1. **RESULTS FROM PRIOR SUPPORT**

The mission of the Hubbard Brook (HBR) LTER program is to improve understanding of the response of the Northern Forest ecosystem to natural and anthropogenic disturbances. The broad conceptual model guiding our research envisions disturbance playing out on a geophysical and historical template that influences the biogeochemistry, vegetation, hydrology and food webs of the northern forest (FIG. 1). Traditionally, we have organized our research around three types of disturbance: 1) disturbance resulting directly or indirectly from regional climate change; 2) disturbance associated with air pollution; and 3) disturbance related to changes in forest structure and composition. Our conceptual model has evolved in response to results (many surprising) from long-term data collection, leading to new emphasis on interactions among disturbances and legacies of past disturbance.

Our activities include: 1) collection, analysis and curation of long-term data sets; 2) plot-scale and small-watershed manipulation experiments; 3) landscape scale field studies on hydrology, soil, vegetation, microbes, birds and other heterotrophs; 4) cross-site surveys and experiments across the Northern Forest region and among LTER sites; 5) development and application of ecosystem models; and 6) educational, outreach and natural resource management projects coordinated by the Hubbard Brook Research Foundation (HBRF). Long-term data, experiments, and ecosystem models are used to synthesize results, evaluate uncertainties, and make projections of future ecosystem structure, function, and services. Below, we review results from the past six years of research, organized by focal disturbances (air pollution, climate change, and forest disturbances) and highlight how new results have driven the evolution of our conceptual model and the development of new research initiatives (Table 1).

|  |
| --- |
| **Table 1. Ten recent signature publications from the Hubbard Brook LTER project.** Full citations are given in literature cited section. Data available on Hubbard Brook and LTER portals. |
| Battles, J. J. et al. 2014. Restoring soil calcium reverses forest decline. Environmental Science & Technology Letters **1**:15-19. |
| Bernal, S., et al. 2012. Complex response of the forest nitrogen cycle to climate change. Proceedings of the National Academy of Sciences **109**:3406-3411. |
| Fahey, T. J. et al. 2015. The promise and peril of intensive-site-based ecological research: insights from the Hubbard Brook ecosystem study. Ecology **96**:885-901. |
| Green, M. B. et al. 2013. Decreased water flowing from a forest amended with calcium silicate. Proceedings of the National Academy of Sciences **110**:5999-6003. |
| Groffman, P. M. et al. 2012. Long-term integrated studies show that climate change effects are manifest in complex and surprising ways in the northern hardwood forest BioScience **62**:1056-1066. |
| Lany, N. K., M. P. Ayres, E. E. Stange, T. S. Sillet, N. L. Rodenhouse, and R. T. Holmes. 2016. Breeding timed to maximize reproductive success in a migratory songbird: the importance of phenological asynchrony. Oikos DOI: 10.1111/oik.02412. |
| Likens, G. E., and D. C. Buso. 2012. Dilution and the elusive baseline. Environmental Science & Technology **46**:4382-4387. |
| McGuire, K. J. et al. 2014. Network analysis reveals multiscale controls on streamwater chemistry. Proceedings of the National Academy of Sciences of the United States of America **111**:7030-7035. |
| Wexler, S. et al. 2014. Isotopic signals of summer denitrification in a northern hardwood forested catchment. Proceedings of the National Academy of Sciences 111:16413-16418 |
| Yanai, R. D. et al. 2013. From missing source to missing sink: Long-term changes in the nitrogen budget of a northern hardwood forest. Environmental Science & Technology **47**:11440-11448. |

* 1. **Air Pollution**

Because of its location downwind of industrialized regions in the east and midwest, HBR has been exposed to high levels of air pollution for decades. Long-term measurements of sulfur (S), nitrogen (N), and mercury (Hg) deposition, and their effects on ecosystem structure and function have played a central role in the development of U.S. national policies controlling S and N oxide emissions to the atmosphere (Likens 2010, Driscoll et al. 2011, 2012). We have measured bulk precipitation chemistry since 1963, wet deposition since 1978 (as part of the National Atmospheric Deposition Program (NADP)) and atmospheric chemistry and dry deposition since 1990 (as part of the EPA Clean Air Status and Trends Network (CASTNet)). Our long-term monitoring of atmospheric deposition shows a continuous decline in S deposition since the early 1970s, a decline in nitrate (NO3-) deposition that started in the early 2000s and no significant change in NH4+ deposition, consistent with changes in pollutant emissions in the U.S. (FIG. 2) (REF). We have also measured major solutes in streams at HBR since 1963, adding acid neutralizing capacity (ANC), fractions of dissolved Al, and dissolved organic carbon (DOC) in 1982. These long-term stream chemistry measurements (FIG. 3) show a pattern of decreases in SO42- concentrations, which are consistent with long-term decreases in atmospheric S deposition. We have found a significant, but erratic, long-term decrease in stream NO3-. These changes have resulted in changes in the acid-base status of streamwater, with increases in pH and ANC, and decreases in monomeric Al (FIG. 3). With the declines in SO42-, NO3-, and the base cations, streamwater is trending toward the solute concentrations we presume it had prior to the industrial revolution (FIG. 4).

In 1998, we initiated an experimental addition of CaSiO3 to an entire watershed (W1) to replace the available calcium (Ca) that was lost from soils by leaching during the 20th century (Nezat et al. 2010, Cho et al. 2012, Johnson et al. 2014). The Ca addition has produced a remarkable cascade of results that continues to surprise us 16 y after the start of the experiment. Unexpectedly, we observed a ~20% increase in evapotranspiration for 3 y following treatment, before returning to pretreatment levels (Green et al. 2013). The Ca amendment reversed the forest decline that had been occurring in the watershed, and W1 supported greater leaf area and aboveground net primary production and lower fine root biomass compared to the untreated reference watershed (Battles et al. 2014, Fahey et al. 2016) (FIG. 5). The Ca amendment also enhanced seedling establishment and survival (Cleavitt et al. 2011, 2014). As the Ca moved downward through the soils, it increased soil exchangeable Ca and pH (Johnson et al. 2014). Late-stage decomposition rate of litter increased (Lovett et al. 2016), and the pools of C and N in the forest floor and upper mineral horizons declined markedly(Johnson et al. 2014). Initially, pools of available N in the soil also declined as tree N uptake was stimulated more than microbial N mineralization (Groffman and Fisk 2011a). However, in recent years there have been marked and unexplained increases in NO3- concentrations in soil solutions and streamwater in the treated watershed (FIG. 6), indicating an oversupply relative to plant and microbial demand. Research to understand these surprising results is proposed in section 2.2.2.

Unlike the Ca-treated watershed, NO3- concentrations in streamwater have remained low in the reference watershed and elsewhere at HBR (Bernal et al. 2012, Yanai et al. 2013). These low NO3- concentrations are surprising given that the forests at HBR are no longer aggrading biomass (Van Doorn et al. 2011), and have experienced elevated atmospheric N deposition for decades, which should foster high rates of hydrologic and gaseous N loss. Hypotheses for these unexpectedly low levels of N leaching, include recent decreases in atmospheric N deposition (Likens and Buso 2012), recovery of forests from past disturbances (Bernal et al. 2012), accumulation of N in mineral soil (Yanai et al. 2013), increases in gaseous losses (Morse et al. 2014, Wexler et al. 2014, Kulkarni et al. 2015, Morse et al. 2015a, 2015c), and changes in dissolved organic matter quantity and quality (Goodale et al. 2005, Fakhraei and Driscoll 2015, Fuss and Driscoll 2015). New research on this topic is proposed in section 2.2.3.

The legacy of ecosystem N enrichment from chronically elevated N deposition has raised important questions about shifting patterns of nutrient limitation of plants and microbes in the HBR forest (Naples and Fisk 2010, Groffman and Fisk 2011b, Minick et al. 2011, Crowley et al. 2012, Fisk et al. 2014). Using integrated modeling and empirical studies, we are finding that plant and microbial allocation processes change significantly in response to varied resource needs (Rastetter et al. 2013). For example, plants increase root foraging for N where N availability is low, and for phosphorus (P) where N availability is high (Naples and Fisk 2010). Plants and microbes allocate more available N to the production of P-mineralizing enzymes where N availability is high (Ratliff and Fisk 2016, Fisk et al. 2015). The tendency of these processes to balance N:P stoichiometry suggests biotic responses to imbalances in the availability of nutrients, an idea that is being tested in a N x P fertilization experiment conducted across a wide gradient of soil fertility at HBR and other regional sites(see section 2.2.4; Fisk et al. 2014). Results indicate that forest productivity in mid-successional and mature stands is limited by P, whereas in early-successional productivity is N-limited (Goswami et al., in prep.). New research on plant and microbial processes that balance N and P stoichiometry are proposed in section 2.2.4.

**1.2 Climate Change**

Long-term climate changes at HBR are consistent with expectations for the broader Northern Forest region (Hayhoe et al. 2007). At the three HBR weather stations with the longest records (48 to 56 years), average annual air temperature has increased by 0.22 to 0.28 °C per decade, with more marked warming in winter than in summer (Hamburg et al. 2013). Precipitation has also increased by 3.5 to 6.7 cm per decade or 13 to 28% over 58 years (FIG. 7) (Campbell et al. 2007). Winter precipitation has not changed significantly, but winter air temperatures have warmed, and as a result 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) (FIG. 8).

Snowpack decline and precipitation increases have in turn influenced streamflow. Snowmelt-induced peak flows in spring have declined (Campbell et al. 2011) and are occurring earlier in the year (Hamburg et al. 2013).Annual average streamflow has increased at a rate of 5.9 cm per decade at the measurement station with the longest record at HBR (FIG. 7). Interestingly, evapotranspiration (ET), estimated as the difference between annual precipitation and streamflow, has shown slight, but significant declines in the hydrologic reference watershed over the period of record (Campbell et al. 2011). The cause of the decline in ET is not known (Groffman et al. 2012) and is one focus of our proposed research (section 2.3.2).

Spring leaf-out has advanced in response to warming climate, which has increased both photosynthesis and net C storage of forests at HBR (Keenan et al. 2014). At the same time, our findings indicate that the changing climate promotes N losses from the ecosystem (Durán et al. 2015a). These seemingly contradictory results suggest that plant and soil processes are not responding in concert, emphasizing the importance of seasonal transitions and the winter dormant period, when plant and soil processes are uncoupled. The winter/spring transition is critical to forest ecosystem biogeochemistry, representing a period when soil microbial mineralization processes are active but trees have not yet become a dominant sink for water or nutrients. This period of the “vernal window” is increasing over time as snow melts and soils warm earlier, while the timing of tree canopy expansion advances at a slower pace (Groffman et al. 2012) New research on climate seasonality is discussed in section 2.3.3.(FIG. 9).

Climate warming over the long-term appears to decrease production of plant available N via N mineralization and nitrification (Durán et al. 2015a) whereas short-term increases in hydrologic and gaseous N losses can occur during the vernal period and during winter by reducing snow cover and increasing soil freezing (Groffman et al. 2010, Reinmann et al. 2012, Durán et al. 2014), further decreasing plant available N and suggesting that climate change may be driving reductions in N availability in HBR forests. The increase in N loss is driven by frost damage to roots, which reduces plant uptake of N (Templer 2012, Comerford et al. 2013, Campbell et al. 2014), and by shifts in hydrologic flowpaths and nutrient transport through soil profiles (Fuss et al. 2015). Patterns across the elevation gradient at HBR are consistent with the hypothesis that climate warming reduces N availability. In valley plots, which are approximately 2oC warmer (mean annual temperature) than high elevation plots, N availability, foliar N, and process rates related to N loss (nitrification, denitrification) are lower that at high elevation plots with similar vegetation and soils (Ross et al. 2011, 2012, Durán et al. 2014, Morse et al. 2015a, 2015c). We propose comparative and experimental work on climate change effects on N cycling (section 2.3.4).

Our research has also elucidated some of the key responses of animals to climate change. The dominant 1° consumers of the green (live plant-based) food web at HBR are caterpillars (Lepidoptera), and caterpillars are the chief food for the dominant 2° consumers, which are birds (Gosz et al. 1972). Dramatic interannual fluctuations in caterpillar abundance (> 30-fold) are related to climatic variation: higher Lepidoptera abundance and bird reproduction are associated with warm springs and long, warm summers (Reynolds et al. 2007, Stange et al. 2011, Townsend et al. 2013, Lany et al. 2015, Sherry et al. 2015, Townsend et al. 2015). Direct effects of temperature on caterpillar development rate and survival may drive this pattern. A competing hypothesis is that interannual variation in foliar N, which is a limiting nutrient for caterpillars, and is itself sensitive to climate, drives the surprising interannual variation in 1o consumers (Lany 2014). Research proposed in sections 2.3.3, 2.3.4, and 2.3.5 will test the hypothesis that effects of climate and disturbance on pools and fluxes of N produce a strong dynamic linkage between biogeochemistry and biodiversity.

Climate change is also altering higher trophic levels in other ways (Rodenhouse et al. 2009). Moose browsing, and their indirect effects on decomposition and N cycling, become more intense as snow depth declines and more vegetation is exposed above the snow (Christenson et al. 2010, 2014; continuing studies in 2.5.3). The abundance of the top predator in streams (spring salamander) is declining from climatic effects on streamflow and stream chemistry (Lowe 2012; continuing studies in 2.4.5). Advances in the timing of spring leaf-out pose a particular challenge to Neotropical migrant birds, which are the dominant terrestrial predators in our system. For the past 25 years, Black-throated Blue Warblers at HBR have been remarkably adept at timing their nesting relative to the timing of spring, but this flexibility may be approaching its limit because the dates at which birds first arrive at HBR from their wintering grounds are relatively inflexible and now similar to the earliest springs (Lany et al. 2015); continuing studies in 2.3.3).

**1.3 Forest Disturbance**

An unprecedented combination of disturbances is buffeting the Northern Forest, including intensified timber harvest, introduction of exotic insects and diseases, migration of more southerly or valley-dwelling species into the upland forests, and climatic phenomena, such as ice storms and “microburst” windstorms. Ecosystem responses to these disturbances continues to be a major focus of long-term research at HBR (Likens 2013).

In the reference watershed, tree species composition has changed and overall biomass has declined in recent years due to dieback of sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) (FIG. 10). In the lower parts of HBR, we have observed increasing density of seedlings of red oak (*Quercus rubra)* and white pine (*Pinus strobus*), two tree species characteristic of lower elevations that have previously been absent from most of the upland forests of HBR. Surprisingly, the boreal conifer species red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), which we would expect to decline due to climate change, have increased in aboveground biomass more than any other tree species at HBR over the last 10 y (Van Doorn et al. 2011). Beech bark disease, produced by an introduced scale insect and native bark-cankering fungi, invaded the HBR valley in the 1970s and has increased both mortality of larger American beech (*Fagus grandifolia*) trees and regeneration by sprouting, leading to a younger population age structure (Gavin and Peart 1993, Hane 2003). Two other highly damaging forest pests, the hemlock woolly adelgid (*Adelges tsugae*) and the emerald ash borer (*Agrilus planipennis*), are not yet present at HBR but are projected to arrive within the term of the next LTER proposal and are the subject of proposed research in sections 2.4.1 and 2.4.2.

Overall bird abundance has declined at HBR over the 40+ y of record, primarily due to the loss of species that nest and forage in mid-successional habitats, which have become less common as the forest has matured (Holmes and Sherry 2001, Holmes 2011)(FIG. 11). Moose re-invaded the HBR forest beginning in the 1980s after a long absence (Groffman et al. 2012), and their browsing affects soil nutrient cycling (Christenson et al. 2010, 2014), tree and shrub layer vegetation dynamics, and consequently bird and lepidopteran populations. We have just begun (in 2015) studies of bats at HBR, and the initial data indicate that the species most susceptible to the exotic fungal disease known as “white-nose syndrome” are already very rare, but that there remains a community of at least three bat species.

Forest harvest experiments at HBR have been used to test fundamental questions about long-term ecosystem response to disturbance. In our earliest experiment watershed 2 (W2) was clear-felled and then treated with herbicides for 3 years to prevent regrowth. Despite extensive nutrient losses from the watershed (Likens et al. 1970), a comparison of 31 y of regrowth on W2 to clear-cut sites in the region showed that aboveground net primary productivity and biomass accumulation fell within the range measured in the other sites (Reiners et al. 2012). This remarkable robustness of ecosystem recovery in response to severe devegetation is difficult to reconcile with our

whole-tree harvest experiment on watershed 5 (W5) which indicates that intensive forest harvest may promote greater calcium (Ca) limitation of forest growth. Long-term monitoring of streamwater chemistry in W5indicates that Ca export has remained elevated relative to the adjacent reference watershed for more than 30 y (Campbell et al. 2016). This ongoing leaching of Ca, coupled with depletion of soil Ca due to chronic acid deposition, suggests that available soil Ca pools in W5 may not be sufficient to sustain growth of the young forest. Indeed the abundance of the most Ca demanding species, sugar maple, has dramatically declined on W5 (Cleavitt et al. In prep.). The rearch on W5 also indicates that soil C pools are more dynamic than previously thought. We calibrated and validated two widely used soil carbon (C) models – RothC and CENTURY – for the prediction of soil C pools under several climate change scenarios (Dib et al. 2014). Neither model captured the rapid recovery of soil C pools on W5 that occurred between post-harvest years 8 and 15. This, combined with observations of large changes in forest floor C pools after the Ca treatment on W1, suggests that the large soil C pool at HBR is more responsive to disturbance than previously thought. These dynamic responses of ecosystem processes to forest harvest will continue to provide…

**1.4 Geophysical and historical template**

A major advance over the past 10 y has been analysis of how the geophysical and historical template influences the biogeochemistry, vegetation, hydrology and food webs in northern forest ecosystems. Variation in hydrology across the landscape influences the formation and distribution of soil types (Bailey et al. 2014, Bourgault et al. 2015, Gillin et al. 2015), which in turn influences chemistry of both surface water and groundwater (Zimmer et al. 2013, Gannon et al. 2014, McGuire et al. 2014, Gannon et al. 2015, Benettin et al. 2015), as well as plant (Bailey 2013), microbial (Morse et al. 2014) and higher trophic level dynamics (Greene et al. 2008). Spatial patterns of vegetation, resulting in part from disturbance history of the landscape, determine the spatial patterns of many songbird populations; these patterns tend to remain nearly constant from year to year despite large changes in songbird abundance (Halworth et al. in prep.) New research on the geophysical and historical template is detailed in section 2.5.

**1.5. Synthesis, integration, models, uncertainty and prediction**

Synthesis of HBR research has been an ongoing activity, dating back to the important books on biogeochemistry (Likens et al. 1977, most recent update in 2013) and vegetation dynamics (Bormann and Likens 1979). We have produced a series of monographs on individual elements (Likens et al. 1994, 1998, 2002, Lovett et al. 2005, Fahey et al. 2005) including a recent synthesis paper on N (Yanai et al. 2014). We also provide synthesis aimed at particular scientific issues (e.g., Bernhardt et al. 2005, Groffman et al. 2012) and have led integrative studies to inform national policy issues (e.g., Driscoll et al. 2001, 2003, 2007, 2015a, Fahey et al. 2010, Raciti et al. 2011, Lovett et al. in press). A more reflective type of synthesis is provided by two of the long-term leaders of the HBR project, Richard Holmes and Gene Likens, who have written a book that illustrates the changes they have seen in the HBR ecosystem over the 50+ years of the study, and further changes that are likely in the future (Holmes and Likens in press).

Models, driven by long-term data, have been widely used at HBR for both synthesis and prediction (Box 1). The PnET series of forest ecosystem models has been used to evaluate how changing climate, atmospheric deposition, solar radiation, and CO2 levels influence ecological processes at HBR (e.g., Pourmokhtarian et al. 2012). The Multiple Element Limitation model (Rastetter et al. 2013) identified allocation mechanisms that are key to N and P cycling in forest ecosystems recovering from disturbance. Terrestrial biosphere models have been used with long-term ground observations of phenology at HBR, satellite indices, and ecosystem-scale CO2 flux measurements to show that changes in phenology have increased carbon uptake through photosynthesis more than C release through respiration (Keenan et al. 2014). Models of the effects of climate change on soil C pools have been tested against long-term data from HBR (Dib et al. 2014).

The long-term data at HBR have allowed for novel analyses of the sources of uncertainty in ecosystem measurements and models including the N content of vegetation (Yanai et al. 2010), patterns in biomass accumulation (Fahey et al. 2005, Battles et al. 2014) and hydrologic export of solutes (Yanai et al. 2015, Campbell et al. in press). The HBR effort on quantifying uncertainty in ecosystem studies has led the LTER network on this issue, spawning a NSF Research Coordination Network (RCN) and a workshop at the 2015 LTER All-Scientists Meeting ([www.esf.edu/quest](http://www.esf.edu/quest)). Another recent effort examined how well HBR represents the broader Northern Forest region, finding that HBR is representative of some regional patterns and processes, such as sensitivity to and recovery from acid deposition, but its mountainous terrain and non-agricultural past make it less representative of others, such as bird community composition (Fahey et al. 2015).

**1.6 Publication and leveraging research funding**

In the current LTER grant cycle,we have produced 216 peer-reviewed papers that have been cited a total of 3379 times; with an H-index of ~30, and an i10-index of 95. HBR investigators have used LTER funding to generate synergies with other funded research from NSF and other agencies including projects on winter climate change, N gas fluxes, landform controls on hydrologic flowpaths and pedogenesis, N sinks in the mineral soil, multiple element limitation of the forest, ice storms, and stream community ecology. Two LTREB grants augment long-term studies of precipitation and stream chemistry and bird populations.

**1.7 Education, outreach and broader impacts**

Many of our education and outreach activities are run by the Hubbard Brook Research Foundation (HBRF), which serves as the interface organization between researchers at HBR and schools and community stakeholder organizations in the region. HBRF’s school-yard LTER program targets middle- and high-school teachers with professional development, teaching resources, and school partnerships. Professional development of K-12 teachers occurs through a Research Experience for Teachers (RET) program, and partnerships, including Project Learning Tree, Project WET, Project WILD, GLOBE, the USDA Forest Service, and the New Hampshire Science Teachers’ Association. We host 8-10 REU students each summer through an on-site REU program that is run jointly by Plymouth State University and HBRF. Our contribution to the LTER schoolyard series, *Seeking the Wolf Tree,* was recently published (Cleavitt 2015). Outreach for the book has included two teacher workshops, student assembly presentations, and distribution of over 500 books, with 550 more soon to be shipped to town libraries and school principals throughout NH. HBR scientists have explored the effects of winter climate change on human dimensions through multiple “Roundtable” discussions with stakeholders including foresters, farmers, ski area operators, snowmobilers, maple sugar producers, and road maintenance personnel. One of these led to a published Op Ed in the Boston Globe.

The Science Links program synthesizes and translates scientific information from HBR for policymakers at regional and national levels (Osmond et al. 2010, Fahey et al. 2010, Driscoll et al. 2011, 2012, Raciti et al. 2012).. A new science communication and outreach initiative, the Science Policy Exchange (SPE), established in collaboration with the HFR, PIE and BES LTER sites, is addressing health and ecosystem effects of coal combustion (Driscoll et al 2015a; Capps et al. in review; Buonocore et al in review ), impacts of forest pests and pathogens (Lovett et al. in press), and green infrastructure (Driscoll et al. 2015b).

**1.8 Response to mid-term review**

Our mid-term site review team, while largely complimentary, identified several important concerns that we have addressed in this proposal. They noted: 1) a lack of clarity in articulating current research questions, in explaining how these questions arose from a synthesis of previous work, and in crystallizing the pressing, future questions that have yet to be answered; 2) that prior data should be synthesized to identify new questions or predictions; 3) microbial and stream ecology did not appear as a strong emphasis of the LTER research; and 4) a seeming reluctance on the part of current HBR LTER researchers to recruit individuals in areas that fall outside of their own expertise, including stream ecology and landscape ecology. In this proposal we have clarified how our long-term and experimental data have led to evolution of our conceptual models, research questions, and inclusion of new participants at HBR. Our proposed research identifies a series of important, integrative questions that have emerged from our long-term data over the past six years that we hope to address in the next six years. We have added new LTER investigators in the fields of stream ecology, hydrology, vertebrate ecology and forest landscape modeling, and we clarify the importance of microbial and stream ecology in our research program.

1. **PROPOSED RESEARCH**

**2.1 Introduction**.

*2.1.1 Background*

Since the establishment of the Hubbard Brook Experimental Forest by the US Forest Service in 1955, research at HBR has focused on the ecology and management of northern forests. The Hubbard Brook Ecosystem Study, founded in 1963 by G. Likens, F. H. Bormann, R. Pierce and their colleagues, developed the small watershed approach to understanding forest ecosystems and advanced the use of whole-ecosystem manipulations to help elucidate the response of forests to disturbance. From the beginning, HBR has sought to bring research results to policy and management, and research from the site has figured strongly in the national debates on air pollution, carbon management, and forest harvesting.

These early efforts were strengthened when HBR joined the LTER network in 1988. The focus on understanding the role of disturbance in the functioning of forest ecosystems continues to this day, but our research team has grown, our research program has evolved and broadened, and our knowledge of the ecosystem has become deeper and more nuanced as we observe long-term trends and seek to explain surprising responses that challenge our understanding. Among the unexpected findings at HBR in recent years are:

* Evapotranspiration in the reference watershed, determined as the difference between annual precipitation and stream discharge, has significantly declined over the period of record despite gradually increasing air temperature..
* Ca is not considered a limiting element in temperate forests, but experimental addition of Ca to a watershed reversed forest decline and had significant impacts on transpiration, tree reproduction, root biomass, litter decomposition, and stream chemistry and biology.
* N export in streamwater of the reference watershed has remained at a very low level through most of the last decade despite the cessation of aboveground biomass accumulation in the forest and the continued accumulation of N from air pollution.
* Net primary production (NPP) is very stable from year to year at HBR, while abundance of the main 1° consumers in the green food web (Lepidoptera) fluctuates dramatically (>30-fold), along with reproduction and abundance of the most important 2° consumers, Neotropical migrant birds.

Each of these surprises emerged from long-term measurements supported by the LTER program. Each has sparked new research to understand the causes of the phenomena, and each has spurred us to re-examine our conceptual and quantitative models, develop new models that better account for the unexpected observations, and make projections about future ecosystem structure, function, and services.

*2.1.2 Research themes and conceptual model*

The overarching research theme of this proposal is the **response of ecosystem structure, composition and function to disturbance**. The disturbance theme retains continuity with previous HBR-LTER proposals, but this proposal extends our research with emphasis on multiple interacting disturbances, legacies of past disturbance, and new directions in experimental and comparative studies.

Disturbances, both natural and anthropogenic, are the most important factors driving change at HBR and throughout the Northern Forest region (Bormann and Likens 1979, Pickett and White 2013). Predicting the future of these forests requires a comprehensive understanding of multiple disturbances and their interactions (Paine et al. 1998, Foster et al. 1997, Foster and Aber 2004). Some of these disturbances are chronic and long-term, such as gradual changes in average temperature and precipitation or the steady progression of the beech bark disease. Others are intense and episodic, such as ice storms, wind storms, and insect outbreaks. Forest ecosystems integrate these multiple disturbances and the response may be additive, synergistic, or antagonistic. Moreover, these disturbances may leave legacies that affect the forest, and its response to future disturbances, for decades or centuries (Compton and Boone 2000). Two examples of these legacies at HBR are the depleted soil Ca availability from chronic acid deposition and the successional dynamics that reflect historical forest harvests. Further, these disturbances play out on a landscape template that imparts spatial heterogeneity to the responses. This template includes geophysical properties of bedrock, glacial till, soils, hydrology and microclimate as well as the spatial patterns of the legacies of past land use history and natural disturbances. Thus, predicting the response to disturbance for an ecosystem requires knowledge not only of its current functioning, but also its spatial context and temporal trajectories.

Our overall conceptual model focuses on three key drivers of change in the HBR ecosystem-- changing atmospheric chemistry, changing climate, and changing biota. These three changes are in some ways intertwined (e.g., climate change or air pollution can change the biota), but they provide a useful structure for grouping the broad range of HBR research into themes. These drivers of change cause perturbations in the interacting ecosystem processes of biogeochemistry, hydrology, vegetation dynamics, and food webs, and the responses may vary across the landscape because of the characteristics of the geophysical and historical template (FIG. 1). Understanding the variation imposed by this template is an important cross-cutting theme of HBR research. While soil parent materials and topography are essentially fixed on ecological time scales, the spatial template structures patterns of ecological processes across the landscape and provides differential responses to disturbances.

In previous cycles of the HBR-LTER we have used “Forest Disturbance” to describe processes such as forest harvesting and windstorms that damage forest structure. Here we have broadened this category to “Changing Biota” to encompass responses to structural disturbances as well as biological changes caused by invasions of non-native species, migrations of more southern or low elevation species into HBR, and shifts in relative abundance of existing species. Biotic change is different from the other two disturbances in several important ways. First, while the drivers of climate change and air pollution are largely external to the HBR ecosystem, biotic change includes forces that are both external (e.g., invasive species) and internal (e.g., succession). Further, climate change and air pollution can alter ecosystem processes in ways that feed back and influence biotic change (FIG. 1).

*2.1.3. Synthesis and integration*

A comprehensive ecosystem study like ours seeks integration across levels of organization and disciplines of study. We propose to focus on five integrative questions that will frame much of our research agenda for the next LTER cycle:

1. How will legacies of past air pollution, particularly depletion of exchangeable cations and accumulation of sulfur and nitrogen in the soil, affect the future functioning of forest and stream ecosystems?
2. What are the soil, microbial and vegetation processes that have permitted nitrogen export in stream water in the reference watershed to remain low despite continued N pollution and cessation of biomass accumulation in the watershed forest?
3. How will simultaneous effects of climate change, air pollution, plant succession, and invasive species, alter the structure, function and biodiversity of forests of HBR?
4. How will changing climate seasonality, particularly changes in spring snowmelt, soil thawing, and phenology of microbes, plants and animals, affect ecosystem functions and food webs?
5. Is N availability a key driver that integrates microbial, plant and animal population dynamics?

Answering these broad questions will challenge us to span disciplines from hydrology and soil chemistry to vegetation dynamics and food web structure, and to span levels of organization from populations to landscapes. Approaches to these synthesis and integration challenges are detailed in section 2.8.

*2.1.4 Research sites*.

HBR (43°56’N, 71°45’W) is a 3160-hectare Experimental Forest owned by the USDA Forest Service and located within the White Mountain National Forest of New Hampshire (Bailey et al. 2003, Campbell et al. 2007). The climate is cool, humid and continental with average monthly air temperatures ranging from -9 °C in January to 18 °C in July. Average annual precipitation is 1400 mm and is distributed fairly evenly throughout the year. A snowpack usually persists from late December until mid-April, with a peak depth in March. We have used the small watershed approach to quantify the response of forest and aquatic ecosystems to disturbance, and several of our monitored watershed have been experimentally manipulated (Table 2). Increasingly we have broadened the scope of our study to encompass the wider Hubbard Brook valley (refs).

The HBR-LTER also encompasses other forested sites in the region that provide further context for studies at the HBR. For example, we conduct complementary research at the Bartlett Experimental Forest (BEF), located about 30 km east of the HBR, where silvicultural treatment of forests on similar sites provides a valuable resource for experimental work (Leak and Smith 1996, Fisk et al. 2014). In the past, steep terrain at HBR precluded installation of an eddy covariance tower to measure C fluxes, so we used data from a tower at a flatter site in the BEF, which we compare with biomass and modeling approaches at HBR and across the region. The BEF facility is part of the [AmeriFlux](http://public.ornl.gov/ameriflux/) network. Recent improvements in techniques for using eddy covariance in complex terrain led us to install a flux tower at HBR in 2015,

and we propose comparative studies to resolve unexplained differences in C budgets between these sites (ref.).HBR researchers also conduct comparative and collaborative studies with researchers at other regional forest study sites, including Cone Pond (NH), Bowl Natural Area (NH), Jeffers Brook (NH), Sleepers River (VT), Bear Brook (ME), Biscuit Brook (NY), Huntington Forest (NY) and other LTER sites such as the Harvard Forest (MA).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Table 2. Monitored small watersheds at HBR.** | | | | |
| **Water-shed** | **N- or S-facing** | **Size (ha)** | **Year measure-ments began** | **Treatment/Disturbance** |
| 1 | S | 11.8 | 1956 | CaSiO3 (Wollastonite) addition 1999. |
| 2 | S | 15.6 | 1957 | Clear felled in winter 1965-66; no products removed. Herbicided 1966-8; left to regrow from 1969. |
| 3 | S | 42.4 | 1958 | None; hydrologic reference watershed |
| 4 | S | 36.1 | 1961 | Clear-cut by strips in three phases, 1970, 1972, 1974. Timber products removed. |
| 5 | S | 21.9 | 1962 | Whole-tree clear-cut to 10 cm diameter, 1983-1984. Timber products removed. |
| 6 | S | 13.2 | 1963 | None; biogeochemical reference watershed. |
| 7 | N | 76.4 | 1965 | None |
| 8 | N | 59.4 | 1969 | None |
| 9 | N | 68.2 | 1986 | None |
| 101 | S | 12.1 | 1970 | Clear-cut in 1970; timber products removed. Note: streamflow quantity is not monitored, only chemistry. |

2.2 **Theme** **1: Changing atmospheric chemistry**

*2.2.1 Overview*

Our long-term research on atmospheric deposition (section 1.1) has revealed several important trends and surprising results that spur our new research in this area. While the atmospheric deposition of pollutants such as S and N have declined in recent years, the legacies of decades of chronic air pollution persist, and have important impacts on current ecosystem function. One such legacy is the depletion of available soil Ca by acid deposition. Our watershed-scale Ca addition explores the consequences of this depletion, and the results of this experiment have continued to surprise us, most recently with major changes to ecosystem C and N pools and fluxes. Another legacy is the accumulation of N in the ecosystem, primarily in the soils. This accumulation has continued to the present, and raises important questions: what processes drive the sinks for N in the ecosystem, and what are the consequences of accumulation of N for a forest that was previously N-limited?

*2.2.2. Impacts of calcium depletion caused by acid deposition* (Contributes to synthesis question 1. Research team: Driscoll, Johnson, Battles, Fahey, Likens, Bernhardt, Rosi-Marshall, Lovett, Fisk, Campbell, Bailey, Green….)

Our long-term nutrient budgets at HBR indicate that a large amount of available Ca has been leached from the soil by decades of elevated SO42- and NO3- associated with acid deposition (Likens et al. 1996, 1998). To test the hypothesis that replacement of this lost Ca would improve ecosystem function and structure, we experimentally added CaSiO3 to W1 in 1999. Under “Results of Prior Support” we described key findings from this study including improvements in forest health, reversal of the forest decline that has continued in the reference watershed, and increases in leaf area and aboveground net primary productivity (Battles et al. 2014; Fahey et al.2016). Recent observations have yielded more unexpected findings. The Ca addition enhanced the late-stage decomposition of leaf litter (Lovett et al. 2016) and, possibly as a result of the increased decomposition, the soil pools of C and N have declined in the Oa (humus) horizon and the upper mineral soil (Johnson et al. 2014). Starting in 2010 we observed marked increases in leaching losses of NO3- in most of our lysimeters in W1 from the forest floor to the mineral soil(FIG 6 NO3 leaching from W1). It is not clear what processes are driving these recent abrupt changes in watershed biogeochemistry.

Key questions for research on the long-term response to this CaSiO3 treatment that we will address over the next six years include:

* What is the mechanism driving the recent loss of soil organic matter and NO3- from W1 and how long will this persist?
* Will the recovery of forest productivity and improvements in sugar maple population growth continue?
* What are the consequences of altered water chemistry for stream ecosystems?
* What is the fate of the Ca added to W1?

*Approach.* To address these research questions we will continue monitoring microbial biomass and activity, vegetation dynamics and net primary productivity, soil, soil solution and stream chemistry in the CaSiO3 treated watershed. To better understand the unexpected perturbations in the N cycle, we will combine multiple datasets to develop N budgets for the watershed before and after Ca addition, allowing us to quantify the sources and fates of N within the watershed. We will conduct time-series analysis and mass balances to examine the transport and fate of added Ca and Si, and evaluate the implications for the recovery of the Ca status, the acid-base chemistry of the watershed, and the long-term health and productivity of the forest. To quantify the fate of the added CaSiO3,we will make detailed measurements in aboveground biomass and complete soil profiles through quantitative soil pits including novel tracer approaches (ref). As a new initiative in this LTER cycle, we will investigate the influence of changing water chemistry (e.g. Likens and Buso 2012) on in-stream C dynamics and macroinvertebrate emergence (details in section 2.3.3).

*2.2.3 Controls on nitrogen losses from forests* (Contributes to synthesis question 2. Research team: Lovett, Groffman, Goodale, Ollinger…)  
The export of N in streamwater draining forested watersheds is an important indicator of N cycling in the forest (Vitousek and Reiners 1975) and N saturation due to air pollution (Aber et al. 1998). It is also a delivery mechanism for excess N flowing to rivers, estuaries, and coastal waters, where it can cause eutrophication (Driscoll et al. 2003). In contrast to the elevated N export from the Ca-treated watershed discussed above, the export of N in the reference watershed has remained surprisingly low in most years (FIG. 3). This contradicts two established ecosystem theories. First, N retention theory predicts that as a forest matures and net biomass accumulation approaches zero, as has occurred at HBR (FIG. 5 ), N export should increase and eventually equal the rate of N input from atmospheric deposition (Vitousek and Reiners 1975). Second, N saturation theory predicts that as a forest accumulates N from atmospheric deposition, its biotic demand will be become saturated and N losses via leaching will increase (Aber et al. 1989). *Our long-term data require re-evaluation of these two widely-accepted theories.*

Our revised conceptual model of N saturation focuses on the fates of N deposited to the ecosystem and the controls on, and consequences of, those fates (Lovett and Goodale 2011). There are four possible N sinks, which can operate simultaneously: (1) incorporation into detritus or soil, (2) incorporation into perennial vegetation structures, (3) losses via leaching, and (4) gaseous losses (FIG. 12). At HBR, two of the four possible fates are well quantified by our long-term data. Stream data indicate that the leaching loss is generally small and forest biomass data indicate that the vegetation is currently a source, not a sink, of N (Yanai et al. 2013). The soil sink and gaseous loss terms are not well constrained and the subject of current and proposed research. The key questions that will drive our N cycling research over the next six years are:

* What is the fate of N in the mineral soil? How much N is retained, by what processes and in what form and in what soil fraction? How does this source or sink change over the course of ecosystem development?
* What factors control the gaseous loss of N from the ecosystem? How does this flux vary in space and time, and what is the time- and space- integrated total loss rate from the ecosystem?

Mineral soil N retention. While the forest floor N pool has been relatively constant over time (Yanai et al. 2013), the mineral soil pool has not been monitored and could constitute a substantial sink for N. The dynamics of N retention and release in the mineral horizons are spatially heterogeneous and may vary over the course of ecosystem development. We hypothesize that the Vitousek and Reiners (1975) model is incomplete because it does not account for exchanges of N with the mineral soil. During periods of rapid vegetation growth and N uptake, the demand for N by plants exceeds supply in atmospheric deposition, and the trees extract stored N from the mineral soil to supply their needs (N “mining”). As vegetation N demand slows to less than the amount supplied by atmospheric deposition, the excess N can re-accumulate in the mineral soil, creating a sink that prevents N leaching. Thus the mineral soil serves as an “N Bank” that can be borrowed from during periods of rapid growth, but is “repaid” during periods of slower growth (FIG. 14 N Bank diagram). N leaching occurs after the re-accumulation of soil N is complete and the soil N pool reaches a steady state. We suggest that the reference watershed (W6) at HBR is in the soil re-accumulation phase, preventing significant amounts of N leaching (FIG. 14). *This represents a substantial revision to a widely-held ecosystem theory.*

*Approach.* To evaluate the conceptual model shown in Fig. 14 we need to understand the fate of N in the mineral soil over the course of ecosystem succession. Mineral soil N pools are large and spatially heterogeneous and thus it is difficult to directly measure small changes (Yanai et al. 2013), but small changes in mineral soil pools are equivalent to very large changes in the vegetation and forest floor. Isotopic measurements provide much better resolution of N fluxes to the soil, and we will add double-labeled (with stable isotopes 13C and 15N) litter to determine the ability of mineral soil horizons to retain C and N in stands across a successional sequence at HBR and surrounding forests. We will use 15N NMR to help determine the form of N retained in the soil organic matter. We will also measure soil and plant C and N pools and root biomass and enzyme activity to observe patterns of root N mining. The data will be used to improve parameterization of the PnET-SOM model, and the model will be used to explore the implications of the results in a successional context. (Box 1).

Gaseous N losses.Although gaseous loss from denitrification has generally not been considered an important process in oxic soils, recent stable isotope (Wexler et al. 2014) and gas flux (Kulkarni et al. 2014, 2015, Morse et al. 2015b, 2015c) evidence from HBR indicates that gaseous losses could be much greater than expected, may be occurring in upland soils and in shallow saturated zones, and that much of the N could be lost as N2 rather than N2O. The recent trend to warmer and wetter conditions could be increasing these gaseous losses.

**Box 1. Quantitative Models.**

At HBR we use quantitative models for synthesizing data and experimental knowledge, identifying knowledge gaps, developing hypotheses, and making predictions of future ecosystem behavior. A variety of models has been used to address a wide range of research questions. Existing models are being adapted to use for specific questions in the project and new models are under development. Here we provide a brief description of models mentioned in this proposal and references for further information.

**PnET Models**: Stand-level ecosystem carbon and nutrient cycling models; originally developed by John Aber et al (e.g., Aber et al. 1997) using data from HBR and other sites. We use several versions:

**PnET-CN**: Includes carbon and nitrogen cycling, forest production and respiration, basic hydrology, climate and disturbance. Has been used for evaluations of effects of land use history, N deposition, climate change and other disturbances on C and N cycling (Aber and Driscoll 1997, Aber et al. 2002 , Ollinger et al. 2002, Ollinger et al. 2008). Will be used for modeling climate, phenology and N deposition impacts on forest productivity and N cycling.

**Pnet-BGC**: Adds major ion chemistry to PnET-CN. Used for simulation of vegetation, soil, and surface water biogeochemistry in response to air pollution, climate change, and land disturbance (e.g., Gbondo-Tugbawa et al. 2002, Pourmokhtarian et al. 2012). Will be used for simulating impacts of depleted soil Ca reserves and forecasting trends in stream chemistry.

**PnET-SOM**: Adds a more detailed soil C and N module to PnET-CN, including more soil C pools and transformations and a denitrification routine (Tonitto et al. 2014). Will be used for modeling soil C and N retention and gaseous losses.

**Spe-CN**: A forest C and N cycling model parameterized for individual tree species; unlike PnET-CN, allows simulate impacts changing species composition on ecosystem C and N dynamics. Recently developed using data from HBR and other sites (Crowley et al. in review). Will be used to assess how vegetation changes due to succession, invasive pests and other disturbances influence nutrient cycling.

**Ecosystem Demography model, version 2.2 (ED2) model**: ED2 combines the logic of forest gap models with a biophysical land surface model by scaling processes from individual trees to regional ecosystems to simulate vegetation dynamics, CO2 exchange, and the energy balance (Medvigy et al. 2009). Will be used in conjunction with the Predictive Ecosystem Analyzer (LeBauer et al. 2013), which facilitates Bayesian model-data assimilation, to simulate vegetation changes within HBR forests.

**Multiple Element Limitation (MEL) model**. The MEL model (Rastetter et al. 1997) couples ecosystem C, N, P and water cycles. The heart of the model is an algorithm that simulates redistribution of plant “uptake effort” to optimize relative acquisition of these resources from the environment. We calibrated and applied the MEL model to forest recovery from disturbance at HBR (Rastetter et al. 2013), and we are now testing the model with a factorial N X P fertilization study at HBR and regional sites.

*Approach.* We have been monitoring a suite of microbial biomass and activity variables (including denitrification potential) at HBR since 1994 (Bohlen et al. 2001, Groffman et al. 2006a, 2010) and

soil:atmosphere fluxes of nitrous oxide since 2001 (Groffman et al. 2006b, 2009, 2010). These measurements have been coupled with more detailed measurements of N2 and N2O fluxes to produce estimates of N gas losses relevant to watershed mass balances. The long-term data have been useful for illustrating how and when changes in overall microbial N cycling processes lead to changes in gas fluxes (Kulkarni et al. 2014, 2015, Morse et al. 2015b, 2015c). We propose to continue these long-term data streams and to use them as a cue for more detailed measurements of actual flux in specific places and times. In addition, our studies of natural abundance stable isotopes (15N and 18O in NO3-) in soil solutions and stream water suggest denitrification in shallow groundwater of upland soils (Wexler et al. 2014). We will expand the isotopic measurements to track seasonal and spatial patterns in denitrification and to relate them to hydrologic fluxes. The results will be used to improve the simulation of denitrification in the PnET-SOM model.

*2.2.4 Multiple element limitation* (Contributes to synthesis question 1. Research team: Fisk, Yanai, Fahey, others…)

According to ecological theory vegetation productivity should tend towards co-limitation by multiple environmental resources, a concept that underlies the MEL model (Rastetter et al. 1997) which we have calibrated and applied to HBR to investigate forest co-limitation by N and P (Rastetter et al. 2013). We advance the concept that a variety of natural and anthropogenic factors challenge the maintenance of balanced N and P nutrition, including the legacy of decades of pollutant N deposition that would be expected to alleviate N limitation and exacerbate P limitation (Fig?). However, several mechanisms could counteract these challenges to balanced nutrition and maintain N and P co-limitation (Fig.). . We are exploring these element interactions in a N and P fertilization experiment in a set of 13 forest stands that span a wide range of soil fertility and forest age (Fisk et al. 2014). We have been adding low levels of N and/or P for five years, and our initial findings indicate that P limits forest biomass accumulation in mid-successional stands (see section 1.1); however, we predict that over time species composition (both above and below-ground) and allocation to acquisition of N vs P will shift, leading to co-limitation with N.

This experiment is designed to answer three key questions:

* How does nutrient limitation or co-limitation of forest productivity develop through time?
* Which plant and soil mechanisms are most important to intermediate-term (5-15 y) responses that maintain N and P co-limitation?
* How do plant and microbial responses to added N and P vary across a native soil fertility gradient?

*Approach.* We will continue N and P fertilization in 13 northern hardwood stands located in three sites (Hubbard Brook, Bartlett Experimental Forest, Jeffers Brook) in the White Mountain region. The sites were chosen to represent regional variation in soil mineralogy. Each stand has four plots (each plot is 0.25 ha in the older stands and 0.16 ha in the younger stands)-- a control plot and three plots treated with N (30 kg N ha-1yr-1), P (10 kg P ha-1yr -1), and both N and P, added annually since spring 2011. These relatively low doses are designed to alter site fertility while minimizing artifacts associated with higher doses of fertilizer.. We will quantify tree growth and mortality, litterfall, total soil respiration, and fine root growth responses to N and P to test for limitation or co-limitation of forest productivity. We will also measure soil enzyme activities, microbial nutrient pools and turnover, rhizosphere allocation, and mycorrhizal functional groups to identify belowground responses that mediate nutrient recycling and plant uptake. The various mechanisms contributing to nutrient recycling and productivity responses will be compared across our suite of 13 stands to evaluate how initial soil fertility and successional stage influence responses. Results will be used in the MEL model for more general application in forest ecosystems and will contribute to our theoretical understanding of nutrient limitation.

**2.3 Theme 2: Changing Climate**

*2.3.1. Overview*

. Our long-term data (section 1.2) reveal numerous intriguing trends that motivate our new research to evaluate physical, chemical, and biological responses to climate change. Of these trends, the decline in evapotranspiration (ET), the decline in snowpack depth and duration, the lengthening of the growing season, and the expansion of the period between snowmelt and tree budburst are of particular interest. Research described below seeks to improve our understanding of these phenomena, place them in the context of other sources of variation, and explore their implications for organisms and ecosystem processes in the forest and streams.

*2.3.2 Changes in ET: Response to climate variability and forest disturbance* (Contributes to synthesis question 3. Research Team: Green, Asbjornsen, Campbell, Matthes, McGuire…)

To investigate the long-term decline in ET, we will utilize methods that can address ET variability across spatial scales from individual trees to the landscape (FIG. 15). Possible reasons for the decline include endogenous factors linked with tree physiology, such as changing nutrition by N and Ca, changes in photosynthesis or water use efficiency due to changing atmospheric CO2 concentrations, or by exogenous drivers such as altered temperature, solar radiation, or humidity. ET can change dramatically in response to ecological disturbances, or over decadal timescales in response to climate. Thus, understanding the dynamics of ET change will improve predictions of how individuals, communities, and ecosystems respond to and control future hydrologic change. Our major research question is:

* What is the relative magnitude, direction, and persistence of ET change in response to climate variability versus forest disturbance?

*Approach.* We will evaluate ET trends at four time scales: long-term forest succession (60 years), decadal response to disturbance (5 to 10 years), seasonal response to annual climate (1 year), and synoptic response to weather (weeks). Causes of trends at all four time scales will be assessed using multiple datasets including: meteorological records, modeling, dendrochronological isotope analysis to assess stem increment growth and the natural abundance 13C and 18O composition of annual tree rings (as a proxy for physiological drivers of ET trends due to stomatal regulation of leaf-level exchange of H2O and CO2), and landscape-scale measurement of micrometeorological ET flux.

Analysis of the response to disturbance will involve retrospective analysis of the forest harvesting treatments at HBR. The seasonal controls will be assessed using eddy covariance at our new flux tower site (see section 2.1.3) and sapflow measurements collected across the HBR. The ET will be assessed for its onset, peak, and decline relative to meteorology and phenology controls. The eddy covariance and sapflow measurements will also be used to assess controls on short-term variability of ET. This work will focus on meteorological and soil moisture controls on ET (e.g., short-term droughts, airmass type, across-canopy moisture flux). Results will be synthesized across time scales with the ED2 model (Box 1).

* + 1. *Changing seasonality* (Three subprojects; all contribute to synthesis question 4)

Vegetation phenology, forest carbon cycling and biosphere-atmosphere interactions. (Research team Richardson, Green, others…) Plant phenology is highly responsive to both weather and climate. Phenology mediates interannual variation in ecosystem productivity and carbon uptake by setting the start and end of the growing season (Richardson *et al.*, 2010; Keenan *et al.*, 2014). Additionally, phenology influences the seasonality of fluxes of CO2, water, energy, and volatile organic compounds (Richardson *et al.*, 2013a). Despite its importance, phenology is one of the least understood, and most poorly represented, processes in current-generation biosphere models (Richardson *et al.*, 2012). Our central question is:

* How does the timing of the start and end of the growing season influence whole-ecosystem photosynthesis, evapotranspiration, and partitioning of the surface energy budget?

*Approach.* We will take advantage of ongoing, long-term data sets collected at HBR and BEF. These data include 25 years of tree phenology data from HBR (Richardson et al., 2006); 8 years of digital camera imagery from BEF and HBR (Richardson et al., 2013b); and 12 years of eddy covariance measurements of ecosystem-scale fluxes of carbon, water, and energy between the forest and the atmosphere from BEF (Jenkins et al., 2007). We will (1) conduct data-driven studies of the response of atmosphere-biosphere exchanges of C, heat and water to changes in the timing of budbreak and leaf senescence; (2) develop new predictive models for spring leaf-out and autumn senescence, and use these to evaluate past and potential future shifts in growing season length; and (3) integrate our new phenological sub-models with the ecosystem model PnET-CN to investigate the potential impact of future shifts in phenology on ecosystem processes related to C and N.

Seasonality and the spring trigger. (Research team: Groffman, others…) The winter/spring transition is critical to forest ecosystem biogeochemistry because soil microbial mineralization processes are active, but plants have not yet become a dominant sink for water or nutrients for the growing season (Muller and Bormann 1976, Zak et al. 1990). This opening of the “vernal window” is lengthening at HBR because the timing of snow melt and associated increases in soil microbial activity is advancing faster than tree leaf out(Groffman et al. 2012) (FIG. 9). We observe a rapid increase in surface soil temperature of up to 8 C, just as snow melts, resulting in an abrupt increase in soil microbial activity-- a “spring trigger” for the opening of the vernal window. (FIG. 9), leading to the question:

* Does variation in the vernal window drive variation in hydrologic and gaseous N losses during the spring period?

*Approach.*  We will address this question with careful monitoring of the timing of the spring trigger combined with ongoing measurements of soil solution and watershed N exports. This will include detailed monitoring of the transition cascade from energy balance (using the eddy covariance tower at HBEF) to snowpack dynamics, to soil moisture and temperature, to stream temperature and chemistry. We will also seek non-LTER funding to manipulate the system though snow removals and additions during the winter/spring transition.

Seasonality and stream carbon dynamics. (Research Team: Rosi-Marshall, Bernhardt, Likens). Spring and autumn are arguably the most important seasons for in-stream carbon processes and invertebrate consumers in headwater streams (ref). At HBR, the greatest watershed export of N occurs in early spring and differences in spring conditions cause substantial interannual variability in watershed export (ref). Historically, allochthonous inputs have dominated C cycling in the streams at HBR and there has been very little contribution by in-stream algal production (Fisher and Likens 1973). However, recently we have observed spring algal blooms in some headwater streams. The causes are not known, but may be related to changing stream chemistry (Likens and Buso 2012). Interestingly, algal blooms have never been observed in the less acidic stream draining the CaSiO3 amended watershed (W1). This leads to the question:

* How does seasonal variation in the spring and autumn interact with changing water chemistry to influence stream carbon dynamics?

*Approach:* We will employ long-term monitoring of in-stream conditions and organic matter dynamics in three streams across a gradient of pH (W6, W1, and W9). Sensors will include data loggers to record in-stream temperature and conductivity, light detectors at the surface of the stream, and cameras (linked into the sensor network) for remote observation of stream conditions. The cameras will allow us to track algal blooms and to estimate the timing and extent of leaf litter inputs in the fall. In the spring, we will deploy tiles in the streams and will collect them every two weeks until canopy closure to estimate algal standing crop. When an algal bloom occurs we will also conduct an extensive survey of algal standing crop throughout reaches of 100 m. In the autumn, we will deploy standard litterbags to measure leaf litter decomposition rates and invertebrate consumers (Entrekin et al. 2008). We will also examine the influence of C dynamics on primary consumers be measuring emergence production using nets constructed over the stream channels (Hall et al 1980). We will measure emergence 3 times during the 6 year LTER cycle, once after a spring algal bloom, once after a spring without an algal bloom and once during the autumn. Data will be compared to past measurements at HBR (e.g. Fisher and Likens 1973) to investigate long-term changes in stream C dynamics. This project involves two new HBR-LTER co-PIs (Rosi-Marshall and Bernhardt) and addresses the mid-term review recommendation to invest in stream ecology research.

*2.3.4 Climate change effects on N cycling* (Contributes to synthesis question 3. Research team: Groffman, Templer, others…) )

We investigate the impacts of climate change on N cycling using both comparative studies and experimental manipulations. The natural elevation gradient at HBR creates an approximately 2oC difference in mean annual temperature between low and high elevation locations, with little difference in soil and vegetation type. The sites at lower elevation have lower net N mineralization and nitrification (FIG. 16 soil microbial process trends), which control the availability of inorganic N for plant uptake, leaching and denitrification. In addition to this comparative study, we initiated a field experiment, the Climate Change Across Seasons Experiment (CCASE), to examine the interaction of climate change in the growing and dormant seasons. Soils are warmed 5 0C with heating cables throughout the growing season (April through October) and snow is removed in winter to induce soil freezing. This combination of experimental treatments allows us to determine the interactive effects of projected warmer soils in the growing season and colder soils in winter (ref). Recent results show that soil freezing in winter damages roots and impairs the ability of maple trees to take up N and water at the beginning of the growing season, but warmer soil temperatures in the growing season allow maple trees to repair the root damage caused by soil freezing.

The key question driving these studies is:

* How does climate change alter the processes of production, uptake, and loss of N in the ecosystem?

*Approach.* We will continue our measurements along the elevational gradient and analyze long-term relationships between mineralization, nitrification, climate and watershed N losses to improve understanding of climate effects on N supply and loss (Groffman et al. 2009, Durán et al. 2014, 2015b). We propose to add measurements of foliar N, spring ephemeral plants, and insect population dynamics to this study. In the CCASE experiment we will continue the treatments and measure soil N cycling (i.e. mineralization, nitrification, denitrification, and N leaching), tree N uptake, root health, and sap flow (i.e. water uptake and transpiration).

*2.3.5 Climate change, N availability, and forest food webs* (Contributes to synthesis questions 4 and 5. Research team: Ayres, Lany, others?...)

Strong seasonality is a prominent feature of animal populations at HBR and north temperate hardwood forests in general. Spring and early summer is the time of maximal biological activity for animals, especially for leaf-eating insects, chiefly caterpillars, which feed at high rates under favorable temperatures (Jones et al. 200?, Reynolds et al. 2007, Lany 2014, Lany et al. 2015), and birds, which are producing eggs and feeding young. A second conspicuous feature of HBR is high interannual variability in the abundance of 1° consumers. Caterpillar abundance and biomass varies by > 30-fold among years (Reynolds et al. 2007). Years of high caterpillar abundance are causally related to high nesting success of birds and increased recruitment of 1-year-old birds the following spring (refs). The variability in 1° consumers at HBR contrasts to net primary production, which is stable to within +/- 20% (Fahey et al. 2005). Thus, if food resources influence the abundance and diversity of animals in HBR it is most likely due to the quality of food rather than the quantity.

The season of highest animal activity in HBR coincides with the availability of relatively high quality plant tissue for herbivores. Caterpillars of HBR grow faster when consuming foliage with higher leaf N (Lany 2014). Leaf N concentration in hardwood trees is highest just after budburst and declines through leaf expansion. Any feature of climate change that affects the availability of foliage with high N for herbivores could affect the green food web in general.

We will evaluate three general pathways by which climate change could influence the diversity and abundance of animals at HBR.

* Summers are getting longer and warmer at HBR. Annual thermal sums have increased by 200 – 300 degree days (~14 %) since 1961. This is related to the abundance of 1° consumers: caterpillar abundance tends to increase following summers that are relatively long and warm (high thermal sums) and to decrease following cool summers (Reynolds et al. 2007).
* The average timing of budburst has advanced by ~ 7 d since 1961, and the two earliest springs in 50 years have been within the last four years (Lany et al. 2015). Changing leafout dates can alter the phenological associations among species. For example, the timing of nest initiation by Black-throated Blue Warblers, a well-studied Neotropical migrant, advances by only about 6 days for a 10-day advance in leaf expansion, and the recent early springs are coming closer to their inflexible dates of arrival on the breeding grounds (Lany et al. 2015).
* Temperatures during leaf expansion are getting cooler. A feature of HBR climate is that when budburst is earlier in the spring, temperatures during leaf expansion and bird nesting are cooler than in an average year. Thus the increasingly frequent early springs at HBR are associated with cooler temperatures at which early season caterpillars feed and grow more slowly (Lany 2014). Lepidoptera that feed on early season leaves are the main source of overall interannual variation in Lepidoptera abundance (Stange et al. 2011).

Key questions regarding effects of climate change on forest food webs are:

* How resilient to climate change is phenological synchrony among plants, insects and birds?
* What are effects on the green food web of temperatures being warmer or cooler during budburst and leaf expansion when foliar N is high and animal activity is maximal?
* What causes interannual variation in leaf N and what are consequences for the green food web?
* Is the brown (detrital) food web buffered from the effects of leaf N variation because of litter mixing and retranslocation of N prior to leaf drop?

*Approach.* To answer these questions we will continue and expand annual long-term tracking of animal populations at HBR. Our studies will take advantage of variability among years and across elevations in temperatures and foliar N. Existing programs include sampling of flying insects with malaise traps and foliage surveys for caterpillars and spiders (Lany et al. 2015); valley-wide monitoring (point counts) for birds and diurnally active small mammals (Holmes et al. 2011); blacklighting for moths (Stange et al. 2011); measurement of foliar N concentrations across dates, species, and elevations (Lany 2014), and surveys for stream salamanders (Greene et al. 2008, Burton and Likens 1975). New measurements will include (1) systematic annual sampling of brown web invertebrates via litter samples, pitfall traps, and soil cores; (2) sampling of bats with automated recorders (Coleman et al. 2014, Froidevaux et al. 2014); (3) estimation of abundance of terrestrial salamanders, which are the top predators in the brown web , permitting comparisons with historical surveys that have become inactive (Burton 1976); and (4) estimates of % herbivory from large samples of leaves examined shortly before abscission begins. To strengthen analyses of interannual patterns we will also add measurements of potential N mineralization and nitrification and extractable NH4+ and NO3- in the soil and extend fine scale measurements of air and soil temperature and soil moisture to provide high coverage across our study sites.

**2.4 Theme 3: Changing biota**

2.4.1 *Overview*

The magnitude and pace of change in forest biota are accelerated by disturbances such as forest harvesting, climate change and species invasions. Several aspects of the long-term record of biotic change at HBR motivate the proposed research in this section. First, the HBR forests are subject to multiple interacting drivers that alter the structure and species composition in complex ways. Climate change, natural successional dynamics, nutrient depletion due to chronic acid deposition, and introduced diseases are simultaneously affecting the dynamics of the forest. In the near future, two new introduced pests, emerald ash borer and hemlock woolly adelgid, are likely to have severe effects.. In the headwater streams, the decline of a top predator, the salamander *Gyrinophilus porphyriticus*, may restructure the stream food web. These trends demand new measurements and a more encompassing models of forest ecosystem dynamics.

2.4.2 *Vegetation dynamics* (Contributes to synthesis question 3. Research team: Battles, Fahey, Cleavitt, Matthes…)

Results from our network of long-term vegetation plots contradict a fundamental premise of the original Hubbard Brook model of ecosystem dynamics – “the shifting mosaic steady state”. As conceived by Bormann and Likens (1979), the end point of succession in northern hardwood forests is defined by vegetation stability where the competitively superior tree species, sugar maple and American beech, replace themselves over time. However these expectations no longer hold. For example, a remarkable proportional increase (up to X%) in American beech in the young adult size class (10-30 cm) in the HBR forest represents a radical shift in the canopy of the future (van Doorn 2014). Drivers of these changes include the depletion of soil nutrients due to acid rain (Likens et al. 1996, Battles et al. 2014), which favors beech over the more nutrient-demanding maple, and the progression of beech bark disease (Lovett et al. 2006), which kills mature beech but increases sapling production through root sprouting.

Such profound shifts in forest structure and composition will alter thethe biogeophysical template that governs other population, community and ecosystem processes. We propose a revision to our conceptual model that accommodates such transient as well as steady-state dynamics. We build on the hierarchical-response framework (HRF) proposed by Smith et al. (2009). Evidence from HBR suggests that directional change through time is characterized by multiple stepped responses (FIG. 17:HRF). Initially the consequence of chronic stress is limited to individual responses (e.g., reduced growth) that do not immediately translate into changes in ecosystem function (FIG.17A). As the stressor persists, demographic trends in tree species are manifested as a re-ordering of species composition (FIG. 17B). These shifts in community composition modify ecosystem function (e.g., declines in productivity *sensu* Smith et al. 2015). Continued exposure (or the inclusion of additional stressors) can result in the introduction of new species via immigration (FIG. 17C) that exacerbate trajectories of decline. The co-occurrence of an episodic disturbance (e.g., windstorms) likely would accelerate directional changes already underway (FIG. 17D).

We assert that it is essential to quantify the patterns and processes of tree recruitment in order to understand the direction and rate of vegetation change. Historically our sampling has emphasized established trees (≥ 2 cm in diameter at breast height or 1.37 m) since they dominate the contribution to carbon and nutrient budgets, but forest transitions start with regeneration. For example, our recent work on seedling demography has begun to outline how episodic reproduction, gradients in light and nutrient availability, and seedling traits interact to influence the likelihood of survival (Cleavitt et al. 2008, Cleavitt et al. 2011, Cleavitt et al. 2014). Yet key questions remain:

* How does tree recruitment success vary across the geophysical and historical template?
* How does the demographic performance of tree species vary between adults and juveniles?
* What is the relative importance of seed dispersal versus seedling survival in constraining the migration of tree species?

*Approach.* We will extend our existing seedling monitoring efforts to incorporate all the major geophysical gradients in the Hubbard Brook Valley. Specifically, we will establish seedling transects in a stratified random subset of our valley-wide permanent plot network. We will identify new germinants each year and track the fate of existing seedlings. We will quantify the light environment with hemispherical photography and measure the seed bed We will directly link these new measurements to the existing data on the population dynamics of adults (i.e., van Doorn et al. 2011) and soil resource availability (Battles and Fahey 2015). Also, we will add identical seedling transects to the six sites where we track leaf and seed production in the reference watershed (W6) and our experimental Ca-addition study (W1). Again the co-location of seedling transects within our existing vegetation monitoring scheme leverages existing data – in this case, seed production and dispersal. The inclusion of seedling transects allows us to track all three steps in tree recruitment: seed production, seed dispersal, and seedling survival. These efforts will allow us to measure incipient changes by calculating population transition probabilities for the trees. The subsequent step of associating these probabilities with drivers such as natural disturbance events, diseases, and immigration will test predictions from the hierarchical response framework.

* + 1. *The incipient loss of Fraxinus from HBR* (Contributes to synthesis question 3. Research team Ayres, Battles, Lovett…)

The emerald ash borer (*Agrilus planipennis*), an invasive insects that kills ash (*Fraxinus*) trees, was within 50 km of HBR as of November 2015. Based on patterns elsewhere, we can expect that it will virtually eliminate ash from HBR and the surrounding region within the next 5-10 years (Herms et al. 2014). North American ash is closely associated with > 40 species of native insects that are judged to be at risk from the extirpation of ash (Gandhi and Herms 2010). In addition, white ash (*F. americana,* the ash species present at HBR) has highly decomposable litter (Lovett et al. 2015) and produces soil organic matter with low C:N ratios and high nitrification rates (Venterea et al. 2002), thus potentially creating hot spots for nitrate leaching and denitrification. Our research on this imminent disturbance will focus on two principal questions:

* What tree species will replace white ash in the forest, and will the traits of the new species cause changes in forest productivity and nutrient cycling?
* Will the loss or severe reduction of ash populations lead to reduced biodiversity in the green and brown food webs, with consequences for ecosystem function (e.g., nutrient cycling, hydrology, and interannual stability of food webs), or will there be sufficient redundancy that the ecosystem will be relatively little changed in structure or function?

*Approach.* We will combine ground vegetation surveys and remote sensing to map the canopy ash trees of HBR and to document their death. We will extend a sampling program started in 2015 to characterize the above- and below-ground invertebrate communities associated with ash vs. other hardwood trees in HBR. Sampling includes (1) beat sheets and vacuum sampling for foliage insects, and (2) pitfall traps, litter samples, and soil cores for brown web insects and fungi living below canopy ash trees. We will add sampling of understory plants (including spring ephemerals) and soil fungi to provide a representative baseline inventory of fauna and flora associated with ash in HBR..

We will use our vegetation survey data to identify the most important co-dominants with ash in different parts of the landscape, and then use the Spe-CN model (Box 1?) to predict how the decline of ash and its replacement will affect C and N cycling in the ecosystem. In a selected set of ash-dominant stands, we will begin monitoring of plant and soil C and N pools (live wood, downed wood, forest floor, and upper mineral soil) prior to the arrival of the emerald ash borer. Many of these pools change slowly, so all of the expected changes will not be manifested during the term of this proposal. However we will continue to monitor these plots at 5-y intervals to determine if the responses are consistent with model predictions.

*2.4.5 Changing stream food webs.* (Contributes to synthesis question 4. Research team: Lowe, Rosi-Marshall, Bernhardt…)

A 12-year data set on the stream salamander *Gyrinophilus porphyriticus* from northern NH showed a significant decline in abundance which may be linked to climate-- abundance is negatively correlated with annual precipitation, and metamorphosing individuals may be killed during spring and fall floods, which have increased in frequency (Lowe 2012). *G. porphyriticus* is the top predator in the fishless headwater streams that dominate the HBR. Therefore, declines in this species may lead to significant changes in the composition, structure, and function of headwater food webs. We tested for these top-down effects on stream invertebrate communities experimentally, using replicate stream mesocosms with treatments that differ in salamander abundance and species composition (i.e., single-species v. multi-species). Surprisingly, we found that *G. porphyriticus* significantly reduces stream invertebrate abundance when occurring alone, but not when it occurs with *Eurycea bislineata*, another widespread stream salamander at HBR and known intra-guild prey of *G. porphyriticus* (Resetarits 1991).

These findings justify further investigation of changes in headwater stream food webs, and represent an excellent opportunity to expand stream research at HBR, as recommended in the mid-term review. Our experimental results also give us the opportunity to explore the ecosystem effects of intra-guild predation, thus linking the long history of steam ecosystem research at HBR to broader community ecology theory and models (Polis and Holt 1992, Rudolf 2006). The key question driving this new research is:

* How do declines in the salamander population (*G. porphyriticus*) affect the stream invertebrate community and stream ecosystem function?

*Approach*. To track changes in headwater food webs, we propose to continue intensive capture-mark-recapture studies of salamander populations (*G. porphyriticus* and *E. bislineata*) in five HBR streams. These surveys were initiated in 2012. We propose to assess the broader effects of changes in top-predator populations by sampling stream community and ecosystem variables in reaches that span gradients of salamander abundance and species composition. These response variables include in-stream invertebrate productivity, stream-to-forest flux of invertebrate subsidies, in-stream primary productivity, and N and P export, and carbon cycling (see section 2.3.3 above).

* 1. **Characterizing the geophysical template and ecosystem responses**

An important recent advance at HBR has been moving beyond the small gauged watersheds that were the subject of most of the early manipulations (Table 2) and developing a more detailed understanding of the spatial heterogeneity present across the entire HBR valley (~3000 ha). We use the term “valley-wide” to describe research at this larger scale. Variations in bedrock, glacial deposits, topography and disturbance history structure the vegetation patterns in the valley. These vegetation patterns combine with physical factors such as climate and soils to influence landscape scale patterns of important ecosystem characteristics such as foliar chemistry (FIG. 18 Foliar N image), N cycling , stream chemistry (FIG 19 Buso and Likens pH map), and bird abundance (FIG. 20). Research on this underlying template and its influence on landscape-level patterns is an important part of the HBR project.

*2.5.1 Hydropedologic research: Validating and extending the model of hydrology and soil formation* (Research team: Bailey, McGuire, Pardo?)

Our recent research has shown that soil units defined by varying expression of podzolization, the dominant soil forming process in the Northern Forest region, are distributed according to distinct regimes in water table fluctuation in soils (FIG. 21) (Bailey et al. 2014, Gannon et al. 2014). We have shown that the distribution of these “hydropedologic units” can be predicted by topographic analysis at the catchment scale (Gillin et al. 2015). The hydropedologic approach has been useful in understanding stream chemistry (Zimmer et al. 2013, McGuire et al. 2014, Gannon et al. 2015) and N dynamics (Morse et al. 2014, Wexler et al. 2014). The next phase in this research is to extend the hydropedological concept, which was developed by careful study of our hydrologic reference watershed (W3), to a broader scale.

Our research question is:

What additional hydropedological units are encountered as we scale up to the entire HBR valley?

Approach. We propose to utilize existing soil descriptions recorded across the valley for previous watershed experiments, the valley-wide network of permanent vegetation monitoring plots, and other studies as validation of a trial application, extending the hydropedologic model beyond W3. We expect that our current model will work well at predicting spatial variation in soils for portions of the valley with similar geologic parent materials and physiographic position, but will not work well across the broader range of conditions. New sampling strategies will be developed to characterize hydropedologic conditions where the model fails to predict existing soil descriptions and used to improve models (e.g., Gillin et al. 2015).

2.5.2 Headwater streams and *Valley-wide stream survey* (Research team: McGuire, Bailey, Likens?…)

A hallmark of HBR research is the ecology of headwater streams and their watersheds (e.g., Fisher and Likens 1972, Bernhardt et al. 2005). Headwater streams across the Hubbard Brook valley display a surprisingly high chemical diversity (e.g. in pH, FIG. 18- Valley wide stream pH) (Likens and Buso 2006, McGuire et al. 2014). This same chemical diversity of streams is present at the small watershed scale when the entire channel network is sampled at a fine spatial scale (Zimmer et al. (2013). These patterns add a great deal of diversity to, and challenge the conceptual model of, controls on stream chemistry presented by Johnson et al. (1981). Moreover, bluelines on USGS topographic maps, the standard inventory of streams in the US, are very incomplete, representing <10% of perennial stream channel length at HBR, and not accounting for an even greater length of seasonally flowing streams (Zimmer et al. 2013). These small headwater stream reaches are dynamic ecotonal systems where hydrologic processes mediate the export of dissolved material such as DOC (Gannon et al. 2015) and N (Wexler et al. 2014). We will undertake a new initiative to begin the process of mapping the complete stream network, including seasonal streams across the HBR valley. We propose to address the following questions: What properties of the geophysical template lead to the initiation of seasonal streams and to the transition to perennial flow? What is the function of seasonal streams in controlling the chemistry of downstream perennial reaches?

Approach.We will undertake detailed mapping of perennial and temporary streams by direct observation in selected catchments, identifying physiographic signatures of flow-permanence/intermittence in these mapped sections, and then using topographic analysis of detailed LiDAR derived DEMs to predict seasonal and permanent stream networks across the entire valley. Direct observations in other catchments will validate the modeled stream distribution. Synoptic stream chemistry surveys will be conducted in several catchments representing the range of chemistry conditions reported by Likens and Buso (2006) to see if similar patterns emerge at the fine scale, and to elucidate the transition from seasonal to perennial streams, as reported by Zimmer et al. (2013) for W3.

*2.5.3 Spatial patterns of animal populations* (Research team: Ayres, Lowe, Christenson, TerHofstede…)

Our measurements of bird abundance at the valley-wide spatial scale have shown that bird populations vary significantly among years but that the spatial pattern of bird abundance and diversity across the HBR valley remains relatively constant. In stream salamanders, we have found surprising, fine-scale (e.g., within stream) patterns of evolutionary divergence within the HBR (Lowe et al. 2012). These patterns set the stage for exciting new research about the linkages and feedbacks among ecological, evolutionary and ecosystem process involving animals in the HBR ecosystem. . We will take advantage of spatial patterning in ecosystem characteristics and processes to test hypotheses about the relative influence of abiotic variables (climate, soil moisture, aspect, etc.), vegetation variables (composition, structure, productivity) and trophic interactions on the abundances and species associations of animals across the landscape. We will address the following question:

Approach. To complement the ongoing surveys of birds, small mammals, Lepidoptera and salamanders, we will monitor the spatial patterns of other key animal groups to evaluate spatial and temporal concordance of patterns across groups and to quantify how these patterns are linked to ecosystem processes playing out on the hydropedologic template. New surveys will include large mammal activity using motion-detecting, infrared game cameras that have been positioned throughout the HBR valley since the fall of 2014. Systematic sampling of bat populations began in 2015 and will continue with a combination of (1) continuous automated recording of bat calls in selected locations known to have high bat use, and (2) short-term sampling (also via ultrasonic detectors) of multiple locations drawn from those of the valley-wide bird studies. To assess patterns and abundances of litter and soil invertebrates (the brown food web), 20 sites, located along two elevational transects within northern hardwood forest (from ~ 300 to 750 m asl, one each with northern and southern aspects) will be monitored each year during two key seasons: late spring and mid-fall. Both litter and soil samples will be processed using the Berlese and Baermann funnel extraction methods (ref xxxx) to identify all invertebrates to at least the level required to infer functional group, and to genera or species when possible.

**2.6 HBR research infrastructure for the 21st century**

*2.6.1 Sensor Technology to Enhance Research and Monitoring (Research team: Rustad, Campbell, Green, Martin…)*

Undoubtedly, scientific breakthroughs of the 21st century will be powered by technologies that help researchers collect and manipulate massive datasets, visualize the results, and elucidate underlying patterns and processes. Over the past five years, HBR has embraced new environmental sensor technologies, wireless communications capabilities, data visualization tools, and streaming, real time QA/QC procedures. We maintain digital sensors at nine stream gauging stations, six full meteorological stations, and six soil climate stations, and run six web cams for automated phenologic monitoring. In addition, we are: deploying stream physical and chemical sensors (water temperature, NO3-, organic matter, pH, conductivity, and dissolved oxygen) in two watersheds; streaming real time data online for three experiments (CCASE and the Throughfall Displacement and Ice Storm Experiments described below); instrumenting a water and carbon flux tower; developing automated dendrometer bands; and developing an automated QA/QC procedure to ensure high quality data. Our data are available to the public on our website (Hubbardbrook.org), and are also foundational datasets for the USFS Smart Forests Environmental Sensor Network (Smartforests.org), and the Northeast Environmental Sensor Network (NESensorNet.sr.unh.edu), both of which link sensor data from individual sites to regional and national scale networks. In addition, we have worked with artists and musicians to encode our data as an artistic rendering and musical sonification of the water cycle, making our data more available to a broader audience (Waterviz.org)

*2.6.2 Rapid Assessment Teams (RATS) to assess extreme weather events (Coordinator: Rustad)*

As the frequency and severity of extreme weather events increases under a changing climate, there is a need to better understand and predict the consequences of these events on the ecosystems we study. But studying these events poses challenges: they are unpredictable in time and space, they present unsafe working conditions, and they require additional funds. To prepare for these challenges, we developed Rapid Assessment Teams (RATS) for specific types of extreme events (Wind RAT, Water RAT, Ice RAT, etc). These teams have access to protocols for responding safely and in a timely manner to a specific extreme event, a stockpile of materials and supplies for rapid sample collection and analyses, and funding for hiring additional local staff to clear trails, access sampling locations, and collect samples as needed.

*2.6.3 Transforming the sample archive* (Coordinators: Pardo, Martin)

The HBR Sample Archive is unique in the LTER network in the breadth and organization of its collection, with a dedicated building housing more than 100,000 samples, 27,000 of which have been bar-coded and fully described in a database (viewable on the HBR website). In the last five years approximately 1500 streamwater samples, 1200 precipitation samples, 45 soil samples and 25 foliage samples have been subsampled from the Archive. During the next LTER cycle, we will transform the Archive by re-organizing the collection to improve efficiency, completing the bar-coding, and linking the archive database to the analytical data for each sample. This will enable queries that return a list of samples matching the specific criteria (e.g., stream samples from W6 in the 1980s with NO3-concentration > 2 mg/L), and corresponding metadata (barcode, physical sample location, volume/weight remaining, chemistry, etc). These improvements will create a state-of-the-art resource which will pinpoint the most appropriate samples for specific questions, further expanding its value to researchers from around the world. The HBR Archive serves as a model for other research sites (including LTER sites) and extends the reach of this LTER site well into the future.

**2.7. Related Research**

The HBR-LTER benefits greatly from collaborative efforts and funding from its many research partners. First and foremost, the USDA Forest Service (USFS) maintains and runs the Hubbard Brook Experimental Forest, our principal research site. USFS maintains the site infrastructure (roads, weather stations, weirs, sensor network, etc.), collects the basic hydrological and meteorological data for the site, does much of the chemical analysis of water samples, maintains the sample archive, and provides intellectual collaboration through its team of project scientists. This USFS effort is essential to the success of the HBR-LTER. In addition, two NSF-LTREB grants support data collection for two of our most prominent long-term data sets: weekly precipitation/stream chemistry measurements and the long-term census of breeding birds. Both of these data sets complement our ongoing LTER research. For example, weekly stream chemistry monitoring at the gaging stations of the experimental watersheds (LTREB) provides a temporally detailed context in which to interpret our spatially detailed, monthly LTER sampling of soil solutions and longitudinal stream chemistry (ref.).

In addition, the long-term data from the HBR-LTER has helped us obtain short-term research grants on many of the topics presented here. These grants illustrate leveraging of the LTER funding. For instance, HBR co-PIs have received grants in the last 6 years on subjects such as winter climate change, multiple element limitation, denitrification, calcium addition, N retention in the mineral soil, landform controls on hydrologic flowpaths and pedogenesis, ice storms, stream community ecology, as well as a site-based REU grant. These grants have benefitted from the long-term data and intellectual interactions provided by the LTER, and they augment HBR-LTER activities, but they are not essential for the continuation of the LTER. We are careful and selective about incorporating these projects into the longer-term LTER suite of measurements to avoid overcommitment of resources, while welcoming new investigators.

For example, we have just begun two externally funded experiments that augment our climate change research:

Throughfall displacement experiment (TDE). To assess the response of the northern hardwood forest ecosystem to drought, a TDE was established at HBR in 2015 (primary funding from USDA Northeastern States Research Cooperative, H. Asbjornsen, PI). Two replicate treatment plots were equipped with a system of gutters constructed in the understory to remove approximately 50% of the throughfall from the plots. This experiment is part of the NSF “Drought-Net” RCN and is leading the development of standard protocols for TDEs in forest ecosystems.

Ice storm experiment. With funding from a NSF-Ecosystems grant (C. Driscoll and L. Rustad, PIs), we began a new experiment in 2015 to study the potential impacts of future ice storms. Using fire hoses ice has been generated in 8 experimental plots atvarying intensity and frequency of ice damage. In addition, long-term responses to the severe ice storm that occurred at HBR in 1998 will be evaluated from field data.

**2.8 Synthesis and Prediction**

*2.8.1 Challenges for synthesis and prediction*

Synthesis at HBR has been conducted through iterative analysis of theory, long-term observations, results from plot and watershed experiments, simulation models, and comparative analyses. These approaches are synergistic, enabling us to improve understanding of how multiple aspects of the northern hardwood forest at HBR have changed over time, and to make projections of ecosystem response to future change. Our predictions have not always been accurate. For example, existing ideas about soil formation processes in upland landscapes have been elaborated by our observations of relationships between water table fluctuations and podzolization processes, leading to new models and measurements of solute flux in headwater catchments . Expanding the scale of these observations will likely reveal additional key processes. This iterative…

Over the next six years, we propose to address several significant synthesis, integration and prediction challenges:

1. *How will legacies of air pollution, particularly depletion of exchangeable cations and accumulation of sulfur and nitrogen in the soil, affect the future functioning of forest and stream ecosystems?* Our long term data indicate that depletion of Ca from decades of acid deposition has affected forest growth, stream chemistry, ecosystem N cycling and soil C storage. In addition, the continued decline of air pollution, coupled with depleted reservoirs of base cations in the soil, is producing extremely dilute streamwater. How quickly will forest ecosystems recover from acid deposition? How dilute will streamwater become and how will this affect stream biota? To address these patterns we will conduct simulations of the potential response of HBR watersheds to anticipated future decreases in atmospheric deposition using PnET-BGC, examining the rate, extent, and timing of soil and stream recovery. We will also convene a task group to look across the fields of soil chemistry, hydrology, vegetation physiology and dynamics, and animal population studies to synthesize the knowledge of the impacts of soil base cation depletion, using geochemical tracers, mass balances, long-term trends, and simulation modeling.
2. *What are the soil, microbial and vegetation processes that have permitted nitrogen export in stream water in the reference watershed to remain low despite continued N pollution and cessation of biomass accumulation in the watershed forest?* One of the most vexing mysteries in the long-term records at HBR is the decline in watershed N exports despite continued N inputs from the atmosphere and the lack of N accumulation in forest biomass. We will use new insights from our work on mineral soil N retention and gaseous N loss in combination with data on soil C and N pools, microbial activity, hydrologic fluxes, climate, atmospheric deposition, and biomass trends to quantify the N sinks in our conceptual model (FIG. 12) and elucidate the controls on N loss from the ecosystem. We will synthesize this information using mass-balance budgeting, process constraints derived from stable isotope data, and trend analysis of N export from reference and manipulated watersheds. The new knowledge will be used to improve the mineral soil N exchange and denitrification modules in the PnET-SOM model, which will allow us to extrapolate to longer time and scales simulate disturbances such as harvesting and climate change.
3. *How will simultaneous effects of climate change, air pollution, plant succession, and invasive species, alter the structure, function and biodiversity of forests of HBR?* Our long-term data show that multiple, concurrent drivers are changing tree species composition and forest structure, which in turn will have important effects on ecosystem function. We plan to use a model-data fusion framework to integrate and evaluate our understanding of the cause and consequence of these transient dynamics in tree demography and ecosystem function. Dietze and Matthes (2014) recently proposed innovations in the Ecosystem Demography Model, version 2.2 (ED2, Medvigy et al. 2009) in conjunction with the Predictive Ecosystem Analyzer (PEcAn) informatics system (LeBauer et al. 2013) that account for the cumulative impact of chronic biotic and abiotic stressors that persist for decades. This framework provides the unique ability to model disturbances due to abiotic forcings like climate change and extreme weather events, in addition to biotic forest disturbances due to native or invasive insects and pathogens, through a generalized ecophysiological scheme. The spatiotemporally rich, long-term datasets from HBR are ideally suited to better characterize and attribute decadal scale changes in ecosystem processes with this framework. The long-term vegetation studies provide data for both forest demography and the functional responses (e.g., beech growth as a function of disease severity, sugar maple seedling survival as a function of Ca availability, forest productivity and transpiration) needed to initialize, parameterize, constrain, and validate the ED2 model for HBR. We have recruited an ecosystem data scientist (Matthes) to lead the model-data assimilation effort over the next cycle.
4. *How will changing climate seasonality affect ecosystem functions and food webs?* Seasonal changes are dramatic at HBR and recent research suggests that advances in spring leaf-out have increased both photosynthesis and net C storage of forests at HBR (Richardson et al. 2006, Keenan et al. 2014) and had marked effects on food webs. Over the next six years, we will use new data to develop predictive models for spring leaf-out and autumn senescence, and use these to evaluate past and potential future shifts in growing season length. By integrating our new phenological sub-models with the ecosystem model PnET-CN, we will investigate the potential impact of future shifts in phenology on a suite of ecosystem processes related to C and N cycling. These data streams will be integrated to make projections about how changes in seasonal timing are likely to influence both the biogeochemistry and biodiversity of forests at HBR over the next 50 -100 years.
5. *Is N availability a key driver that integrates microbial, plant and animal population dynamics?* Perhaps the most enduring synthesis and integration challenge at HBR is integrating the long-term datasets on biodiversity (primarily birds and invertebrates) and biogeochemistry (Gosz et al. 1978). We now have accumulating evidence for the importance of seasonal and interannual variation in foliar N to primary consumers (chiefly Lepidoptera). Furthermore, recent advances using the elevation gradient and variation in the geophysical template at HBR have created new opportunities for understanding interconnections among biogeochemistry, foliar chemistry, and forest fauna (Rodenhouse et al. 2009, Groffman et al. 2012). Over the next six years, we will integrate climate, biogeochemical and biodiversity datasets using hierarchical statistical modeling to improve understanding of how changes in vegetation, invertebrates, bird, and mammals over the next 30 years are linked to changes in climate and biogeochemistry, especially foliar N and soil N dynamics but also including Ca and acid/base status.

*2.8.2 Understanding uncertainty to improve ecosystem science.*(Research team: Yanai, Campbell, Battles..)

The long history of intensive sampling at HBR provides a unique opportunity to quantify the uncertainty in our understanding of the ecosystem and to explore efficient means to improve the precision and accuracy of our measurements. We have taken advantage of this opportunity to reduce bias in our forest biomass calculations and to refine our streamflow estimates (Yanai et al. 2010, Yanai et al. 2014). These improvements have directly contributed to new insights regarding forest productivity (Battles et al. 2014) and ecosystem nitrogen dynamics (Yanai et al. 2013). Most recently, we found that the greatest uncertainty in hydrologic input-output budgets was due to missing observations in precipitation chemistry (Campbell et al. 2016). On the other hand, the weekly schedule of sampling of streams was unnecessarily frequent given the variance during base flow (summer time) but not frequent enough during the fluctuating flows associated with snowmelt. We plan to follow-up on these results with the strategic addition of precipitation collectors and dilution gaging during high flows in order to assess alternative monitoring strategies for these key aspects of the hydrologic budget. At HBR and other LTER sites, the diversity of the data we collect and the duration of the record we manage pose unique challenges. Thus our larger goal for this proposal is to expand our focus and develop best practices for the collection, analysis, and curation of ecosystem data over the long-term. By collaborating with colleagues in the LTER Network and in the QUEST research coordinating network (<http://www.esf.edu/quest/>), we will help lead the effort to make the best measurements possible given the resources available.

* 1. **Education And Outreach** (Leaders: Garlick, J. Wilson, G. Wilson)

*2.9.1 Schoolyard and outreach activities*

The Hubbard Brook Research Foundation (HBRF) serves as an interface organization between HBR researchers and schools and community stakeholder organizations in the region. HBRF’s Schoolyard activities with K-12 local schools, done under the rubric of its Environmental Literacy Program, include: development of classroom curricula and other resources; teacher professional development, through HBRF’s Research Experience for Teachers (RET) program which trains teachers to adapt real-world data for use in middle- and high-school classrooms; and long-term school partnerships. Policy-oriented activities that share cutting-edge research information with stakeholder organizations are organized around HBRF’s Science Links Program, which synthesizes policy-relevant research, and the Forest Science Dialogues Program, which uses facilitated roundtables and other activities to foster two-way conversations between researchers and stakeholders. In addition, HBRF leverages its education and policy activities by assuming leadership roles with two regional organizations, the Science Policy Exchange (SPE) and the Northeastern States Research Cooperative (NSRC). Continuing and new activities in education and outreach will include:

* Maintaining partnerships with science education providers in NH and running teacher professional development programs, including the RET program.
* Maintaining close working relationships with the five public K-12 schools closest to HBR, as well as with others who have requested our involvement.
* Creating classroom lessons for middle- and high-school teachers based on studies and data from experimental forests and other research sites.
* Providing tours, assistance in data acquisition, and classroom usage, and interface with the research community as requested by other schools in the region.
* Providing support to HBR scientists to partner with the Science Policy Exchange and NSRC on regional broader-impact projects.
* Expanding the Forest Science Dialogues project beyond NH to other Northern Forest states.
* Developing two new Science Links projects on migratory birds and winter climate change.

*2.9.2 Supporting REU programs*

Protecting the region’s forests in the future will depend in part on training new scientists to conduct vital research and monitoring. HBRF’s Research Experience for Undergraduates (REU) program, done in partnership with Plymouth State University, provides on-the-ground research opportunities, while also allowing students to participate in the vibrant scientific community at HBR, for example, by attending and presenting at the annual HBR Cooperators’ Meeting. Between 8 and 10 students/y perform independent research under the mentorship of HBR scientists and present their research at a culminating annual REU conference. This effort is primarily supported by a site NSF site REU grant, with partial funding from the LTER program. We plan to continue this successful program during the next LTER cycle.

* 1. CROSS-SITE AND NETWORK ACTIVITIES
  2. LTER Core areas??? Table of core data sets???

1. DATA MANAGEMENT AND ACCESSIBILITY **(5 p extra)**)

The Information Management System at HBR addresses several major goals; (1) maintaining a catalog of HBR data, with an emphasis on high quality data/documentation and data preservation (2) enabling data discovery/access to serve the HBR, LTER, and broader scientific communities (3) maintaining a physical sample archive. The primary role of the HBR Information Manager is to support the HBR information management system and to provide expertise in Information Management for scientists conducting research projects and data syntheses. The Information Manager also contributes to LTER network IM activities and serves on network-level committees (NISAC [2014-2017], Databits (co)Editor [fall 2014, spring 2015], and ad-hoc working groups [sensorNIS]). The HBR Information Manager is based at the University of New Hampshire in the Earth Systems Research Center (ESRC)

**Governance**

Information management (IM) activities at HBR are supervised by an Information Oversight Committee (IOC). The IOC addresses topics such as the HBR data catalog (data quality assurance and quality control, metadata, contributions to LTER-Network Information System), the sample archive, and the HBR website (updating the content, structure, and design). The IOC meets formally twice each year (January/July) and reports to the Scientific Coordinating Committee (governing body for HBR). The IOC includes a representative cross-section of HBR participants.

**IT Resources**

IT support for HBR IM is provide through the UNH Research Computing and Instrumentation (RCI) center. RCI provides support to researchers in ESRC, as well as to the wider University research community, State of NH, and Federal Agencies. ESRC has had a long-standing Service Level Agreement (SLA) with RCI (more than 20 years). In addition to overall IT support described in the RCI also provides the personnel for as-needed project support. This gives the HBR-IM team access to expertise for special projects, without the need to provide full-time support for personnel on the IM team for programming, web design, etc.

Create Table here with IM key features: website, catalogs (biblio, personnel, data, site locations)

Number of datasets in hubbardbrook.org catalog and in LTER-NIS (list # data packages and total number of entities), databases – MYSQL for HBR data, Postgres for metadata management, PostGIS for spatial data access online.

|  |  |
| --- | --- |
| Feature | Details, software, resources |
| Website: http://hubbardbrook.org | html, css, php, xslt, javascript, apache |
| Bibliography | Zotero, MYSQL, bibutils |
| Data Catalog | MYSQL |
| Metadata | Postgres, metabase2 (adopted from GCE/MCR/SBC) |
| Computer Hardware | Dell Poweredge R510, desktop and laptop linux systems. |
| Backup | BackupPC |

**Database Detail**

Tabular data for all HBR datasets are stored in a MYSQL database, and retrieved by website queries via php code. Both a live and development database are used to test and stage datasets for review and approval. A

Postgres database handles the metabase content – see details in metadata section. All databases are backed up daily, and data is easily restored for the entire database, or for individual tables as necessary.

**HBR Website**

The HBR website is the primary means by which HBR information is disseminated, with additional non-digital data (charts, maps, photographs) made available upon request. The HBR website was redesigned in 2012, following the Guidelines for LTER Web Site Design and Content. All updates to the website undergo initial testing and review on a development version of the website. The HBR website is hosted on the main webserver managed by RCI, with temperature control and power backup. add some figure from google analytics that demonstrates level of website use, and use by user category from our local download file.

Personnel database – A personnel database, including curriculum vitas, is maintained on the HBR website. Individuals update their own vitas via a password-protected web form. Updates can be made any time and reminders (and subsequent follow-ups) are sent out twice annually to ensure that the information is current.

Current Research – A description of current research activities is available through the HBR website to keep the public abreast of research initiatives and preliminary findings. Updates reflect changes in the development and scope of current research.

Photo archive *–* The website has a searchable archive of digital images that are frequently used in publications, presentations and textbooks. Many of the historical HBR photographs and slides have been scanned at high resolution to ensure that these irreplaceable images are preserved in perpetuity. The online photo gallery was recently updated with the installation of Piwigo (http://piwigo.org) on the website server. This full-featured photo management software allows for photo upload, tagging, search, and for user accounts with varying permission levels. An Epson V800 slide scanner is now available for HBR, and we are in the process of identifying additional historical slides to be added to the digital collection.

Data catalog – The HBR data catalog is available on the HBR website as well as the LTER NIS. A complete inventory of data is available in section XX. When users view or download data from the local HBR data catalog, they self-identify, by entering their name, affiliation, email address. This information is stored in a database and provides statistics on data use. Datasets accessed through the LTER-NIS data portal are tracked through 'Data Package Access Reports'.

UPDATE THIS SECTION On average, 3,705 HBR datasets are downloaded per year (approximately 10 per day) by users representing 29 countries, 156 degree granting institutions, 15 government agencies, and 17 identifiable K-12 schools or districts.

External links – The HBR website provides links to LTER information and data resources, the US Forest Service site for Hubbard Brook, and the Hubbard Brook Research Foundation.

Internal Website

Password protected intranet access is available to the core HBR research teams. This was developed as a means of sharing ideas, information, and documents among the approximately 50 geographically dispersed members of the Committee of Scientists. The site mostly contains internal communications such as meeting minutes, NSF reviews, presentations, and proposals.

**Publications**

The publication list for HBR dates back to 1955, and includes more than 2,400 publications (books, journal articles, conference presentations, and theses). This publication list is accessible in a searchable format on the HBR website. New HBR publications are identified through self-reporting by investigators, annual reports, and Google Scholar alerts. Citations are managed locally with Zotero (http://zotero.org). This open source bibliography management software allows for export to standard reference management exchange formats, harvests citation information and associated pdf's easily through a browser, and provides cite-as-you-write support for MSWord and Open/LibreOffice. A custom formatting style has been written to generate an upload format compatible with the current HBR bibliography database table. A new citation plugin for Zotero provides the capability to update and attach publication citation metrics. Early publications are archived in paper at the Cary Institute; publications since 2011 are archived in pdf format. The pre-2011 publications are being converted to digital format by downloading pdfs from the publisher, and scanning original paper copies when digital version is unavailable. For the past several years, publications have been added to the list with the inclusion of a hyperlinked DOI to improve access to the documents. In addition, we often have USDA Forest Service authors on HBR publications; in these cases, the publications are open access through <http://www.treesearch.fs.fed.us/>, and we have begun to add links directly to the treesearch page for those publications.

**Data Access Policy**

HBR adheres to the LTER Network Data Access Policy that was approved by the LTER Coordinating Committee in 2005. To date, all the data collected at HBR are considered Type I, with a goal of release to the general public within 2 years from the time of collection.

*Create a Download Summary Table – by year, by type of institution*

**Metadata**

HBR researchers have a long history of data sharing, and were among the first LTER sites to provide dial-up access to datasets. Within a year of LTER EML adoption, all HBR data were available on-line with EML documentation. Due to the early adoption of EML, many data packages became out of sync with the EML Best Practices developed by the LTER community (over the course of a decade). During this past renewal cycle, all datasets were brought into compliance with EML Best Practices, as demonstrated through their availability in the NIS data catalog.

The most important task ahead with regard to metadata, is the harvest of information from our existing eml into the metabase schema. We have been able to leverage resources from other sites for this process, in particular GCE, SBC, and MCR. The latter two sites have built the metabase schema in Postgres, and have just completed migrating flat xml file content to the database. They have shared an export of the metabase schema, which we imported to the HBR Postgres database, as well as xsl files for the extraction of key eml components - attributes, personnel, keywords, etc. Once the database is populated, we will also leverage MCR/SBC code resources that generate eml from the metabase. Once complete, all HBR metadata will be generated from the information stored in metabase; a model that will streamline data package development and help to increase our productivity.

**Data Lifecycle**

Research at HBR is conducted by a geographically dispersed group of cooperating scientists from many institutions. The data collected by these scientists include core data sets that comprise the long-term monitoring program, as well as data from shorter-term studies. Scientists who wish to conduct new research at HBR obtain permission from the Research Approval Committee (RAC; spring and fall submission periods). As part of this process, they submit an on-line proposal submission form, providing detailed information on research location, data collection, sampling methods, and a safety plan. The information on the proposal submission form is appended to a database, and approved projects are tracked over time until completion. In the next RAC cycle (spring 2016), we will implement a number of changes that have been developed by the RAC chair and the Information Manager. These changes will improve our ability to track status, progress, data, and publications for all projects at the Hubbard Brook Experimental Forest. Three important changes will be 1) the requirement for a data management plan that will be signed off by both RAC and IM, prior to the initiation of a project, 2) a formalized data policy that requires *all* researchers at the Experimental Forest to contribute the data obtained in the study, and accompanying metadata, to the HBR Information Manager, and 3) a formalized annual reporting requirement, implemented with the Qualtrics Survey Research Suite (a Web-based survey and data analysis service licensed by UNH). The new RAC-IM integration will increase the number of opportunities for PI-IM interaction over the data lifecycle, and will increase the number and quality of datasets that we develop.

Since data collected at HBR are diverse and often highly specialized, individual researchers are responsible for developing their own data management protocols (e.g., database design, QA/QC) prior to submission to the centralized data catalog. The Information Manager is available to provide guidance and assistance at the onset and through all phases of research to ensure the integrity and safety of the data and metadata. Data and metadata forms are submitted to the Information Manager for review. The IM then reviews submissions (data formatting and QA/QC checks, LTER-NIS PASTA congruency evaluation) prior to uploading data to the data catalog.

**Sensor Network/transition from charts to digital/adoption of GCE Toolbox**

There is a fair amount to write here, and there are ongoing developments – I'll get to this section soon

**Sample Archive**

More than 20 years ago, HBR made a commitment to the permanent storage of physical samples (e.g., streamwater, precipitation, vegetation, soil). A dedicated building on-site serves as the archive facility, and now houses approximately 40,000 samples. After samples are collected and analyzed, they are stored in a physical sample archive building located at HBR. Samples are preserved, barcoded, and cataloged with accompanying metadata in the HBR centralized database, a process that ensures the discoverability and access to samples for future research. A sample archive subsampling policy has been developed to 1) to maintain the chemical integrity of these samples; 2) to document the use of these samples, and any resulting changes; 3) inform principal investigators of interest in sample use; and 4) to acknowledge the appropriate funding sources for their original collection. Requests for reanalysis of these samples (e.g. isotopic analyses, heavy metals) are received periodically, and have resulted in a number of publications. Details from Amey. During this current funding cycle, the establishment of the HBR Archive Committee, and archive support from LTER supplemental funding, have improved our capability to identify samples valuable to this collection, and to move forward in cataloging and storing additional samples. We have been able to make e**xtensive updates to the inventory, organization, and sample volume data for the streamwater and precipitation samples. The development of a data entry station in the archive building that incorporates bar-code scanning and direct scale-to-computer entry of sample weights has streamlined this process.**

Although all samples in the archive are described in detail in a database, a shortcoming of the current system, is that tables have not been keyed to enable queries integrating both physical sample and analytical data. In an initial proof-of-concept, we have worked with some of the existing sample and analytical data tables to generate keys that allow more comprehensive queries. The goal of this effort is to enable queries such as “generate a list of all soil samples from the Oe horizon in watershed 5 from 1980-1990 with %N > threshold”. This type of query now returns a list of all physical samples meeting that criteria, their location within the archive (room/shelf/bin), and the amount of sample remaining. This initial exercise has been informative – existing sample and analytical data were not prepared with this type of sample/data access in mind, and will be challenging to retrofit; however, lessons learned provide insight on the path forward as we archive more physical samples, and catalog associated analytical data tables. During this next funding cycle, we expect to make progress on the integration of archive sample information and analytical data by supporting a paid, in-residence intern from the Syracuse University School of Information Studies, who will work closely with the HBR-IM during the summer(s).

**HBR Information Management Milestones:**

**Response to prior IM reviews:** How we addressed (1) 'Dataset Search by LTER core area' (2) the fact that

website services were seen as 'for us' not broader audience – I think the new virtual tour done in arc storymaps will be a nice inviting feature, and should be done by end of year (3) proposals, reports, coop meeting agenda/abstracts online (done).

1. SITE AND PROJECT MANAGEMENT (**Lovett 3 p extra**)

The Hubbard Brook Ecosystem Study is governed by a Committee of Scientists (COS), which consists of the core group of active PI-level scientists working at the site (currently 67 members). A Scientific Coordinating Committee (SCC) functions as an executive committee for the COS, providing leadership, vision, and coordination. The SCC has seven members: four elected by the COS, the Lead Scientist for the Forest Service HB project, the Executive Director of the Hubbard Brook Research Foundation, and the PI of the HBR-LTER grant. There is also one non-voting external advisor, currently Ivan Fernandez of the University of Maine. The SCC elects a chair from within its membership and appoints members to three standing committees (Education and Outreach, Information Management, and Research Approval), as well as *ad hoc* committees constituted as needed.

The COS meets quarterly for full-day meetings that center on science topics (new initiatives, synthesis activities, etc.) as well as project business. These meetings generally draw 30-40 attendees and include students and postdocs as well as lead scientists. The winter meeting spans 2 days and includes a mixer and dinner to facilitate social interaction and cohesion with the HBR project. The winter, spring and fall meetings are typically held at the Cary Institute in Millbrook, NY, a relatively central location for the more than X institutions that participate in the project. The summer meeting is held at Hubbard Brook. In addition to the quarterly meetings, the Hubbard Brook Cooperator’s Meeting is held every year in early July at Hubbard Brook, a tradition dating back to the early days of the project in the 1960s. This 2-day meeting is intended to share information on activities at the site, present new data, and promote collaboration; it includes brief presentations by everyone doing research at HBR, including undergraduate and graduate students. The meeting is attended by many people not actively doing research, but who are interested in what is going on at the site, including Forest Service land managers, outside scientists, and non-governmental organizations (NGOs). This meeting also includes time for social interaction, including a dinner and a barn dance. The 2015 Cooperator’s meeting had XXX attendees, a number which has been increasing every year.

*HBR-LTER Leadership and Transition Plans.*

While there are many research grants active at HBR, the LTER grant is the glue that holds the project together. It provides baseline support for long-term measurements and experiments, elucidates an overall project structure that joins researchers from diverse disciplines, and provides support to recruit new investigators to work at the site. The LTER grant is integrated within the overall project structure (described above) in that the LTER PI sits on the SCC, and the full COS is actively engaged in the preparation of the LTER proposal. Since the inception of the HBR-LTER project in 1988, Tim Fahey from Cornell University and Charley Driscoll from Syracuse University have been the LTER PIs, leading the project through its birth and four renewal cycles. Fahey and Driscoll decided to step down as PIs for this cycle (though both will remain active researchers in the project), and after consultation with the SCC, asked Gary Lovett and Peter Groffman of the Cary Institute to lead the current LTER renewal proposal. This selection was endorsed by the COS. Lovett and Groffman have both been active researchers in the HBR-LTER project since the first cycle of the study, and both have been actively involved in project leadership, having each chaired the SCC at different times. The current LTER grant was transferred from Cornell to the Cary Institute in February 2016, with Lovett as titular PI, to allow the submission of a renewal proposal from the Cary Institute. Lovett and Groffman led the preparation of this LTER proposal with the assistance of a “Leadership Team” consisting of 8 scientists chosen to represent a range of career stages and disciplinary interests. In addition to the PIs and Leadership Team, the broader COS provided ideas and feedback at several stages in the process through meetings and reviewing draft documents, and Fahey and Driscoll have shared their insights and experience.

Looking to the future, Lovett (age 62) will step down as lead PI for the next cycle of the grant, but Groffman (age 58) will continue, along with a second lead PI who will be chosen well in advance of the proposal preparation process. While we understand NSF’s need for a single titular PI for the project, we have found that having two co-lead PIs spreads the administrative burden and leads to better decision making. This PI teamwork will be especially important as we bring younger scientists into the PI role for future cycles. The Leadership Team will continue to provide help, advice, and a sounding board for the PIs for grant administration and proposal preparation. Groffman has recently taken a position at the City University of New York, but this change will not reduce his involvement in the HBR-LTER project. He retains a position of Senior Research Fellow at the Cary Institute, as well as his Cary Institute laboratory.

*Site management.*

The Hubbard Brook Experimental Forest (HBEF) is managed by the USDA Forest Service (USFS). The collaboration between the USFS and academic partners has been a crucial part of the HBR-LTER since its inception. The USFS maintains the buildings, roads, weirs, and other infrastructure at the HBEF, supports the hydrologic and meteorological monitoring, and has several scientists actively engaged in HBR-LTER research. The USFS also employs a site manager (currently Ian Halm) with overall responsibility for management of the HBR, and the USFS Lead Scientist (currently Scott Bailey) chairs the Research Approval Committee of the HBR. Close collaboration between the USFS and the HBR-LTER project have been essential to the success of the site.

Anyone wishing to initiate new research at HBR (current COS members or new investigators) must submit (via an online form) a brief research proposal to the Research Approval Committee (RAC). Proposals are evaluated based on consistency with the mission of HBR, possible interference with ongoing research, and potential for damage to the site. The RAC also seeks to coordinate research to assure that investigators working on similar topics are aware of one another’s past and current research. Most proposals are approved after simple review by the RAC, but proposals for major manipulations are brought to the full COS for discussion before the RAC makes its decision.

The HBR-LTER employs a data manager (Mary Martin at the University of New Hampshire) for the project and a technician stationed at Hubbard Brook for field and laboratory work. Other technicians, students and postdocs are employed by collaborating institutions with LTER funding and are under the direction of co-PIs for specific HBR-related projects.



Figure 1 caption: Conceptual diagram





Figure 3 caption- W6 stream chemistry

Figure 2 caption—bulk and wet deposition



Figure 4 Caption

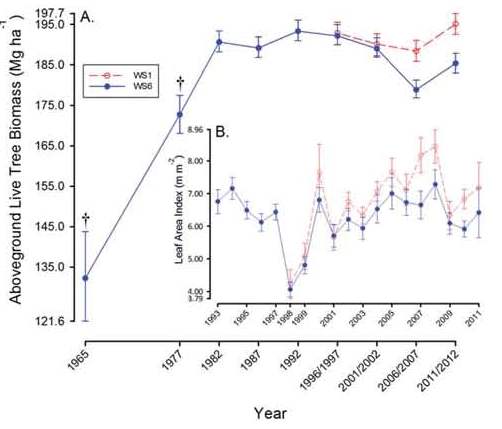


Figure 5 Caption**. Tree biomass and LA on W1 and W6**



Figure 6 caption . W1 NO3 trend



Fig 8 caption. Snowpack duration

Fig 7 caption. Precip and ET

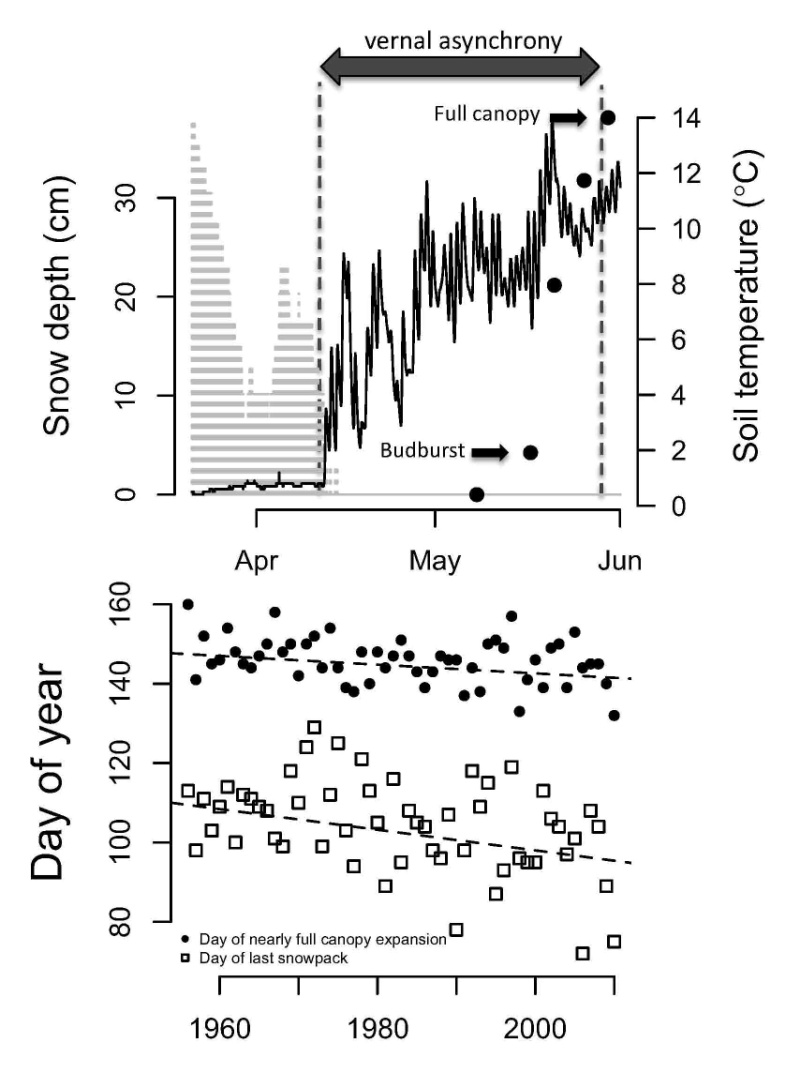


Figure 11 Caption**. Bird species trends**

Figure 10 Caption**. Tree spp changes in reference sites**

Figure 9 Caption**. Vernal asynchrony**



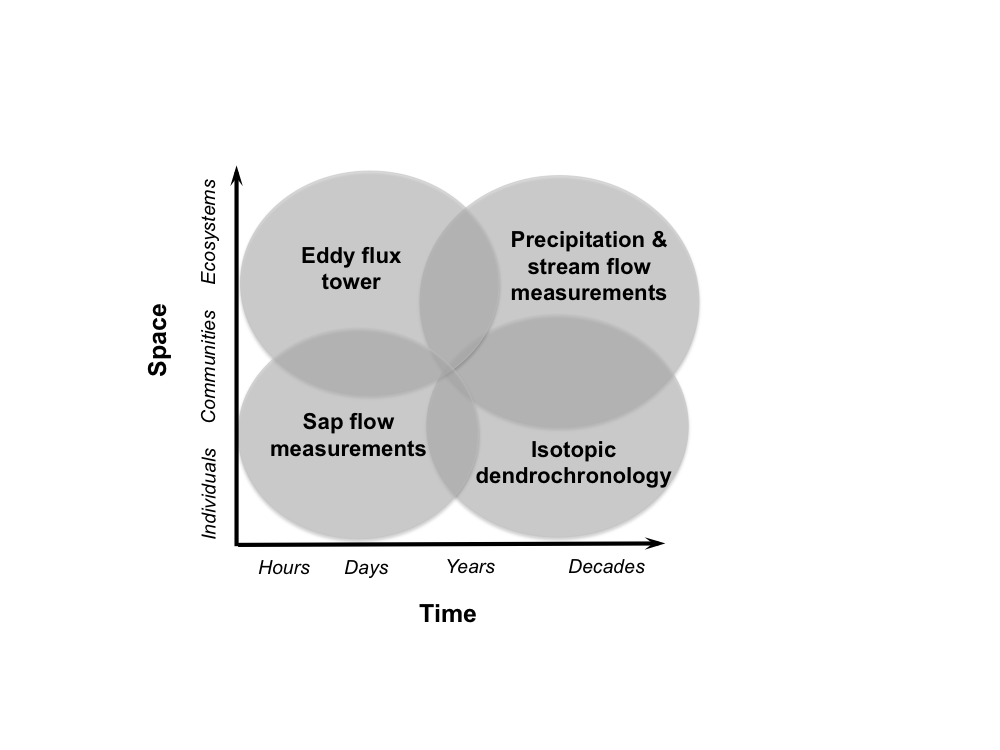
Figure 12 Caption**. N conceptual model**



Figure 13 Caption**. N mass balance**



Figure 14 caption: N Bank model



Historic potential mineralization.tif

Historic potential nitrification.tif

Figure 15 caption: ET Scales

Figure 16 Changes in potential net N mineralization and nitrification rates at the Hubbard Brook Experimental Forest, New Hampshire, USA over the past 40 years. From Duràn et al. (2015)



Figure 17: Heirarchical Response framework

Figure 18 Valley-wide foliar N from AVIRIS

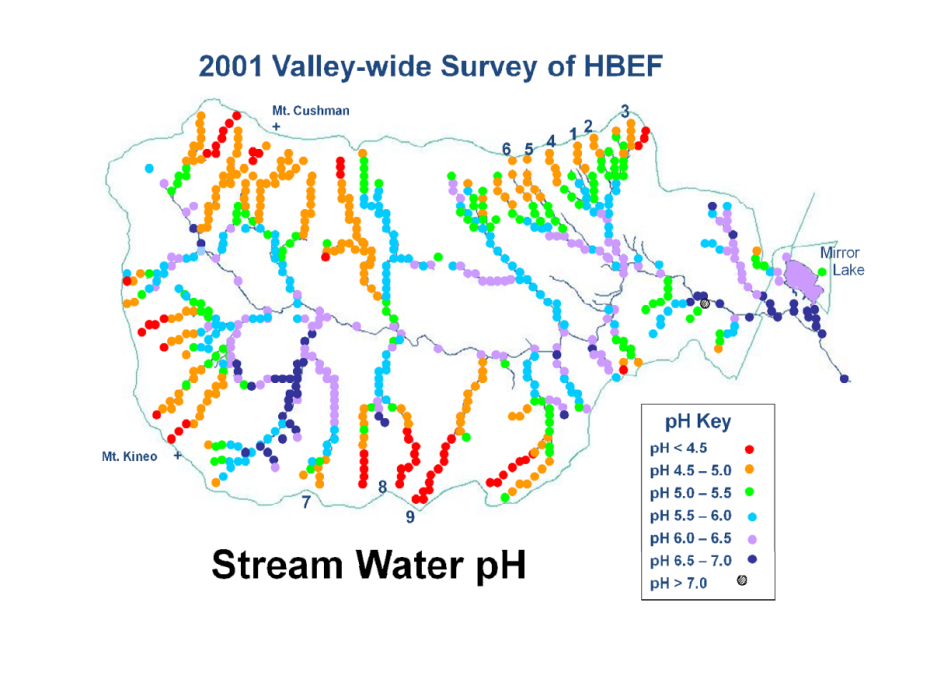


Figure 19 caption- Valley wide stream pH

Figure 20 Valley wide birds.



Figure 20 caption- Hydropedology diagram

FIGure 23 caption:

FIGure 9 caption

Figure 1. Conceptual model for the Hubbard Brook LTER program showing how different types of disturbance paly out on a geophysical and historical template that influences the effects of these disturbances in biogeochemistyr, vegetation, hydrology and food webs.

**FIGure 4. (A) Trends in aboveground live tree biomass and leaf area index in the reference watershed (WS6) and the Ca-treated watershed (WS1) at HBR. Aboveground live tree biomass (trees ≥2 cm in diameter at breast height, 1.37 m) from 1965 to 2012 for WS6 and from 1996 to 2011 for WS1. (B) Leaf area index from 1993 to 2011 for WS6 and from 1998 to 2011 for WS1. Means are plotted with 95% confidence intervals.**

**FIGure 2. The relationship between loss of snowpack, soil temperature, and spring leaf phenology (above) and changes in the modeled day of nearly complete canopy expansion and last snowpack at a middle elevation at HBR, 1960-2010 (below). At the top, disappearance of snowpack (horizontal shading) coincides with an abrupt increase in soil temperature at 4 cm (solid line). Closed circles represent spring leaf development and the arrow denotes the period of ‘vernal asynchrony’ that has increased over time. Below, spring leaf out (closed circles) is becoming earlier at a rate of -1.40± 0.53 days/decade (p<0.01) while the day of last snowpack (open squares) is becoming earlier at a rate of -3.58± 1.05 days/decade (p<0.002); thus the length of the period between snowmelt and full canopy development has increased by approximately 11 days in 55 years. From Groffman et al. (2012).**

Figure X. A conceptual model of ecosystem dynamics in a novel disturbance regime. Adapted from hierarchical response framework of Smith et al. 2009 and informed by trends in long-term observations from HBR. Chronic changes in the biogeochemical template lead to series of stepped, vegetational responses that in turn influence ecosystem function.

Haven’t even begun to organize these yet……

**References cited**

Aber, J. D., K. J. Nadelhoffer, P. Steudler, and J. M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. BioScience **39**:378-386.

Bailey, A. S., J. W. Hornbeck, J. L. Campbell, and C. Eagar. 2003. Hydrometeorological database for Hubbard Brook Experimental Forest: 1955-2000. General Technical Report NE-305. U.S. Department of Agriculture, Forest Service, Newtown Square, PA.

Bailey, S. W. 2013. Two fern species new to New Hampshire, with comments on the generation of calcareous-like habitate by base-poor rocks. Rhodora **115**:286-289.

Bailey, S. W., P. A. Brousseau, K. J. McGuire, and D. S. Ross. 2014. Influence of landscape position and transient water table on soil development and carbon distribution in a steep, headwater catchment. Geoderma **226**:279-289.

Battles, J. J., T. J. Fahey, C. T. Driscoll, Jr., J. D. Blum, and C. E. Johnson. 2014. Restoring soil calcium reverses forest decline. Environmental Science & Technology Letters **1**:15-19.

Bernal, S., L. O. Hedin, G. E. Likens, S. Gerber, and D. C. Buso. 2012. Complex response of the forest nitrogen cycle to climate change. Proceedings of the National Academy of Sciences **109**:3406-3411.

Bohlen, P. J., P. M. Groffman, C. T. Driscoll, T. J. Fahey, and T. G. Siccama. 2001. Plant-soil-microbial interactions in a northern hardwood forest. Ecology **82**:965-978.

Bormann, F. H., and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.

Bourgault, R. R., D. S. Ross, and S. W. Bailey. 2015. Chemical and morphological distinctions between vertical and lateral podzolization at Hubbard Brook. Soil Science Society of America Journal **79**:428-439.

Brooks, P. D., P. Grogan, P. H. Templer, P. M. Groffman, M. G. Oquist, and J. Schimel. 2011. Carbon and nitrogen cycling in snow-covered environments. Geography Compass **5/9**:682-699.

Campbell, J. L., C. T. Driscoll, C. Eagar, G. E. Likens, T. G. Siccama, C. E. Johnson, T. J. Fahey, S. P. Hamburg, R. T. Holmes, A. S. Bailey, and D. C. Buso. 2007. Long-term trends from ecosystem research at the Hubbard Brook Experimental Forest. General Technical Report NRS-17. U.S. Department of Agriculture, Forest Service, Northern Research Station Newtown Square, PA.

Campbell, J. L., C. T. Driscoll, A. Pourmokhtarian, and K. Hayhoe. 2011. Streamflow responses to past and projected future changes in climate at the Hubbard Brook Experimental Forest, New Hampshire, USA. Water Resources Research **doi:10.1029/2010WR009438**

Campbell, J. L., S. V. Ollinger, G. N. Flerchinger, H. Wicklein, K. Hayhoe, and A. S. Bailey. 2010. Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA. Hydrological Processes **24**:2465-2480.

Campbell, J. L., A. M. Socci, and P. H. Templer. 2014. Increased nitrogen leaching following soil freezing is due to decreased root uptake in a northern hardwood forest. Glob Chang Biol **20**:2663-2673.

Chen, L., and C. T. Driscoll. 2005a. Strategies for emission controls to mitigate snowmelt acidification. Geophysical Research Letters **32**:L20401.

Chen, L. M., and C. T. Driscoll. 2005b. A two-layer model to simulate variations in surface water chemistry draining a northern forest watershed. Water Resources Research **41**.

Cho, Y., C. Driscoll, C. Johnson, J. Blum, and T. Fahey. 2012. Watershed-level responses to calcium silicate treatment in a northern hardwood forest. Ecosystems **15**:416-434.

Christenson, L. M., M. J. Mitchell, P. M. Groffman, and G. M. Lovett. 2010. Winter climate change implications for decomposition in Northeastern forests: Comparisons of sugar maple litter to herbivore fecal inputs. Global Change Biology **16**: 2589-2601.

Christenson, L. M., M. J. Mitchell, P. M. Groffman, and G. M. Lovett. 2014. Cascading effects of climate change on forest ecosystems: Biogeochemical links between trees and moose in the northeast USA. Ecosystems **17**:442-457.

Cleavitt, N. L., J. J. Battles, T. J. Fahey, and J. D. Blum. 2014a. Determinants of survival over 7 years for a natural cohort of sugar maple seedlings in a northern hardwood forest. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **44**:1112-1121.

Cleavitt, N. L., J. J. Battles, T. J. Fahey, and J. D. Blum. 2014b. Determinants of survival over 7 years for a natural cohort of sugar maple seedlings in a northern hardwood forest. Canadian Journal of Forest Research **44**:1112-1121.

Cleavitt, N. L., T. J. Fahey, and J. J. Battles. 2011. Regeneration ecology of sugar maple (Acer saccharum): seedling survival in relation to nutrition, site factors, and damage by insects and pathogens. Canadian Journal of Forest Research **42**:235-244.

Comerford, D., P. Schaberg, P. Templer, A. Socci, J. Campbell, and K. Wallin. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia **171**:261-269.

Compton, J. E., and R. D. Boone. 2000. Long-erm impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology **81**:2314-2330.

Crowley, K. F., B. E. McNeil, G. M. Lovett, C. D. Canham, C. T. Driscoll, L. E. Rustad, E. Denny, R. A. Hallett, M. A. Arthur, J. L. Boggs, C. L. Goodale, J. S. Kahl, S. G. McNulty, S. V. Ollinger, L. H. Pardo, P. G. Schaberg, J. L. Stoddard, M. P. Weand, and K. C. Weathers. 2012. Do nutrient limitation patterns shift from nitrogen toward phosphorus with increasing nitrogen deposition across the northeastern United States? Ecosystems **15**:940-957.

Dib, A. E., C. E. Johnson, C. T. Driscoll, T. J. Fahey, and K. Hayhoe. 2014. Simulating effects of changing climate and CO2 emissions on soil carbon pools at the Hubbard Brook experimental forest. Global Change Biology **20**:1643-1656.

Driscoll, C. T., K. F. Lambert, F. Stuart Chapin, D. J. Nowak, T. A. Spies, F. J. Swanson, D. B. Kittredge, and C. M. Hart. 2012. Science and society: The role of long-term studies in environmental stewardship. BioScience **62**:354-366.

Driscoll, C. T., K. F. Lambert, and K. C. Weathers. 2011. Integrating science and policy: A case study of the Hubbard Brook Research Foundation Science Links program. BioScience **61**:791-801.

Durán, J., J. L. Morse, P. M. Groffman, J. L. Campbell, L. M. Christenson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, G. E. Likens, J. M. Melillo, M. J. Mitchell, P. H. Templer, and M. A. Vadeboncoeur. 2015. Climate change decreases nitrogen supply in a northern hardwood forest. Ecosphere **Submitted**.

Durán, J., J. L. Morse, P. M. Groffman, J. L. Campbell, L. M. Christenson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, M. J. Mitchell, and P. H. Templer. 2014. Winter climate change affects growing-season soil microbial biomass and activity in northern hardwood forests. Global Change Biology **20**:3568-3577.

Fahey, T. J., T. G. Siccama, C. T. Driscoll, G. E. Likens, J. Campbell, C. E. Johnson, J. J. Battles, J. D. Aber, J. J. Cole, M. C. Fisk, P. M. Groffman, S. P. Hamburg, R. T. Holmes, P. A. Schwarz, and R. D. Yanai. 2005. The biogeochemistry of carbon at Hubbard Brook. Biogeochemistry **75**:109-176.

Fahey, T. J., P. H. Templer, B. T. Anderson, J. J. Battles, J. L. Campbell, C. T. Driscoll, Jr., A. R. Fusco, M. B. Green, K.-A. S. Kassam, N. L. Rodenhouse, L. Rustad, P. G. Schaberg, and M. A. Vadeboncoeur. 2015. The promise and peril of intensive-site-based ecological research: insights from the Hubbard Brook ecosystem study. Ecology **96**:885-901.

Fahey, T. J., P. B. Woodbury, J. J. Battles, C. L. Goodale, S. P. Hamburg, S. V. Ollinger, and C. W. Woodall. 2010. Forest carbon storage: ecology, management, and policy. Frontiers in Ecology and the Environment **8**:245-252.

Fakhraei, H., and C. T. Driscoll. 2015. Proton and aluminum binding properties of organic acids in surface waters of the northeastern U.S. Environmental Science & Technology **49**:2939-2947.

Federer, C. A. 2015. BROOK 90: A Simulation Model for Evaporation, Soil Water and Stream Flow, Version 4.7. <http://www.ecoshift.net/brook/brook90.htm>.

Fisk, M., T. Ratliff, S. Goswami, and R. Yanai. 2014. Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests. Biogeochemistry **118**:195-204.

Foster, D. R., and J. D. Aber, editors. 2004. Forests in Time: The Environmental Consequences of 1,000 Years of Change in New England. Yale University Press, New Haven.

Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and F. A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. BioScience **47**:437-445.

Fuss, C. B., and C. T. Driscoll. 2015. Recovery from chronic and snowmelt seasonal acidification: Long-term trends in stream and soil water chemistry at the Hubbard Brook Experimental Forest. Journal of Geophysical Research - Biogeosciences **In revew**.

Fuss, C. B., C. T. Driscoll, M. B. Green, and P. M. Groffman. 2015. Hydrologic flowpaths during snowmelt in forested headwater catchments under differing winter climatic and soil frost regimes. Hydrological Processes **In review**.

Gannon, J. P., S. W. Bailey, and K. J. McGuire. 2014. Organizing groundwater regimes and response thresholds by soils: A framework for understanding runoff generation in a headwater catchment. Water Resources Research **50**:8403-8419.

Gannon, J. P., S. W. Bailey, K. J. McGuire, and J. B. Shanley. 2015. Flushing of distal hillslopes as an alternative source of stream dissolved organic carbon in a headwater catchment. Water Resources Research **In press**.

Garnas, J. R., M. P. Ayres, A. M. Liebhold, and C. Evans. 2011. Subcontinental impacts of an invasive tree disease on forest structure and dynamics. Journal of Ecology **99**:532-541.

Gavin, D. G., and D. R. Peart. 1993. Effects of beech bark disease on the growth of American Beech (*Fagus Grandifolia*). Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **23**:1566-1575.

Gillin, C. P., S. W. Bailey, K. J. McGuire, and J. P. Gannon. 2015. Mapping of hydropedologic spatial patterns in a steep headwater catchment. Soil Science Society of America Journal **79**:440-453.

Goodale, C. L., J. D. Aber, P. M. Vitousek, and W. H. McDowell. 2005. Long-term decreases in stream nitrate: Successional causes unlikely; possible links to DOC? Ecosystems **8**:334-337.

Gosz, J. R., R. T. Holmes, G. E. Likens, and F. H. Bormann. 1978. The flow of energy in a forest ecosystem. Scientific American **238**:92-102.

Green, M. B., A. S. Bailey, S. W. Bailey, J. J. Battles, J. L. Campbell, C. T. Driscoll, T. J. Fahey, L. C. Lepine, G. E. Likens, S. V. Ollinger, and P. G. Schaberg. 2013. Decreased water flowing from a forest amended with calcium silicate. Proceedings of the National Academy of Sciences of the United States of America **110**:5999-6003.

Groffman, P., J. Hardy, S. Fashu-Kanu, C. Driscoll, N. Cleavitt, T. Fahey, and M. Fisk. 2010. Snow depth, soil freezing and nitrogen cycling in a northern hardwood forest landscape. Biogeochemistry **102**:223-238.

Groffman, P. M., and M. C. Fisk. 2011a. Calcium constrains plant control over forest ecosystem nitrogen cycling. Ecology **92**:2035–2042.

Groffman, P. M., and M. C. Fisk. 2011b. Phosphate additions have no effect on microbial biomass and activity in a northern hardwood forest. Soil Biology and Biochemistry **43**:2441-2449.

Groffman, P. M., M. C. Fisk, C. T. Driscoll, G. E. Likens, T. J. Fahey, C. Eagar, and L. H. Pardo. 2006a. Calcium additions and microbial nitrogen cycle processes in a northern hardwood forest. Ecosystems **9**:1289-1305.

Groffman, P. M., J. P. Hardy, C. T. Driscoll, and T. J. Fahey. 2006b. Snow depth, soil freezing, and fluxes of carbon dioxide, nitrous oxide and methane in a northern hardwood forest. Global Change Biology **12**:1748-1760.

Groffman, P. M., J. P. Hardy, M. C. Fisk, J. T. Fahey, and C. T. Driscoll. 2009. Climate variation and soil carbon and nitrogen cycling processes in a northern hardwood forest. Ecosystems **12**:927-943.

Groffman, P. M., L. E. Rustad, P. H. Templer, J. L. Campbell, L. M. Christenson, N. K. Lany, A. M. Socci, M. A. Vadeboncouer, P. G. Schaberg, G. F. Wilson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, C. L. Goodale, M. B. Green, S. P. Hamburg, C. E. Johnson, M. J. Mitchell, J. L. Morse, L. H. Pardo, and N. L. Rodenhouse. 2012. Long-term integrated studies show that climate change effects are manifest in complex and surprising ways in the northern hardwood forest BioScience **62**:1056-1066.

Hamburg, S. P., M. A. Vadeboncoeur, A. D. Richardson, and A. S. Bailey. 2013. Climate change at the ecosystem scale: A 50-year record in New Hampshire. Climatic Change **116**:457-477.

Hane, E. N. 2003. Indirect effects of beech bark disease on sugar maple seedling survival. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **33**:807-813.

Holmes, R. T. 2011. Avian population and community processes in forest ecosystems: Long-term research in the Hubbard Brook Experimental Forest. Forest Ecology and Management **262**:20-32.

Holmes, R. T., and T. W. Sherry. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. The Auk **118**:589-609.

Johnson, C. E., C. T. Driscoll, J. D. Blum, T. J. Fahey, and J. J. Battles. 2014. Soil chemical dynamics after calcium silicate addition to a northern hardwood forest. Soil Science Society of America Journal **78**:1458-1468.

Keenan, T. F., J. Gray, M. A. Friedl, M. Toomey, G. Bohrer, D. Y. Hollinger, J. W. Munger, J. O/'Keefe, H. P. Schmid, I. S. Wing, B. Yang, and A. D. Richardson. 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. Nature Clim. Change **4**:598-604.

Kulkarni, M., A. Burgin, P. Groffman, and J. Yavitt. 2014. Direct flux and 15N tracer methods for measuring denitrification in forest soils. Biogeochemistry **117**:359-373.

Kulkarni, M. V., P. M. Groffman, J. B. Yavitt, and C. L. Goodale. 2015. Complex controls of denitrification at ecosystem, landscape and regional scales in northern hardwood forests. Ecological Modelling **298**:39-52.

Lany, N. K. 2014. Effects of temperature on species interactions in northern hardwood forests. Dissertation. Dartmouth College, Hanover, NH, USA.

Lany, N. K., M. P. Ayres, E. E. Stange, T. S. Sillet, N. L. Rodenhouse, and R. T. Holmes. 2015a. Breeding timed to maximize reproductive success in a migratory songbird: The importance of phenological asynchrony. Submitted.

Lany, N. K., M. P. Ayres, E. E. Stange, T. S. Sillet, N. L. Rodenhouse, and R. T. Holmes. 2015b. Breeding timed to maximize reproductive success in a migratory songbird: the importance of phenological asynchrony. Oikos **In press**.

Likens, G. E. 2010. The role of science in decision making: does evidence-based science drive environmental policy? Frontiers in Ecology and the Environment **8**:e1-e9.

Likens, G. E. 2013. Biogeochemistry of a Forested Ecosystem, 3rd Edition. Springer-Verlag, New York.

Likens, G. E., and D. C. Buso. 2012. Dilution and the elusive baseline. Environmental Science & Technology **46**:4382-4387.

Lovett, G., and C. Goodale. 2011. A new conceptual model of nitrogen saturation based on experimental nitrogen addition to an oak forest. Ecosystems **14**:615-631.

Lovett, G. M., G. E. Likens, D. C. Buso, C. T. Driscoll, and S. W. Bailey. 2005. The biogeochemistry of chlorine at Hubbard Brook, New Hampshire, USA. Biogeochemistry **72**:191-232.

Lowe, W. H. 2012. Climate change is linked to long-term decline in a stream salamander. Biological Conservation **145**:48-53.

McGuire, K. J., C. E. Torgersen, G. E. Likens, D. C. Buso, W. H. Lowe, and S. W. Bailey. 2014. Network analysis reveals multiscale controls on streamwater chemistry. Proceedings of the National Academy of Sciences of the United States of America **111**:7030-7035.

Minick, K. J., M. C. Fisk, and P. M. Groffman. 2011. Calcium and phosphorus interact to reduce mid-growing season net nitrogen mineralization potential in organic horizons in a northern hardwood forest. Soil Biology & Biochemistry **42**:271-279.

Morse, J. L., J. Durán, F. Beall, E. Enanga, I. F. Creed, I. J. Fernandez, and P. M. Groffman. 2015a. Soil denitrification fluxes from three northeastern North American forests ranging in nitrogen availability. Oecologia **177**:17-27.

Morse, J. L., J. Duran, and P. M. Groffman. 2015b. Soil denitrification fluxes in a northern hardwood forest: The importance of snowmelt and implications for ecosystem N budgets. Ecosystems **18**:520-532.

Morse, J. L., S. F. Werner, C. Gillen, S. W. Bailey, K. J. McGuire, and P. M. Groffman. 2014. Searching for biogeochemical hotspots in three dimensions: Soil C and N cycling in hydropedologic units in a northern hardwood forest. Journal of Geophysical Research Biogeosciences **119**:1596-1607.

Muller, R. N., and F. H. Bormann. 1976a. Role of Erythronium americanum Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. Science **193**:1126-1128.

Muller, R. N., and F. H. Bormann. 1976b. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. Science **193**:1126-1128.

Naples, B., and M. Fisk. 2010. Belowground insights into nutrient limitation in northern hardwood forests. Biogeochemistry **97**:109-121.

Nezat, C. A., J. D. Blum, and C. T. Driscoll. 2010. Patterns of Ca/Sr and Sr-87/Sr-86 variation before and after a whole watershed CaSiO3 addition at the Hubbard Brook Experimental Forest, USA. Geochimica Et Cosmochimica Acta **74**:3129-3142.

Osmond, D. L., N. M. Nadkarni, C. T. Driscoll, E. Andrews, A. J. Gold, S. R. Broussard Allred, A. R. Berkowitz, M. W. Klemens, T. J. Loecke, M. A. McGarry, K. Schwarz, M. L. Washington, and P. M. Groffman. 2010. The role of interface organizations in science communication and understanding. Frontiers in Ecology and the Environment **8**:306-313.

Pickett, S. T., and P. S. White. 2013. The ecology of natural disturbance and patch dynamics. Elsevier.

Pourmokhtarian, A., C. T. Driscoll, J. L. Campbell, and K. Hayhoe. 2012. Modeling potential hydrochemical responses to climate change and increasing CO2 at the Hubbard Brook Experimental Forest using a dynamic biogeochemical model (PnET-BGC). Water Resources Research **48**:W07514.

Raciti, S. M., T. J. Fahey, R. Q. Thomas, P. B. Woodbury, C. T. Driscoll, F. J. Carranti, D. R. Foster, P. S. Gwyther, B. R. Hall, S. P. Hamburg, J. C. Jenkins, C. Neill, B. W. Peery, E. E. Quigley, R. Sherman, M. A. Vadeboncoeur, D. A. Weinstein, and G. Wilson. 2012. Local-scale carbon budgets and mitigation opportunities for the northeastern United States. BioScience **62**:23-38.

Rastetter, E. B., R. D. Yanai, R. Q. Thomas, M. A. Vadeboncoeur, T. J. Fahey, M. C. Fisk, B. L. Kwiatkowski, and S. P. Hamburg. 2013. Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. Ecological Applications **23**:621-642.

Reiners, W., K. Driese, T. Fahey, and K. Gerow. 2012. Effects of three years of regrowth inhibition on the resilience of a clear-cut northern hardwood forest. Ecosystems **15**:1351-1362.

Reinmann, A. B., P. H. Templer, and J. L. Campbell. 2012. Severe soil frost reduces losses of carbon and nitrogen from the forest floor during simulated snowmelt: A laboratory experiment. Soil Biology and Biochemistry **44**:65-74.

Reynolds, L. V., M. P. Ayres, T. G. Siccama, and R. T. Holmes. 2007. Climatic effects on caterpillar fluctuations in northern hardwood forests. Canadian Journal of Forest Research **37**:481-491.

Rodenhouse, N. L., L. M. Christenson, D. Parry, and L. E. Green. 2009. Climate change effects on native fauna of northeastern forests. Canadian Journal of Forest Research **39**:249-263.

Ross, D. S., S. W. Bailey, G. B. Lawrence, J. B. Shanley, G. Fredriksen, A. E. Jamison, and P. A. Brousseau. 2011. Near-surface soil carbon, carbon/nitrogen ratio, and tree species are tightly linked across northeastern United States watersheds. Forest Science **57**:460-469.

Ross, D. S., J. B. Shanley, J. L. Campbell, G. B. Lawrence, S. W. Bailey, G. E. Likens, B. C. Wemple, G. Fredriksen, and A. E. Jamison. 2012. Spatial patterns of soil nitrification and nitrate export from forested headwaters in the northeastern United States. Journal of Geophysical Research-Biogeosciences **117**.

Sherry, T. W., S. Wilson, S. Hunter, and R. T. Holmes. 2015. Impacts of nest predators and weather on reproductive success and population limitation in a long-distance migratory songbird. Journal of Avian Biology:n/a-n/a.

Stange, E. E., M. P. Ayres, and J. A. Bess. 2011. Concordant population dynamics of Lepidoptera herbivores in a forest ecosystem. Ecography **34**:772-779.

Templer, P. 2012. Changes in winter climate: soil frost, root injury, and fungal communities. Plant and Soil **353**:15-17.

Templer, P., A. Schiller, N. Fuller, A. Socci, J. Campbell, J. Drake, and T. Kunz. 2012. Impact of a reduced winter snowpack on litter arthropod abundance and diversity in a northern hardwood forest ecosystem. Biology and Fertility of Soils **48**:413-424.

Tonitto, C., C. Goodale, M. Weiss, S. Frey, and S. Ollinger. 2014. The effect of nitrogen addition on soil organic matter dynamics: a model analysis of the Harvard Forest Chronic Nitrogen Amendment Study and soil carbon response to anthropogenic N deposition. Biogeochemistry **117**:431-454.

Townsend, A. K., E. G. Cooch, T. S. Sillet, N. L. Rodenhouse, R. T. Holmes, and M. S. Webster. 2015. The interacting effects of food, spring temperature, and global climate cycles on population dynamics of a migratory songbird. Global Change Biology **In press**.

Townsend, A. K., T. S. Sillett, N. K. Lany, S. A. Kaiser, N. L. Rodenhouse, M. S. Webster, and R. T. Holmes. 2013. Warm springs linked to longer breeding seasons and higher fecundity in a North American migratory bird. PLoS ONE **8**:e59467.

Van Doorn, N. S., J. J. Battles, T. J. Fahey, T. G. Siccama, and P. A. Schwarz. 2011. Links between biomass and tree demography in a northern hardwood forest: A decade of stability and change in Hubbard Brook Valley, New Hampshire. Canadian Journal of Forest Research **41**:1369-1379.

Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: A hypothesis. BioScience **25**:376-381.

Wexler, S., C. L. Goodale, K. J. McGuire, S. W. Bailey, and P. M. Groffman. 2014. Isotopic signals of summer denitrification in a northern hardwood forested catchment. Proceedings on the National Academy of Sciences **111**:16413-16418.

Yanai, R. D., J. J. Battles, A. D. Richardson, C. A. Blodgett, D. M. Wood, and E. B. Rastetter. 2010. Estimating uncertainty in ecosystem budget calculations. Ecosystems **13**:239-248.

Yanai, R. D., N. Tokuchi, J. L. Campbell, M. B. Green, E. Matsuzaki, S. N. Laseter, C. L. Brown, A. S. Bailey, P. Lyons, C. R. Levine, D. C. Buso, G. E. Likens, J. D. Knoepp, and K. Fukushima. 2015. Sources of uncertainty in estimating stream solute export from headwater catchments at three sites. Hydrological Processes **29**:1793-1805.

Yanai, R. D., M. A. Vadeboncoeur, S. P. Hamburg, M. A. Arthur, C. B. Fuss, P. M. Groffman, T. G. Siccama, and C. T. Driscoll. 2013. From missing source to missing sink: Long-term changes in the nitrogen budget of a northern hardwood forest. Environmental Science & Technology **47**:11440-11448.

Zak, D. R., P. M. Groffman, K. S. Pregitzer, S. Christensen, and J. M. Tiedje. 1990. The vernal dam: Plant microbe competition for nitrogen in northern hardwood forests. Ecology **71**:651-656.

Zimmer, M. A., S. W. Bailey, K. J. McGuire, and T. D. Bullen. 2013. Fine scale variations of surface water chemistry in an ephemeral to perennial drainage network. Hydrological Processes **27**:3438-3451.

Additional refs from John Battles:

Dietze, M. C., and J. H. Matthes. 2014. A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems. Ecology Letters 17:1418-1426.

Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience 56:395-40.

Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. Journal of Geophysical Research-Biogeosciences 114:G01002.

Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. Ecology 90:3279-3289.

Smith, M. D., K. J. La Pierre, S. L. Collins, A. K. Knapp, K. L. Gross, J. E. Barrett, S. D. Frey, L. Gough, R. J. Miller, J. T. Morris, L. E. Rustad, and J. Yarie. 2015. Global environmental change and the nature of aboveground net primary productivity responses: insights from long-term experiments. Oecologia 177:935-947.

van Doorn, N. S. 2014. Patterns and process of forest growth: the role of neighborhood dynamics and tree demography in a northern hardwood forest. PhD Dissertation, University of California Berkeley; 131 pages.

From Andrew:

**References**

**Jenkins JP, Richardson AD, Braswell BH, Ollinger S V., Hollinger DY, Smith ML**. **2007**. Refining light-use efficiency calculations for a deciduous forest canopy using simultaneous tower-based carbon flux and radiometric measurements. *Agricultural and Forest Meteorology* **143**: 64–79.

**Keenan TF, Gray J, Friedl MA, Toomey M, Bohrer G, Hollinger DY, Munger JW, O’Keefe J, Schmid HP, Wing IS, *et al.*** **2014**. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* **4**: 598–604.

**Richardson AD, Anderson RS, Arain MA, Barr AG, Bohrer G, Chen G, Chen JM, Ciais P, Davis KJ, Desai AR, *et al.*** **2012**. Terrestrial biosphere models need better representation of vegetation phenology: Results from the North American Carbon Program Site Synthesis. *Global Change Biology* **18**: 566–584.

**Richardson AD, Bailey AS, Denny EG, Martin CW, O’Keefe J**. **2006**. Phenology of a northern hardwood forest canopy. *Global Change Biology* **12**: 1174–1188.

**Richardson AD, Black TA, Ciais P, Delbart N, Friedl MA, Gobron N, Hollinger DY, Kutsch WL, Longdoz B, Luyssaert S, *et al.*** **2010**. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**: 3227–3246.

**Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M**. **2013a**. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* **169**: 156–173.

**Richardson AD, Klosterman S, Toomey M**. **2013b**. Near-surface sensor-derived phenology. In: Schwartz MD, ed. Phenology: An Integrative environmental science. Dordrecht: Springer Netherlands, 413–430.

**Refs from synthesis section**

**References cited**

Aber, J. D., K. J. Nadelhoffer, P. Steudler, and J. M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. BioScience **39**:378-386.

Bailey, A. S., J. W. Hornbeck, J. L. Campbell, and C. Eagar. 2003. Hydrometeorological database for Hubbard Brook Experimental Forest: 1955-2000. General Technical Report NE-305. U.S. Department of Agriculture, Forest Service, Newtown Square, PA.

Bailey, S. W. 2013. Two fern species new to New Hampshire, with comments on the generation of calcareous-like habitate by base-poor rocks. Rhodora **115**:286-289.

Bailey, S. W., P. A. Brousseau, K. J. McGuire, and D. S. Ross. 2014. Influence of landscape position and transient water table on soil development and carbon distribution in a steep, headwater catchment. Geoderma **226**:279-289.

Battles, J. J., T. J. Fahey, C. T. Driscoll, Jr., J. D. Blum, and C. E. Johnson. 2014. Restoring soil calcium reverses forest decline. Environmental Science & Technology Letters **1**:15-19.

Bernal, S., L. O. Hedin, G. E. Likens, S. Gerber, and D. C. Buso. 2012. Complex response of the forest nitrogen cycle to climate change. Proceedings of the National Academy of Sciences **109**:3406-3411.

Bohlen, P. J., P. M. Groffman, C. T. Driscoll, T. J. Fahey, and T. G. Siccama. 2001. Plant-soil-microbial interactions in a northern hardwood forest. Ecology **82**:965-978.

Bormann, F. H., and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.

Bourgault, R. R., D. S. Ross, and S. W. Bailey. 2015. Chemical and morphological distinctions between vertical and lateral podzolization at Hubbard Brook. Soil Science Society of America Journal **79**:428-439.

Campbell, J. L., C. T. Driscoll, C. Eagar, G. E. Likens, T. G. Siccama, C. E. Johnson, T. J. Fahey, S. P. Hamburg, R. T. Holmes, A. S. Bailey, and D. C. Buso. 2007. Long-term trends from ecosystem research at the Hubbard Brook Experimental Forest. General Technical Report NRS-17. U.S. Department of Agriculture, Forest Service, Northern Research Station Newtown Square, PA.

Campbell, J. L., C. T. Driscoll, A. Pourmokhtarian, and K. Hayhoe. 2011. Streamflow responses to past and projected future changes in climate at the Hubbard Brook Experimental Forest, New Hampshire, USA. Water Resources Research **doi:10.1029/2010WR009438**

Campbell, J. L., S. V. Ollinger, G. N. Flerchinger, H. Wicklein, K. Hayhoe, and A. S. Bailey. 2010. Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA. Hydrological Processes **24**:2465-2480.

Campbell, J. L., A. M. Socci, and P. H. Templer. 2014. Increased nitrogen leaching following soil freezing is due to decreased root uptake in a northern hardwood forest. Global Change Biology **20**:2663-2673.

Cho, Y., C. Driscoll, C. Johnson, J. Blum, and T. Fahey. 2012. Watershed-level responses to calcium silicate treatment in a northern hardwood forest. Ecosystems **15**:416-434.

Christenson, L. M., M. J. Mitchell, P. M. Groffman, and G. M. Lovett. 2010. Winter climate change implications for decomposition in Northeastern forests: Comparisons of sugar maple litter to herbivore fecal inputs. Global Change Biology **16**: 2589-2601.

Christenson, L. M., M. J. Mitchell, P. M. Groffman, and G. M. Lovett. 2014. Cascading effects of climate change on forest ecosystems: Biogeochemical links between trees and moose in the northeast USA. Ecosystems **17**:442-457.

Cleavitt, N. L., J. J. Battles, T. J. Fahey, and J. D. Blum. 2014. Determinants of survival over 7 years for a natural cohort of sugar maple seedlings in a northern hardwood forest. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **44**:1112-1121.

Cleavitt, N. L., T. J. Fahey, and J. J. Battles. 2011. Regeneration ecology of sugar maple (Acer saccharum): seedling survival in relation to nutrition, site factors, and damage by insects and pathogens. Canadian Journal of Forest Research **42**:235-244.

Comerford, D., P. Schaberg, P. Templer, A. Socci, J. Campbell, and K. Wallin. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia **171**:261-269.

Compton, J. E., and R. D. Boone. 2000. Long-erm impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology **81**:2314-2330.

Crowley, K. F., B. E. McNeil, G. M. Lovett, C. D. Canham, C. T. Driscoll, L. E. Rustad, E. Denny, R. A. Hallett, M. A. Arthur, J. L. Boggs, C. L. Goodale, J. S. Kahl, S. G. McNulty, S. V. Ollinger, L. H. Pardo, P. G. Schaberg, J. L. Stoddard, M. P. Weand, and K. C. Weathers. 2012. Do nutrient limitation patterns shift from nitrogen toward phosphorus with increasing nitrogen deposition across the northeastern United States? Ecosystems **15**:940-957.

Dib, A. E., C. E. Johnson, C. T. Driscoll, T. J. Fahey, and K. Hayhoe. 2014. Simulating effects of changing climate and CO2 emissions on soil carbon pools at the Hubbard Brook experimental forest. Global Change Biology **20**:1643-1656.

Driscoll, C. T., K. F. Lambert, F. Stuart Chapin, D. J. Nowak, T. A. Spies, F. J. Swanson, D. B. Kittredge, and C. M. Hart. 2012. Science and society: The role of long-term studies in environmental stewardship. BioScience **62**:354-366.

Driscoll, C. T., K. F. Lambert, and K. C. Weathers. 2011. Integrating science and policy: A case study of the Hubbard Brook Research Foundation Science Links program. BioScience **61**:791-801.

Durán, J., J. L. Morse, P. M. Groffman, J. L. Campbell, L. M. Christenson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, G. E. Likens, J. M. Melillo, M. J. Mitchell, P. H. Templer, and M. A. Vadeboncoeur. 2015a. Climate change decreases nitrogen supply in a northern hardwood forest. Ecosphere **In press**.

Durán, J., J. L. Morse, P. M. Groffman, J. L. Campbell, L. M. Christenson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, G. E. Likens, J. M. Melillo, M. J. Mitchell, P. H. Templer, and M. A. Vadeboncoeur. 2015b. Climate change decreases nitrogen supply in a northern hardwood forest. Ecosphere **Submitted**.

Durán, J., J. L. Morse, P. M. Groffman, J. L. Campbell, L. M. Christenson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, M. J. Mitchell, and P. H. Templer. 2014. Winter climate change affects growing-season soil microbial biomass and activity in northern hardwood forests. Global Change Biology **20**:3568-3577.

Fahey, T. J., T. G. Siccama, C. T. Driscoll, G. E. Likens, J. Campbell, C. E. Johnson, J. J. Battles, J. D. Aber, J. J. Cole, M. C. Fisk, P. M. Groffman, S. P. Hamburg, R. T. Holmes, P. A. Schwarz, and R. D. Yanai. 2005. The biogeochemistry of carbon at Hubbard Brook. Biogeochemistry **75**:109-176.

Fahey, T. J., P. H. Templer, B. T. Anderson, J. J. Battles, J. L. Campbell, C. T. Driscoll, Jr., A. R. Fusco, M. B. Green, K.-A. S. Kassam, N. L. Rodenhouse, L. Rustad, P. G. Schaberg, and M. A. Vadeboncoeur. 2015. The promise and peril of intensive-site-based ecological research: insights from the Hubbard Brook ecosystem study. Ecology **96**:885-901.

Fahey, T. J., P. B. Woodbury, J. J. Battles, C. L. Goodale, S. P. Hamburg, S. V. Ollinger, and C. W. Woodall. 2010. Forest carbon storage: ecology, management, and policy. Frontiers in Ecology and the Environment **8**:245-252.

Fakhraei, H., and C. T. Driscoll. 2015. Proton and aluminum binding properties of organic acids in surface waters of the northeastern U.S. Environmental Science & Technology **49**:2939-2947.

Fisk, M., T. Ratliff, S. Goswami, and R. Yanai. 2014. Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests. Biogeochemistry **118**:195-204.

Foster, D. R., and J. D. Aber, editors. 2004. Forests in Time: The Environmental Consequences of 1,000 Years of Change in New England. Yale University Press, New Haven.

Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and F. A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. BioScience **47**:437-445.

Fuss, C. B., and C. T. Driscoll. 2015. Recovery from chronic and snowmelt seasonal acidification: Long-term trends in stream and soil water chemistry at the Hubbard Brook Experimental Forest. Journal of Geophysical Research - Biogeosciences **In revew**.

Fuss, C. B., C. T. Driscoll, M. B. Green, and P. M. Groffman. 2015. Hydrologic flowpaths during snowmelt in forested headwater catchments under differing winter climatic and soil frost regimes. Hydrological Processes **In review**.

Gannon, J. P., S. W. Bailey, and K. J. McGuire. 2014. Organizing groundwater regimes and response thresholds by soils: A framework for understanding runoff generation in a headwater catchment. Water Resources Research **50**:8403-8419.

Gannon, J. P., S. W. Bailey, K. J. McGuire, and J. B. Shanley. 2015. Flushing of distal hillslopes as an alternative source of stream dissolved organic carbon in a headwater catchment. Water Resources Research **In press**.

Garnas, J. R., M. P. Ayres, A. M. Liebhold, and C. Evans. 2011. Subcontinental impacts of an invasive tree disease on forest structure and dynamics. Journal of Ecology **99**:532-541.

Gavin, D. G., and D. R. Peart. 1993. Effects of beech bark disease on the growth of American Beech (*Fagus Grandifolia*). Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **23**:1566-1575.

Gillin, C. P., S. W. Bailey, K. J. McGuire, and J. P. Gannon. 2015. Mapping of hydropedologic spatial patterns in a steep headwater catchment. Soil Science Society of America Journal **79**:440-453.

Goodale, C. L., J. D. Aber, P. M. Vitousek, and W. H. McDowell. 2005. Long-term decreases in stream nitrate: Successional causes unlikely; possible links to DOC? Ecosystems **8**:334-337.

Gosz, J. R., R. T. Holmes, G. E. Likens, and F. H. Bormann. 1978. The flow of energy in a forest ecosystem. Scientific American **238**:92-102.

Green, M. B., A. S. Bailey, S. W. Bailey, J. J. Battles, J. L. Campbell, C. T. Driscoll, T. J. Fahey, L. C. Lepine, G. E. Likens, S. V. Ollinger, and P. G. Schaberg. 2013. Decreased water flowing from a forest amended with calcium silicate. Proceedings of the National Academy of Sciences of the United States of America **110**:5999-6003.

Groffman, P., J. Hardy, S. Fashu-Kanu, C. Driscoll, N. Cleavitt, T. Fahey, and M. Fisk. 2010. Snow depth, soil freezing and nitrogen cycling in a northern hardwood forest landscape. Biogeochemistry **102**:223-238.

Groffman, P. M., and M. C. Fisk. 2011a. Calcium constrains plant control over forest ecosystem nitrogen cycling. Ecology **92**:2035–2042.

Groffman, P. M., and M. C. Fisk. 2011b. Phosphate additions have no effect on microbial biomass and activity in a northern hardwood forest. Soil Biology and Biochemistry **43**:2441-2449.

Groffman, P. M., M. C. Fisk, C. T. Driscoll, G. E. Likens, T. J. Fahey, C. Eagar, and L. H. Pardo. 2006a. Calcium additions and microbial nitrogen cycle processes in a northern hardwood forest. Ecosystems **9**:1289-1305.

Groffman, P. M., J. P. Hardy, C. T. Driscoll, and T. J. Fahey. 2006b. Snow depth, soil freezing, and fluxes of carbon dioxide, nitrous oxide and methane in a northern hardwood forest. Global Change Biology **12**:1748-1760.

Groffman, P. M., J. P. Hardy, M. C. Fisk, J. T. Fahey, and C. T. Driscoll. 2009. Climate variation and soil carbon and nitrogen cycling processes in a northern hardwood forest. Ecosystems **12**:927-943.

Groffman, P. M., L. E. Rustad, P. H. Templer, J. L. Campbell, L. M. Christenson, N. K. Lany, A. M. Socci, M. A. Vadeboncouer, P. G. Schaberg, G. F. Wilson, C. T. Driscoll, T. J. Fahey, M. C. Fisk, C. L. Goodale, M. B. Green, S. P. Hamburg, C. E. Johnson, M. J. Mitchell, J. L. Morse, L. H. Pardo, and N. L. Rodenhouse. 2012. Long-term integrated studies show that climate change effects are manifest in complex and surprising ways in the northern hardwood forest BioScience **62**:1056-1066.

Hamburg, S. P., M. A. Vadeboncoeur, A. D. Richardson, and A. S. Bailey. 2013. Climate change at the ecosystem scale: A 50-year record in New Hampshire. Climatic Change **116**:457-477.

Hane, E. N. 2003. Indirect effects of beech bark disease on sugar maple seedling survival. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **33**:807-813.

Holmes, R. T. 2011. Avian population and community processes in forest ecosystems: Long-term research in the Hubbard Brook Experimental Forest. Forest Ecology and Management **262**:20-32.

Holmes, R. T., and T. W. Sherry. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. The Auk **118**:589-609.

Johnson, C. E., C. T. Driscoll, J. D. Blum, T. J. Fahey, and J. J. Battles. 2014. Soil chemical dynamics after calcium silicate addition to a northern hardwood forest. Soil Science Society of America Journal **78**:1458-1468.

Keenan, T. F., J. Gray, M. A. Friedl, M. Toomey, G. Bohrer, D. Y. Hollinger, J. W. Munger, J. O/'Keefe, H. P. Schmid, I. S. Wing, B. Yang, and A. D. Richardson. 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. Nature Clim. Change **4**:598-604.

Kulkarni, M., A. Burgin, P. Groffman, and J. Yavitt. 2014. Direct flux and 15N tracer methods for measuring denitrification in forest soils. Biogeochemistry **117**:359-373.

Kulkarni, M. V., P. M. Groffman, J. B. Yavitt, and C. L. Goodale. 2015. Complex controls of denitrification at ecosystem, landscape and regional scales in northern hardwood forests. Ecological Modelling **298**:39-52.

Lany, N. K., M. P. Ayres, E. E. Stange, T. S. Sillet, N. L. Rodenhouse, and R. T. Holmes. 2015. Breeding timed to maximize reproductive success in a migratory songbird: the importance of phenological asynchrony. Oikos **In press**.

Likens, G. E. 2010. The role of science in decision making: does evidence-based science drive environmental policy? Frontiers in Ecology and the Environment **8**:e1-e9.

Likens, G. E. 2013. Biogeochemistry of a Forested Ecosystem, 3rd Edition. Springer-Verlag, New York.

Likens, G. E., and D. C. Buso. 2012. Dilution and the elusive baseline. Environmental Science & Technology **46**:4382-4387.

Lovett, G., and C. Goodale. 2011. A new conceptual model of nitrogen saturation based on experimental nitrogen addition to an oak forest. Ecosystems **14**:615-631.

Lovett, G. M., G. E. Likens, D. C. Buso, C. T. Driscoll, and S. W. Bailey. 2005. The biogeochemistry of chlorine at Hubbard Brook, New Hampshire, USA. Biogeochemistry **72**:191-232.

Lowe, W. H. 2012. Climate change is linked to long-term decline in a stream salamander. Biological Conservation **145**:48-53.

McGuire, K. J., C. E. Torgersen, G. E. Likens, D. C. Buso, W. H. Lowe, and S. W. Bailey. 2014. Network analysis reveals multiscale controls on streamwater chemistry. Proceedings of the National Academy of Sciences of the United States of America **111**:7030-7035.

Minick, K. J., M. C. Fisk, and P. M. Groffman. 2011. Calcium and phosphorus interact to reduce mid-growing season net nitrogen mineralization potential in organic horizons in a northern hardwood forest. Soil Biology & Biochemistry **42**:271-279.

Morse, J. L., J. Durán, F. Beall, E. Enanga, I. F. Creed, I. J. Fernandez, and P. M. Groffman. 2015a. Soil denitrification fluxes from three northeastern North American forests across a range of nitrogen depositon. Oecologia **177**:17-27.

Morse, J. L., J. Durán, F. Beall, E. Enanga, I. F. Creed, I. J. Fernandez, and P. M. Groffman. 2015b. Soil denitrification fluxes from three northeastern North American forests ranging in nitrogen availability. Oecologia **177**:17-27.

Morse, J. L., J. Duran, and P. M. Groffman. 2015c. Soil denitrification fluxes in a northern hardwood forest: The importance of snowmelt and implications for ecosystem N budgets. Ecosystems **18**:520-532.

Morse, J. L., S. F. Werner, C. Gillen, S. W. Bailey, K. J. McGuire, and P. M. Groffman. 2014. Searching for biogeochemical hotspots in three dimensions: Soil C and N cycling in hydropedologic units in a northern hardwood forest. Journal of Geophysical Research Biogeosciences **119**:1596-1607.

Muller, R. N., and F. H. Bormann. 1976. Role of Erythronium americanum Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. Science **193**:1126-1128.

Naples, B., and M. Fisk. 2010. Belowground insights into nutrient limitation in northern hardwood forests. Biogeochemistry **97**:109-121.

Nezat, C. A., J. D. Blum, and C. T. Driscoll. 2010. Patterns of Ca/Sr and Sr-87/Sr-86 variation before and after a whole watershed CaSiO3 addition at the Hubbard Brook Experimental Forest, USA. Geochimica Et Cosmochimica Acta **74**:3129-3142.

Osmond, D. L., N. M. Nadkarni, C. T. Driscoll, E. Andrews, A. J. Gold, S. R. Broussard Allred, A. R. Berkowitz, M. W. Klemens, T. J. Loecke, M. A. McGarry, K. Schwarz, M. L. Washington, and P. M. Groffman. 2010. The role of interface organizations in science communication and understanding. Frontiers in Ecology and the Environment **8**:306-313.

Pickett, S. T., and P. S. White. 2013. The ecology of natural disturbance and patch dynamics. Elsevier.

Pourmokhtarian, A., C. T. Driscoll, J. L. Campbell, and K. Hayhoe. 2012. Modeling potential hydrochemical responses to climate change and increasing CO2 at the Hubbard Brook Experimental Forest using a dynamic biogeochemical model (PnET-BGC). Water Resources Research **48**:W07514.

Raciti, S. M., T. J. Fahey, R. Q. Thomas, P. B. Woodbury, C. T. Driscoll, F. J. Carranti, D. R. Foster, P. S. Gwyther, B. R. Hall, S. P. Hamburg, J. C. Jenkins, C. Neill, B. W. Peery, E. E. Quigley, R. Sherman, M. A. Vadeboncoeur, D. A. Weinstein, and G. Wilson. 2012. Local-scale carbon budgets and mitigation opportunities for the northeastern United States. BioScience **62**:23-38.

Rastetter, E. B., R. D. Yanai, R. Q. Thomas, M. A. Vadeboncoeur, T. J. Fahey, M. C. Fisk, B. L. Kwiatkowski, and S. P. Hamburg. 2013. Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. Ecological Applications **23**:621-642.

Reiners, W., K. Driese, T. Fahey, and K. Gerow. 2012. Effects of three years of regrowth inhibition on the resilience of a clear-cut northern hardwood forest. Ecosystems **15**:1351-1362.

Reinmann, A. B., P. H. Templer, and J. L. Campbell. 2012. Severe soil frost reduces losses of carbon and nitrogen from the forest floor during simulated snowmelt: A laboratory experiment. Soil Biology and Biochemistry **44**:65-74.

Reynolds, L. V., M. P. Ayres, T. G. Siccama, and R. T. Holmes. 2007. Climatic effects on caterpillar fluctuations in northern hardwood forests. Canadian Journal of Forest Research **37**:481-491.

Richardson, A. D., A. S. Bailey, E. G. Denny, C. W. Martin, and J. O'Keefe. 2006. Phenology of a northern hardwood forest canopy. Global Change Biology **12**:1174-1188.

Rodenhouse, N. L., L. M. Christenson, D. Parry, and L. E. Green. 2009. Climate change effects on native fauna of northeastern forests. Canadian Journal of Forest Research **39**:249-263.

Ross, D. S., S. W. Bailey, G. B. Lawrence, J. B. Shanley, G. Fredriksen, A. E. Jamison, and P. A. Brousseau. 2011. Near-surface soil carbon, carbon/nitrogen ratio, and tree species are tightly linked across northeastern United States watersheds. Forest Science **57**:460-469.

Ross, D. S., J. B. Shanley, J. L. Campbell, G. B. Lawrence, S. W. Bailey, G. E. Likens, B. C. Wemple, G. Fredriksen, and A. E. Jamison. 2012. Spatial patterns of soil nitrification and nitrate export from forested headwaters in the northeastern United States. Journal of Geophysical Research-Biogeosciences **117**.

Sherry, T. W., S. Wilson, S. Hunter, and R. T. Holmes. 2015. Impacts of nest predators and weather on reproductive success and population limitation in a long-distance migratory songbird. Journal of Avian Biology:n/a-n/a.

Stange, E. E., M. P. Ayres, and J. A. Bess. 2011. Concordant population dynamics of Lepidoptera herbivores in a forest ecosystem. Ecography **34**:772-779.

Takagi, K., A. Kurtz, S. Bailey, and T. Bullen. 2015. Assessing the impact of clear-cutting on the forest calcium cycle using Ca stable isotopes. Submitted to ?

Templer, P. 2012. Changes in winter climate: soil frost, root injury, and fungal communities. Plant and Soil **353**:15-17.

Townsend, A. K., E. G. Cooch, T. S. Sillet, N. L. Rodenhouse, R. T. Holmes, and M. S. Webster. 2015. The interacting effects of food, spring temperature, and global climate cycles on population dynamics of a migratory songbird. Global Change Biology **In press**.

Townsend, A. K., T. S. Sillett, N. K. Lany, S. A. Kaiser, N. L. Rodenhouse, M. S. Webster, and R. T. Holmes. 2013. Warm springs linked to longer breeding seasons and higher fecundity in a North American migratory bird. PLoS ONE **8**:e59467.

Van Doorn, N. S., J. J. Battles, T. J. Fahey, T. G. Siccama, and P. A. Schwarz. 2011. Links between biomass and tree demography in a northern hardwood forest: A decade of stability and change in Hubbard Brook Valley, New Hampshire. Canadian Journal of Forest Research **41**:1369-1379.

Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: A hypothesis. BioScience **25**:376-381.

Wexler, S., C. L. Goodale, K. J. McGuire, S. W. Bailey, and P. M. Groffman. 2014. Isotopic signals of summer denitrification in a northern hardwood forested catchment. Proceedings on the National Academy of Sciences **111**:16413-16418.

Yanai, R. D., J. J. Battles, A. D. Richardson, C. A. Blodgett, D. M. Wood, and E. B. Rastetter. 2010. Estimating uncertainty in ecosystem budget calculations. Ecosystems **13**:239-248.

Yanai, R. D., N. Tokuchi, J. L. Campbell, M. B. Green, E. Matsuzaki, S. N. Laseter, C. L. Brown, A. S. Bailey, P. Lyons, C. R. Levine, D. C. Buso, G. E. Likens, J. D. Knoepp, and K. Fukushima. 2015. Sources of uncertainty in estimating stream solute export from headwater catchments at three sites. Hydrological Processes **29**:1793-1805.

Yanai, R. D., M. A. Vadeboncoeur, S. P. Hamburg, M. A. Arthur, C. B. Fuss, P. M. Groffman, T. G. Siccama, and C. T. Driscoll. 2013. From missing source to missing sink: Long-term changes in the nitrogen budget of a northern hardwood forest. Environmental Science & Technology **47**:11440-11448.

Zak, D. R., P. M. Groffman, K. S. Pregitzer, S. Christensen, and J. M. Tiedje. 1990. The vernal dam: Plant microbe competition for nitrogen in northern hardwood forests. Ecology **71**:651-656.

Zimmer, M. A., S. W. Bailey, K. J. McGuire, and T. D. Bullen. 2013. Fine scale variations of surface water chemistry in an ephemeral to perennial drainage network. Hydrological Processes **27**:3438-3451.

From MattAyres

Burton, T. M., G. E. Likens. 1975. Salamander Populations and Biomass in Hubbard Brook Experimental Forest, New-Hampshire. Copeia :541-546.

Coleman, L. S., W. M. Ford, C. A. Dobony, and E. R. Britzke. 2014. A Comparison of Passive and Active Acoustic Sampling for a Bat Community Impacted by White-Nose Syndrome. Journal of Fish and Wildlife Management 5:217-226.

Froidevaux, J. S. P., F. Zellweger, K. Bollmann, and M. K. Obrist. 2014. Optimizing passive acoustic sampling of bats in forests. Ecology and Evolution 4:4690-4700.

Greene, B. T., W. H. Lowe, and G. E. Likens. 2008. Forest succession and prey availability influence the strength and scale of terrestrial-aquatic linkages in a headwater salamander system. Freshwater Biology 53:2234-2243.

Holmes, R. T. 2011. Avian population and community processes in forest ecosystems: Long-term research in the Hubbard Brook Experimental Forest. Forest Ecology and Management 262:20-32.

Lany N.K. Effects of temperature on species interactions in northern hardwood forests. Hanover, NH: Dartmouth College; 2014.

Lany, N. K., M. P. Ayres, E. E. Stange, T. S. Sillett, N. L. Rodenhouse, & R. T. Holmes. 2015. Breeding timed to maximize reproductive success for a migratory songbird: the importance of phenological asynchrony. Oikos DOI: 10.1111/oik.02412;

Stange, E. E., M. P. Ayres, and J. A. Bess. 2011. Concordant population dynamics of Lepidoptera herbivores in a forest ecosystem. Ecography 34: 772-779

* Daniel J. Bain,
* Mark B. Green,
* John L. Campbell,
* John F. Chamblee,
* Sayo Chaoka,
* Jennifer M. Fraterrigo,
* Sujay S. Kaushal,
* Sherry L. Martin,
* Thomas E. Jordan,
* Anthony J. Parolari,
* William V. Sobczak,
* Donald E. Weller,
* Wilfred M. WolLheim,
* Emery R. Boose,
* Jonathan M. Duncan,
* Gretchen M. Gettel,
* Brian R. Hall,
* Praveen Kumar,
* Jonathan R. Thompson,
* James M. Vose,
* Emily M. Elliott,
* and David S. Leigh

Legacy Effects in Material Flux: Structural Catchment Changes Predate Long-Term Studies *BioScience (2012) 62 (6): 575-584 doi:10.1525/bio.2012.62.6.8*

Driscoll, C.T., E.B. Cowling, P. Grennfelt, J. Galloway, and R. Dennis. 2010. Integrated assessment of ecosystem effects of atmospheric deposition: Lessons available to be learned. EM. Nov. 2010:6-13.

Fisk MC, Ratliff TJ, Goswami S, Yanai RD. 2014. Synergistic soil response to nitrogen plus phosphorus fertilization in hardwood forests. Biogeochemistry 118: 195-204.

Paine, Robert T., Mia J. Tegner, and Edward A. Johnson. "Compounded perturbations yield ecological surprises." *Ecosystems* 1.6 (1998): 535-545.