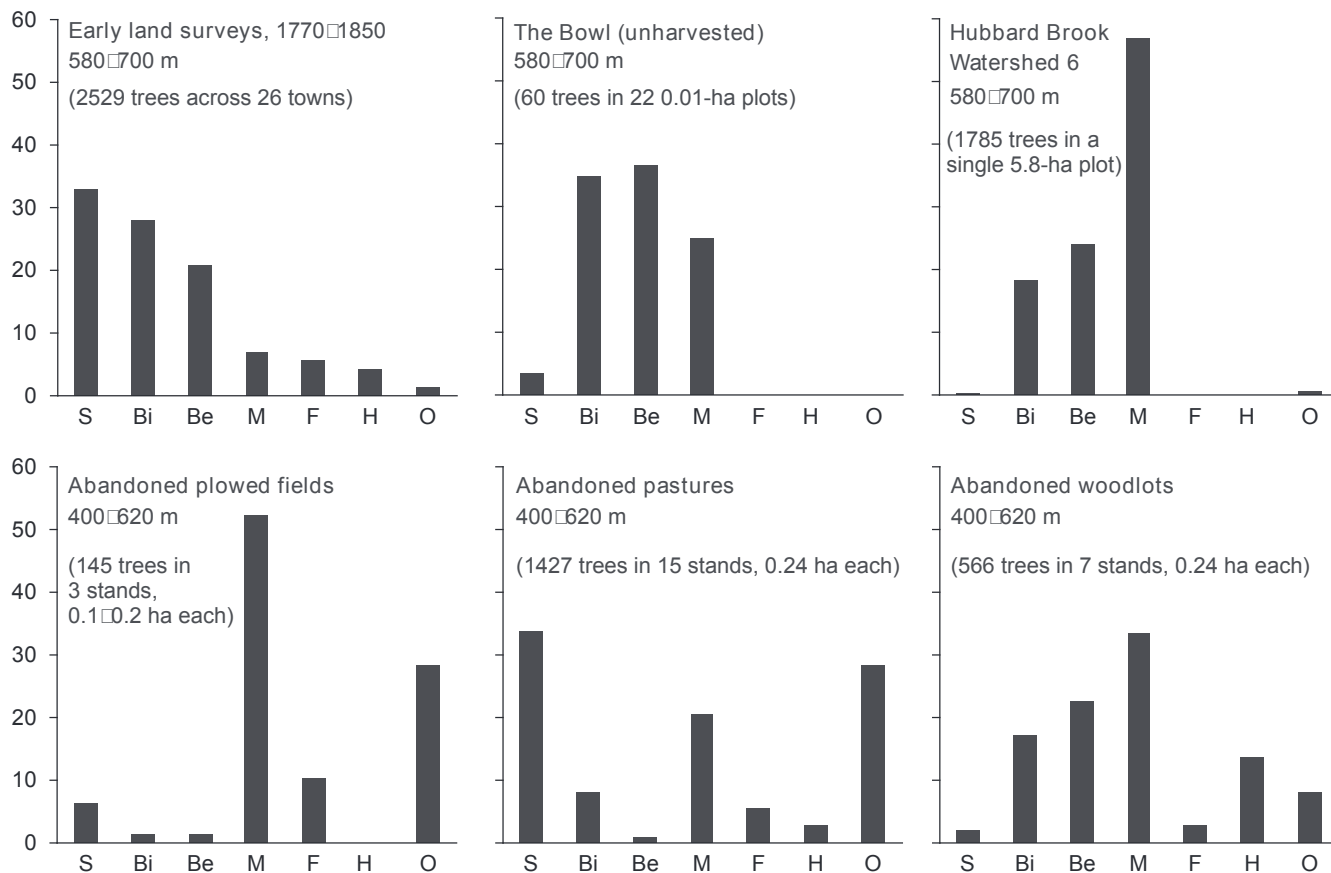
Figure 5. A comparison of forest composition of trees cited as boundary markers in early land surveys in central New Hampshire (580 700 m) with modern forest plots representing a range of disturbance histories at similar elevations illustrates how the local effects of climate change on vegetation are often confounded by the interactions of natural and anthropogenic factors that overshadow the effects of changes in climate on ecosystems. The data are the percentage of stems that were greater than 20 centimeters diameter at breast height. Spruce has declined regionally due to clearing, changes in climate and acid deposition, except where selected for by grazing on abandoned lands, while beech has not successfully recolonized abandoned agricultural lands. Maples are more common on the landscape than they were prior to settlement. The data are from Vadeboncoeur and colleagues (2012). Abbreviations: Be, beech; Bi, birch; F, r; H, hemlock; ha, hectare; m, meters; M, maple; O, other; S, spruce.

and hydrologic owpaths) and interacts with many human and natural factors at multiple temporal and spatial scales, various effects of climate change cannot be predicted from the broad constraints of temperature and precipitation alone on ecosystem properties.

We argue that long-term integrated studies, such as those conducted over the past 50 years at the HBEF, should be an essential component of climate change research and assessment. A combination of long-term and in-depth measurements is essential for understanding the interplay between climate and forest ecosystem dynamics. At the HBEF, that interplay has produced surprising effects on hydrologic variables (e.g., evapotranspiration, stream ow, soil moisture); changes in phenology and water, carbon, and nitrogen uxes during critical seasonal transition periods; winter climate change effects on plant and animal community composition

and ecosystem services; and complex interactions with anthropogenic disturbances and land-use changes that in uence plant community composition. Further research on how site-speci c climate change affects multiple components of ecosystem structure and function should be useful for revealing the key determinants of plant and animal community composition, uxes of water, element dynamics, and the human valuation and use of ecosystems in many areas of the globe. The results from these detailed studies need to be incorporated into macroscale approaches in an iterative process of modeling, experiments, and long-term monitoring at multiple scales. We suggest that the coordination of long-term research efforts and the development of common approaches will improve our understanding of and response to the overarching challenge that climate change presents to science and society.

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