Overview:

The Hubbard Brook (HBR) LTER is an interdisciplinary research program focused on improving the understanding of the response of Northern Forest ecosystems to natural and anthropogenic disturbances. The principal research site is the Hubbard Brook Experimental Forest in the White Mountain region of New Hampshire, but the research is extended through comparative studies with other sites in the Northeastern U.S. and throughout the world. The research involves long-term studies of the biological composition, productivity, hydrology, biogeochemistry, and food webs of forest and stream ecosystems. Results of the research are used to test and revise conceptual and quantitative models of ecosystem functioning, to inform policy and management decisions regionally and nationally, and to bring ecological knowledge to students and teachers at levels from K-12 to graduate school.

Intellectual Merit :

The overarching research theme of this proposal is the long-term response of ecosystem structure. composition and function to disturbance. The broad conceptual model underpinning the HBR-LTER envisions three principal types of disturbance acting as drivers of change in the ecosystem: changing atmospheric chemistry, changing climate, and changing biota. The effects of these drivers play out on a geophysical and historical template that includes variation across the landscape in bedrock, soils, hydrology, climate and history of past disturbance. Within the ecosystem, the disturbances affect the interacting processes of hydrology, biogeochemistry, vegetation dynamics and food web dynamics. Proposed research on the changing atmosphere is focused primarily on the legacies of past air pollution, particularly the depletion of nutrient cations such as calcium from the soil and the accumulation of nitrogen in soil and vegetation. Proposed climate change research is focused on causes of the observed long-term decline in evapotranspiration at the site and the effects of changing timing and duration of seasonal transitions (such as the winter/spring transition) on plants, soils, microbes, animals and stream ecosystems. Proposed research on biotic change is focused on the changing composition and structure of the forests caused by multiple interacting stressors including climate change. new plant species immigrations, invasive forest pests, and altered disturbance regimes. In addition, a cross-cutting theme of the research is understanding the factors that control the spatial variability of soils, streams, and populations of plants and animals across the HBR landscape. Five challenging guestions about the future of the HBR ecosystem provide a nexus for synthesis and integration of the project across different disciplines of study and spatiotemporal scales.

Broader Impacts :

The team of HBR-LTER scientists and outreach specialists is committed to using the results of HBR research to improve education, inform forest management, and provide needed scientific synthesis for policy debates at the regional and national level. Proposed outreach to local K-12 schools includes hosting class visits and tours of HBR, providing data for class exploration, and training teachers by providing them with hands-on learning experiences working with scientists in the field. Undergraduate college students will be brought to the site in the summer to do independent research projects under the mentorship of HBR researchers, and graduate students will be given the opportunity to do their research in a diverse and collegial intellectual environment. Outreach programs are proposed that synthesize results of research done at HBR and elsewhere, and communicate the science to local stakeholders through ?round table? discussions, to the public through targeted media, and to policy makers through briefings and publications prepared to address specific policy questions.

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 associated with air pollution, (2) disturbance resulting directly or indirectly from regional climate change; and (3) disturbance related to changes in forest structure and species composition. Cutting across these themes is research on the geophysical and historical template (e.g., soil, topography, disturbance history) that drives spatial variation within our site and across the broader region. 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 encompassing the five core areas of LTER research (primary production, population studies, movement of organic matter, movement of inorganic matter, and disturbance patterns); (2) plot-scale and small-watershed manipulation experiments; (3) landscape-scale field studies on hydrology, biogeochemistry, soil, vegetation, microbes, birds and other animals; (4) multi-site surveys and experiments across the Northern Forest region and among LTER sites; (5) development and application of ecosystem models; and 6) communication of our results to students, educators, natural resource managers and poicymakers. 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 shaped our conceptual models and motivated new research initiatives. Ten signature publications that characterize our research are listed in 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., et al. 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.



Figure 1. Overall conceptual model underlying HBR-LTER research. Disturbances drive changes in the interacting components of the ecosystem-- vegetation, food webs, hydrology and biogeochemistry. These changes play out on a template that includes the geophysical and historical characteristics of the landscape. The ecosystem responses may feed back to modify the template and alter biotic change. The template and the functional responses change through time in response to the disturbances and internal drivers.

1.1 Air Pollution

Because of its location downwind of industrialized regions in the East and Midwest. HBR has been exposed to elevated levels of air pollution for decades. Long-term measurements of sulfur (S), nitrogen (N), and mercury 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 and mercury (Hg) emissions to the atmosphere (Likens 2010, Driscoll et al. 2011, 2012, 2013). We have measured bulk precipitation chemistry since 1963, wet deposition since 1978 (as part of the National Atmospheric Deposition Program (NADP)) (Fig. 2) 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 (Sickles and Shadwick 2015). We have also measured major solutes in streams at HBR since 1963, adding acid neutralizing capacity (ANC), fractions of monomeric AI, and dissolved organic carbon (DOC) in 1982. These long-term stream chemistry measurements (Fig. 3) show decreases in SO₄² concentrations that 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 inorganic, monomeric Al (Ali) (Fig. 3). With the declines in SO_4^2 , NO_3 , and the base cations, streamwater is trending toward a chemical condition that probably last occurred prior to the industrial revolution (Likens and Buso 2012) (Fig. 4).

In 1998, we initiated an experimental addition of $CaSiO_3$ to an entire watershed, watershed 1 (W1), to replace the available soil calcium (Ca) that was lost from soils during the 20th century by acid depositioninduced leaching (Nezat et al. 2010, Cho et al. 2012, Johnson et al. 2014). The Ca addition has produced a remarkable cascade of ecosystem impacts that continues 16 y after the start of the experiment. The Ca amendment reversed the forest decline that had previously been occurring in the watershed, and W1 supported more leaf area, greater 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).



125 100 75 (heq/L) SOA 50 25 60 50 (heq/L) 40 NO3 30 20 10 5.50 5.25 Чd 5.00 4.75 4.50 40 ANC (µeq/L) 20 0 -20 -40 Ali (µmol/L) 15 10 5 250 (µmol C/L) 200 DOC 150 100 50 0 1970 1980 1990 2000 2010 2020 1960

Figure 2. Trends in chemistry of wet deposition from the NADP site (open circles) and bulk deposition from the reference watershed (W6) (filled circles). Decreases in $SO_4^{2^-}$ and NO_3^- and increases in pH reflect national reductions in emissions of S and N oxides.



Figure 3. Trends in stream chemistry for the biogeochemical reference watershed (W6). Declines in $SO_4^{2^-}$ and Ali and increases in pH reflect declines in acid deposition to the site.

Figure 4. Relation between the sum of acid anions $(SO_4^{2-} + NO_3)$ and the sum of base cations for the W6 stream over time. The red circle labeled "PIR" is an estimate of likely concentrations prior to the industrial revolution. The dashed line from PIR to 1963 shows the inferred trend prior to the start of HBR measurements. The regression line (solid) includes the period 1970-2013, and shows that the concentrations are trending toward estimated PIR values. Updated from Likens and Buso (2012); see that reference for further detail.

Unexpectedly, we observed a ~20% increase in evapotranspiration for the 3 y following treatment, before returning to pretreatment levels (Green et al. 2013). The Ca amendment also enhanced seedling establishment and survival (Cleavitt et al. 2011). As the Ca moved downward through the soils, it

increased soil exchangeable Ca and pH (Johnson et al. 2014). Late-stage litter decomposition increased (Lovett et al. 2016a), 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 unexpected increases in NO₃⁻ concentrations in soil solutions and streamwater in the treated watershed (Fig. 6), indicating an oversupply of N relative to plant and microbial demand. Research to understand these surprising results is proposed in section 2.2.2.



Figure 5. Aboveground live tree biomass in the reference watershed (WS6, solid blue line) and the Ca-treated watershed (WS1, dashed red line, begun in 1996). Means and 95% confidence limits are plotted. The Ca was applied to WS1 in 1999. The inset graph shows leaf area index in the two watersheds from the start of measurements in 1993. From Battles et al.2014.

Figure 6. NO₃⁻ concentration in streamwater at a midelevation site in the Catreated watershed (W1). An ice storm in 1998 increased NO3 concentrations in streams throughout the HBR valley prior to the Ca addition, which occurred in 1999. Note increasing concentrations after 2010.

Unlike the Ca-treated watershed, streamwater NO₃⁻ concentrations have generally remained low (with occasional brief spikes associated with ice storm or soil freezing events) for the last two decades in the reference watershed (Fig. 3) 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 (Fig. 5, for reference watershed) (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, 2015b), 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 maintain N:P stoichiometry suggests biotic control of 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 early-successional productivity is N-limited (Goswami et al. in prep.). Microbial processes also show evidence of P limitation; high N availability consistently suppresses microbial C mineralization, while high P availability enhances it when present in combination with new organic matter inputs (Fisk et al. 2015). New research on plant and microbial processes that balance N and P stoichiometry is proposed in section 2.2.4.

1.2 Climate Change

Long-term trends in climate 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 summer (Hamburg et al. 2013). Precipitation has 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. 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).

Precipitation increases and snowpack decline have in turn influenced streamflow. 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). Snow melt-induced peak flows in spring have declined (Campbell et al. 2011) and are occurring earlier in the year (Hamburg et al. 2013). Interestingly, evapotranspiration (ET), measured indirectly as the difference between annual precipitation and streamflow, has shown slight, but significant declines over the period of record (Fig. 7) (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).

The warming climate has altered conditions at the winter/spring transition, which is critical for forest ecosystem biogeochemistry because during this period soil microbial mineralization processes become active before trees become a dominant sink for water and nutrients. The duration of this "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 (Fig. 8) (Groffman et al. 2012), creating a series of complex effects. First, the longer growing season increases both photosynthesis and net carbon (C) storage of forests at HBR (Keenan et al. 2014). At the same time, asynchrony between plant and microbial processes increases the potential for episodic hydrologic and gaseous N losses (Muller and Bormann 1976). These losses are driven by the lack of plant uptake of water and nutrients during this period, and can be particularly severe when low snow cover increases soil freezing and causes frost damage to roots (Groffman et al. 2010, Reinmann et al. 2012, Templer 2012, Comerford et al. 2013, Durán et al. 2014, Campbell et al. 2014). The freezing and root damage cause shifts in hydrologic flowpaths and nutrient transport through soil profiles (Fuss et al. 2015), and increase gaseous N losses (Morse et al. 2015b). Adding to the complexity are long-term observations showing that climate warming decreases production of plant available N via N mineralization and nitrification (Durán et al. 2016). These observations are supported by elevation gradient analyses at HBR showing that plots in the valley bottom have lower N availability, foliar N, nitrification and denitrification than high elevation plots that are approximately 2°C cooler (mean annual temperature) but have similar vegetation and soils (Ross et al. 2011, 2012, Durán et al. 2014, Morse et al. 2015a, 2015b). Thus overall mean patterns of climate change appear to drive the system toward a tighter N cycle with lower N losses, while the changing vernal window may drive it toward higher N losses. Both of these phenomena, in addition to long-term changes in forest biomass accumulation and atmospheric N deposition, likely contribute to the unexpected NO₃ export patterns shown in Fig. 3. A more comprehensive understanding of the complex N cycle at HBR is the focus of new comparative and experimental studies (sections 2.3.3 and 2.3.4) and integration and synthesis efforts (section 2.8.1).



Figure 7 Trends in precipitation, streamflow, and estimated evapotranspiration at watershed 3, the station with the longest record at HBR. Evapotranspiration is calculated as the difference between precipitation and streamflow on a water-year basis. All regression lines are statistically significant. Updated from Campbell et al. 2010.

Our research has also elucidated the pervasive impact of climate change on the food web. The dominant 1° consumers of the green (live plant-based) food web at HBR are caterpillars (Lepidoptera), and caterpillars are the chief food for birds, which are the dominant 2° consumers (Gosz et al. 1978, Holmes 1990). 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. 2016, Sherry et al. 2015, Townsend et al. 2016). This pattern may result from direct effects of temperature on caterpillar development rate and survival. 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 1° 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 intriguing ways (Rodenhouse et al. 2009). Moose browsing, and its 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 phenology, but this flexibility may be approaching its limit because the earliest springs are now approaching the relatively inflexible dates at which birds first arrive at HBR from their wintering grounds (Lany et al. 2016).

1.3 Forest Disturbance

An unprecedented combination of disturbances is buffeting the Northern Forest, including intensified timber harvesting, introduction of exotic insects and diseases, migration of more southerly or valleydwelling species into the upland forests, and extreme weather phenomena such as ice storms and "microburst" windstorms. Ecosystem response to these disturbances continues to be a major focus of long-term research at HBR (Fahey et al. 2015, Holmes and Likens 2016).



Figure 8. 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. 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 davs/decade (p<0.01) while the day of last snowpack (open squares) is becoming earlier at a rate of -3.58± 1.05 davs/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).

In the reference watershed (W6), tree species composition has changed and overall biomass has declined (Fig. 5) in recent years due mainly to dieback of sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*). The 10-30 cm diameter class of trees, which represents the canopy of the future, shows a marked increase in the relative dominance of American beech (*Fagus grandifolia*) (Fig. 9). Recently 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 largely absent from 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 (BBD), caused by an introduced scale insect and native bark-cankering



Figure 9 Relative dominance of 10-30 cm dbh trees of the three major species in the reference watershed (W6). Relative dominance is measured as relative basal area. Points are plot means with errors expressed as 95% confidence intervals. fungi, invaded the HBR valley in the 1970s and has increased both mortality of larger beech trees and regeneration of beech by sprouting, leading to a younger population age structure (Gavin and Peart 1993, Hane 2003). In an interesting interaction of disturbances, BBD-infected trees were more susceptible to crown damage during a severe ice storm in 1998 (Rhoads et al. 2002), but beech saplings increased their understory dominance in areas where the canopy was damaged by this storm (Weeks et al. 2009). 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. The future of the changing forest is the subject of new research in sections 2.4.2 and 2.4.3.

Forest change is also affecting food webs. Total bird abundance has declined at HBR over the 47 y of record, primarily due to the loss of Neotropical migrant species (Fig. 10). Most of the decline has been in 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). 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 due to the disease, but a community of at least three bat species remains.



Figure 10. Trends in the total number of birds, all species combined, breeding on a 10ha study area at Hubbard Brook in 47 consecutive years. 1969 to 2015. The decline in total abundance (black line) is due primarily to decreasing numbers of Neotropical migrants (red line), while the numbers of short-distance migrants (green line) and permanent residents (blue line) have remained relatively stable. (From Holmes and Likens 2016, modified and updated from Holmes 2007).

Forest harvest experiments have been used to test fundamental questions about long-term ecosystem response to disturbance at HBR. Our earliest experiment was a devegetation of watershed 2 (W2) in which the forest was clear-felled (with the dead vegetation left on site) 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 on W2 fell within the range measured in the other sites (Reiners et al. 2012). This similarity indicates a remarkably robust ecosystem recovery despite severe devegetation.

A whole-tree harvest experiment on watershed 5 (W5) provides evidence that intensive forest harvest may promote greater Ca limitation of forest growth. Long-term monitoring of streamwater chemistry in W5 indicates 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 tree species, sugar maple, has dramatically declined on W5 (Cleavitt et al. in prep.). The research on W5 also indicates that soil C pools are more dynamic than previously thought. Data from W5 were used to calibrate and validate two

widely used soil 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 recovery, 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.

1.4 Geophysical and historical template

In the last six years we have made much progress in understanding 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, reflecting the disturbance history of the landscape as well as the geophysical template, determine the spatial patterns of many songbird populations; these spatial patterns of birds tend to remain nearly constant from year to year despite large changes in bird abundance (Halworth et al. submitted). 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, including early books on biogeochemistry (Likens et al. 1977, most recent update in 2013) and vegetation dynamics (Bormann and Likens 1979) and a series of monographs on individual elements (Likens et al. 1994, 1998, 2002, Lovett et al. 2005, Fahey et al. 2005) and a recent synthesis paper on N (Yanai et al. 2013). 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. 2012, Lovett et al. 2016b). 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 titled *Hubbard Brook-The Story of a Forest Ecosystem* that highlights major findings from the HBR ecosystem over the 50+ years of the study, and suggests changes that are likely in the future (Holmes and Likens 2016).

Models, driven by long-term data, have been used extensively 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., Ollinger et al. 2008, 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. Comparisons of terrestrial biosphere models with long-term ground observations of phenology at HBR, satellite indices, and ecosystem-scale CO₂ flux measurements show that the models do not accurately simulate the temperature sensitivity of forest phenology, and 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 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). We have led the LTER network on the issue of quantifying uncertainty in ecosystem studies, including workshops at the 2012 and 2015 LTER All-Scientists Meetings, two Synthesis Working Groups, and a Research Coordination Network (RCN) (www.esf.edu/quest). Recently, we examined how well HBR represents the broader Northern Forest region, finding that although HBR is representative of some regional patterns and processes, such as sensitivity to and recovery from acid deposition, its mountainous terrain and non-agricultural past make it less representative of others, such as bird community composition (Fahey et al. 2015). Further work on understanding uncertainty and improving the efficiency of long-term measurement strategies is proposed in section 2.8.2.

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 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 and colleagues (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 improved using C and N pool, flux and isotope data and used for modeling soil C and N retention and gaseous losses under current and future conditions.

Spe-CN: A forest C and N cycling model parameterized for individual tree species; unlike PnET-CN, it allows simulation of the impacts of 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: 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, carbon and water exchange, and the energy balance (Medvigy et al. 2009). Will be used in conjunction with the Predictive Ecosystem Analyzer (PEcAn)(LeBauer et al. 2013), which facilitates Bayesian model-data assimilation, to simulate vegetation and hydrologic changes within HBR forests.

Multiple Element Limitation (MEL) model. The MEL model (Rastetter et al. 1997) couples ecosystem C, N, P and water cycles, using an algorithm that simulates redistribution of plant "uptake effort" to optimize relative acquisition of these resources from the environment. MEL has been calibrated and applied to forest recovery from disturbance at HBR (Rastetter et al. 2013), and will be tested with a factorial N X P fertilization study at HBR and regional sites.

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 hydrology and pedogenesis, N sinks in the mineral soil, multiple element limitation of the forest, ice storms, stream community ecology, developing practices to engage scientists and stakeholders, and new approaches to integrate science with the arts. Two LTREB grants augment long-term studies of precipitation and stream chemistry and bird populations, and a site REU grant enhances undergraduate participation in the HBR-LTER project.

1.7 Education, outreach and broader impacts

The Hubbard Brook Research Foundation (HBRF) 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, 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 book 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 Northern Forest communities through "Roundtable" discussions with stakeholders including foresters, farmers, ski area operators, snowmobilers, maple sugar producers, and road maintenance personnel.

Our Science Links program (Driscoll et al. 2011) has been very successful at synthesizing and translating scientific information from HBR and the region for policymakers at regional and national levels (Osmond et al. 2010, Fahey et al. 2010, Driscoll et al. 2012, Raciti et al. 2012). We are also collaborating with regional LTER sites (HFR, PIE and BES) and universities in a new science communication and outreach initiative, the Science Policy Exchange (SPE). Following the Science Links model, SPE produces scientific synthesis papers coupled with outreach targeted to media, land managers and policy makers. Current SPE topics, led by HBR scientists, include the health and ecosystem co-benefits of the EPA's Clean Power Plan (Driscoll et al. 2015a), impacts of invasive forest pests and pathogens (Lovett et al. 2016b), 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 better 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 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 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.

2. 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. E. Likens, F. H. Bormann, R. S. Pierce, and N.M. Johnson, developed the small watershed approach to understanding forest ecosystems and advanced the use of whole-ecosystem manipulations to quantify 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 emissions, and forest management (Holmes and Likens 2016).

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, 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, conduct long-term experiments, 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, estimated as the difference between annual precipitation and stream discharge, has significantly declined over the period of record despite gradually increasing air temperature.
- Although Ca is generally not considered a limiting element in temperate forests, experimental addition of Ca to a watershed reversed forest decline and had significant impacts on transpiration, tree reproduction, litter decomposition, and stream chemistry and biology.
- N export in streamwater of the reference watershed has remained low 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 quite stable from year to year at HBR, but abundance of the main 1° consumers in the green food web (Lepidoptera) fluctuates dramatically (>30-fold), driving fluctuations in the 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 reexamine 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 forested landscapes 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 beech bark disease. Others are intense and episodic, such as ice storms, wind storms, and insect outbreaks. Moreover, these disturbances may leave legacies that affect the forest, and its response to future disturbances, for decades or centuries (Foster et al. 2003). 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. Our overall conceptual model (Fig. 1) illustrates that these drivers of change cause perturbations in the interacting ecosystem processes of biogeochemistry, hydrology, vegetation dynamics, and food webs, and that the responses may vary across the landscape because of the characteristics of the geophysical and historical template. Understanding the variation imposed by this template is an important fourth, cross-cutting, theme of HBR research. While soil parent materials and topography are essentially fixed on ecological time scales, other aspects of the spatial template (such as vegetation structure) can vary in response to disturbances.

Within the framework of this conceptual model, our research encompasses the five LTER core areas-primary production, population studies, movement of organic matter, movement of inorganic matter, and disturbance patterns.

In previous cycles of the HBR-LTER we 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 also encompass biological changes caused by invasions of non-native species and migrations of more southern or low elevation species into HBR. While the biota is always changing, disturbances such as forest harvest and invasive species can accelerate the rate of change. Importantly, "Changing Biota" includes streams as well as forests. Biotic change differs 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

Synthesis and integration across levels of organization and disciplines are ongoing challenges in longterm, comprehensive ecosystem studies like ours. We propose to focus on five integrative questions that will frame, focus and motivate synthesis and integration for the next LTER cycle:

- 1. How will legacies of past air pollution, particularly depletion of exchangeable cations and accumulation of organic matter, S and N in the soil, affect the future structure and functioning of forest and stream ecosystems?
- 2. What are the soil, microbial and vegetation processes that have permitted N 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 and interactive effects of climate change, air pollution, plant succession, and invasive species alter the structure, function and biodiversity of the future 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 integrative 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. We will return to these synthesis and integration questions in section 2.8.

2.1.4 Research sites.

HBR (43°56'N, 71°45'W) is a 3160-hectare Experimental Forest operated 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 watersheds have been experimentally manipulated (Table 2). Increasingly we have broadened our study to encompass the wider HBR valley.

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 near the experimental watersheds at HBR precluded installation of an eddy covariance tower to measure energy and 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 <u>AmeriFlux</u> network. Recent advances in techniques for using eddy covariance in complex terrain (Belcher et al. 2012, Novick et al. 2014) and reconsideration of other locations within HBR with more favorable topography led us to install a flux tower at HBR in 2015, and we will compare the HBR and BEF eddy covariance data during the term of this proposal. The comparison will focus on the energy budget because it is less sensitive than the C flux to inaccuracies caused by non-ideal terrain. HBR researchers

also conduct comparative studies and collaborate 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 | CaSiO ₃ (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 | Ν | 76.4 | 1965 | None | |
| 8 | Ν | 59.4 | 1969 | None | |
| 9 | Ν | 68.2 | 1986 | None | |
| 101 | S | 12.1 | 1970 | Clear-cut in 1970; timber products removed. Streamflow quantity is not monitored, only chemistry. | |

2.2 Theme 1: Changing atmospheric chemistry

2.2.1 Overview

Although the atmospheric deposition of S and N has declined in recent years (section 1.1), 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. Another legacy is the accumulation of N in the ecosystem, primarily in the soils. This accumulation continues to the present, and raises important questions about the processes that regulate N sinks in the ecosystem, and the consequences of N accumulation in 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, Groffman.)

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 $SO_4^{2^-}$ and NO_3^- 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, resumption of forest biomass accumulation and reversal of the forest decline that has continued in the reference watershed (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. 2016a) 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 horizons (Johnson et al. 2014). Starting in 2010 we observed marked increases in NO_3^- in soil solutions and streamwater in this watershed (Fig 6). 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 from forest decline and improvements in sugar maple health 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 vegetation dynamics and net primary productivity, microbial biomass and activity, soil, soil solution and stream chemistry in the CaSiO₃ treated and reference watersheds. To better understand the unexpected perturbations in the N cycle, we will combine multiple datasets to develop N and C 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 timeseries analysis and determine mass balances to examine the transport and fate of added Ca and Si, and evaluate the implications for the recovery of soil Ca pools, 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 nutrient measurements in aboveground biomass and complete soil profiles in quantitative soil pits. 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, Johnson, Pardo, Bernhardt, Driscoll.)

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 pattern 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 the atmosphere (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 plant tissues, (3) leaching losses, and (4) gaseous losses (Fig. 11). At HBR, two of the four sinks are well quantified by our long-term data-- stream data indicate that the leaching loss is generally small, and vegetation data indicate that the forest biomass is declining, thus the vegetation is currently a source of N to the ecosystem, rather than a sink (Fig. 12) (Yanai et al. 2013). The soil sink and gaseous loss terms are poorly constrained, making it difficult to evaluate their relative importance. Therefore 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? 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?

<u>Mineral soil N retention</u>. 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. Vitousek and Reiners (1975) proposed that changes in net biomass accumulation during succession provide a strong internal N sink that controls the leaching losses of N. We hypothesize that the Vitousek and Reiners (1975) model is incomplete because it does not account for exchanges of N between vegetation and 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



Figure 11. Conceptual model of the fates of N added to a forest by atmospheric deposition or fertilization. N has four possible fates. shown by the four arrows, and can move to all of these fates simultaneously. Some of the known controls on the strength of these sinks and loss processes are shown next to each arrow. Some ecosystem responses to N movement to each of these fates are shown below the horizontal line. From Lovett and Goodale (2011).

Figure 12. Change in the ecosystem-scale mass balance of N in the forest of the reference watershed (W6) for □ total atmospheric periods between 1965 and 2007. The "missing term" (brown bar) was calculated as the difference between sources and sinks. and changed from a missing source early in the record to a missing sink later. Note that the biomass *increment (green bar)* created a net sink for N prior to 1992, but was a net source thereafter. From Yanai et al. (2013).

mineral soil, creating a sink that limits 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. 13). Nitrogen leaching occurs after the re-accumulation of soil N is complete and the soil N pool reaches a new 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. 13). This represents a substantial revision to a widely-held ecosystem theory.

Approach. To evaluate the conceptual model shown in Fig. 11 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. 2012), but even a small percentage change in the mineral soil pool can represent an N sink that is large compared to input and output fluxes. Isotopic measurements provide much better resolution of N sink strengths in 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, N and ¹⁵N pools, rates of adsorption of dissolved organic N in the soil, and root biomass and exoenzyme 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 over longer time scales (Box 1).



Figure 13 Revision of the Vitousek and Reiners (1975) conceptual model of N dynamics during succession. (a) Biomass accumulation. (b) N accumulation in plant biomass follows biomass curve in panel a. When plant N accumulation is greater than N deposition, soil mining occurs. When biomass N accumulation falls below N deposition, reaccumulation of soil N occurs. (c) N leaching occurs only when combined biomass + soil N sinks are less than N deposition. We hypothesize that W6 is in the soil reaccumulation phase (panel b) and therefore has low N leaching despite low biomass N accumulation.

<u>Gaseous N losses</u>. Although gaseous loss from denitrification has generally not been considered an important process at HBR, recent stable isotope (Wexler et al. 2014) and gas flux (Kulkarni et al. 2014, 2015, Morse et al. 2015b) evidence indicates that gaseous losses could be much greater than previously 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 (Groffman 2012).

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 N_2O since 2001 (Groffman et al. 2006b, 2009, 2010). These measurements have been coupled with more detailed measurements of N_2 and N_2O fluxes and soil O_2 levels to produce estimates of N gas losses relevant to watershed mass balances. The long-term data illustrate 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). We propose to continue these measurements and to extend them across soil depths, topographic positions, and seasons to identify locations across the geophysical

template that have high potential for denitrification (Morse et al. 2014). Through collaborations with microbiologists at Cornell University (James Shapleigh and C. Armanda Roco) we will use metagenomics shotgun sequencing of community DNA (Illumina HiSeq platform) to provide initial characterization of how microbial community composition and function vary with soil depth. Preliminary results show that microbial community composition varies distinctly by horizon and that, for example, the relative abundance of genes for nitrification peaks in the top 20 cm of mineral soil, while the relative abundance of genes for nitrification peaks in the top 20 cm of mineral soil, while the relative abundance of genes for 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 NO₃⁻ isotopic measurements to identify seasonal, depth, and topographic patterns in denitrification in the HBR watersheds. Results from the denitrification measurements will be used in concert with the mineral soil N work to improve the simulation of N balance in the PnET-SOM model.

2.2.4 Multiple element limitation (Contributes to synthesis question 1. Research team: Fisk, Yanai, Fahey, Goodale, Hamburg.)

According to ecological theory, vegetation productivity should tend towards co-limitation by multiple environmental resources, a concept that underpins the MEL model (Box 1) (Rastetter et al. 1997). We have calibrated and applied MEL 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. 14). However, several mechanisms could counteract these challenges to balanced nutrition and maintain N and P co-limitation (Fig.14). 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 and mature stands (see section 1.1); however, we hypothesize 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 change over the course of succession?
- Which plant and soil mechanisms are most important for maintaining N and P co-limitation?
- How do plant and microbial responses to added N and P vary across a native gradient in soil fertility?



Figure 14. Conceptual model of N vs P limitation in forests, showing factors that cause systems to deviate from colimitation by N and P and the mechanisms that favor co-limitation by conserving or acquiring the more limiting nutrient.

Approach. We will continue N and P fertilization in 13 northern hardwood stands located in three sites in the White Mountain region (HBR, BEF, and Jeffers Brook) that were chosen to represent regional variation in soil fertility. 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 plot fertility while minimizing artifacts associated with higher doses of fertilizer. For comparison with the WS1 Ca treatment other plots in these stands received a onetime wollastonite (CaSiO3) addition in 2012. 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 allow us to evaluate and improve 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 climate data (section 1.2) reveal several intriguing trends that motivate our new research to evaluate physical, chemical, and biological responses to climate change. Of these trends, the declines in evapotranspiration (ET) and 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 because they directly influence ecosystem function and challenge our ability to anticipate the future of the ecosystem. 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, Kelsey, Asbjornsen, Campbell, Matthes, McGuire, Vadeboncoeur.)

Understanding the long-term decline in ET is challenging because ET is controlled by multiple factors operating at a range of spatial and temporal scales. Possible reasons for the decline include successional changes in forest structure or composition; changing nutrition by N, P, and Ca; changes in photosynthesis or water use efficiency due to changing atmospheric CO₂ concentrations or air pollutant levels; and exogenous drivers such as changing temperature, solar radiation, and humidity. We will utilize methods that can address ET variability across spatial scales from individual trees to the landscape (Fig. 15). This will allow us to place the decline in the context of other sources of variability. Understanding the dynamics of ET change on multiple scales will improve predictions of how individuals, communities, and ecosystems respond to and control future hydrologic change. Our major research questions are:

- What is the relative magnitude, direction, and persistence of ET change in response to climate variability versus forest disturbance?
- What is the relative contribution of the various biological and physical drivers of ET change?

Approach. We will evaluate ET trends at four time scales: long-term forest succession (60 years), 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, analysis of tree rings to assess stem increment growth and the natural abundance of ¹³C and ¹⁸O (as a proxy for physiological drivers of ET trends due to stomatal regulation of leaf-level exchange of H₂O and CO₂).

Analysis of the response to disturbance will involve ET

calculations from the long-term hydrologic data from the forest harvesting treatments at HBR (Table 2). The seasonal controls will be assessed using eddy covariance at our new flux tower site (see section 2.1.3) and sapflow



Figure 15. Methods used to study evapotranspiration across temporal and spatial scales.

measurements collected at multiple sites across the HBR valley, for which the seasonal onset, peak, and decline of ET will be evaluated relative to meteorology and phenology. The eddy covariance and sapflow measurements will also be used to assess regulation of 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). We will use the ED2 model and PEcAn data assimilation system (Box 1) to understand current controls on ET and to predict the response to future climate and disturbance scenarios, by synthesizing measurements across temporal scales and conducting modeling experiments that elucidate the roles of different ET drivers.

2.3.3 Changing seasonality (Three subprojects; all contribute to synthesis question 4.)

We predict that changing seasonality, e.g. earlier spring, longer vernal window and warmer autumn, and altered plant phenology, will have important consequences for numerous aspects of terrestrial and aquatic ecosystems at Hubbard Brook. Here we describe three projects that are linked through consideration of changing plant phenology and its impacts on carbon and energy exchange, the forest floor, and embedded stream ecosystems.

<u>Vegetation phenology, forest carbon cycling and biosphere-atmosphere interactions</u>. (Research team: Richardson, Green, Ollinger, Campbell, Rustad.) 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 including 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 biosphere-atmosphere exchanges of CO₂, heat and water vapor 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 cycling.

<u>Seasonality and the spring trigger.</u> (Research team: Groffman, Rustad, Driscoll, Fisk, Pardo, Fahey, Templer, Christenson.) 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 (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 (Fig. 8). 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. 8), leading to the question:

 Does variation in the vernal window drive variation in hydrologic and gaseous N losses from forest soils 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. Continuously recorded (hourly) soil temperature data are available from 26 sites across an elevation gradient, where we will be able to observe the abrupt temperature rise signaling the "soil trigger". Snow depth and soil temperature are both continuously recorded at one site (a Soil Climate Analysis Network (SCAN) site), which will be used to establish the relationship between snowpack depth and soil temperature in the spring (e.g., Fig. 8). These data will be combined with phenology data (described above) to quantify variation in the period of vernal asynchrony (Groffman et al. 2012). This variation will be compared with monthly watershed N

exports and soil solution chemistry data collected to evaluate relationships between asynchrony and nutrient loss. We are also seeking non-LTER funding to manipulate the length of the period of asynchrony though snow removals and additions during the winter/spring transition.

Seasonality and in-stream carbon dynamics. (Research Team: Rosi-Marshall, Bernhardt, Likens, Burchsted, Lowe.) Changes in forest phenology and attendant changes in soil nutrient dynamics have consequences for stream ecosystems. Spring and autumn are arguably the most important seasons for in-stream carbon processes and invertebrate consumers in headwater streams (Tank et al. 2010). At HBR, the greatest watershed export of N occurs in early spring, and differences in spring conditions cause substantial interannual variability in watershed export (Bernhardt et al. 2005). 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 of these algal blooms are not known, but may be related to changing stream chemistry (Likens and Buso 2012) or altered seasonality, e.g., a longer "vernal window" before foliage shades the streams. Interestingly, algal blooms have never been observed in the less acidic stream draining the CaSiO₃ amended watershed (W1). The autumn litter input to streams also fuels in-stream nutrient removal and primary consumers. If the autumn season is warmer and longer, increased litter mineralization may fuel nutrient removal in streams and provide more food resources for stream invertebrates. These predictions lead to the question:

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

Approach: We will initiate a program of monitoring in-stream conditions and organic matter dynamics in three streams across a gradient of pH (W1, W6, and W9; pH ~ 5.4, 5.2, and 4.4, respectively). Sensors will record in-stream temperature and conductivity and light at the surface of the stream, and 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 litterbags to measure leaf litter decomposition rates and invertebrate consumers (Entrekin et al. 2008). We will also examine the influence of changing C dynamics (more available algae or leaf litter) on primary consumers by 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, Hall et al. 1980) to investigate long-term changes in stream C dynamics. This project involves several new HBR-LTER co-PIs (Rosi-Marshall, Bernhardt and Lowe) 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, Driscoll, Fahey, Fisk, Pardo, Rustad, Goodale, Christenson.)

The effects of climate change on N cycling are complex and involve changes in optimal allocation of N within plants, ensuing changes in litter quality, and alteration of belowground processes. We will investigate the impacts of climate change on N cycling using both comparative studies along an elevation gradient and experimental manipulations. The elevation gradient at HBR creates an approximately 2°C 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 foliar N, net N mineralization and nitrification (Fig. 16), 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°C with heating cables from 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 (Groffman et al. 2012). 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 may allow trees to repair the root damage caused by soil freezing.

The key question driving these studies is:

• How does climate change alter the availability, uptake, and loss of N in the ecosystem?



Figure 16. Potential net nitrification (left) and mineralization (right) versus elevation in 20 plots along the elevation gradient at HBR, spring 2011. From Duràn et al. (2014)

Approach. We will continue our measurements along the elevation gradient and analyze long-term relationships among N mineralization, nitrification, soil temperature, soil moisture, snow depth, soil frost and watershed N losses to improve understanding of climate effects on N supply and loss (Groffman et al. 2009, Durán et al. 2014, 2016). We will add measurements of foliar N, spring ephemeral plants, and insect population dynamics to this study (see section 2.3.5). 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 (e.g., Campbell et al. 2014), root health, and sap flow (using the Granier method).

2.3.5 *Climate change, N availability, and forest food webs* (Contributes to synthesis questions 4 and 5. Research team: Ayres, Lany, Lovett, Sillett, Holmes, TerHofstede, Lowe, Christenson, Groffman.)

Strong seasonality is a prominent feature of animal populations at HBR and north temperate hardwood forests in general. Spring and early summer is the period of maximal biological activity for leaf-eating insects such as caterpillars (Reynolds et al. 2007, Lany 2014, Lany et al. 2016), and birds, which are producing eggs and feeding young. Another 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), and years of high caterpillar abundance produce high nesting success in birds (Sillett et al. 2000, Townsend et al. 2016). The variability in 1° consumers at HBR contrasts with that of net primary production, which is stable to within \pm 20% among years (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, as leaf N concentration in hardwood trees is highest just after budburst and declines during leaf expansion. Caterpillars grow most rapidly when consuming foliage with higher leaf N (Lany 2014). 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:

• Longer and warmer summers should favor the abundance of 1° consumers. Annual thermal sums have increased by 200 – 300 degree days (~14 %) since 1961. 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).

- Phenological mismatching may occur as animal population fail to track earlier budburst. The average timing of budburst has advanced by ~ 7 d since 1961, and the two earliest springs in 50 years have occurred in the last four years (Lany et al. 2016). However, 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 (Lany et al. 2016).
- Temperatures during leaf expansion are becoming cooler, potentially slowing caterpillar growth and lowering survivorship. When budburst is earlier in the spring, temperatures during leaf expansion and bird nesting are cooler than in an average year, and early-season caterpillars 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 is phenological synchrony among plants, insects and birds affected by climate?
- What causes interannual variation in leaf N, and what are consequences for the green food web?
- How does temperature during the leaf expansion period affect green food web dynamics?
- To what extent is the brown (detrital) food web buffered from the effects of leaf N variation by retranslocation of foliar N prior to leaf drop and by mixing of fresh litter with old litter in the forest floor?

Approach. To answer these questions we will continue and expand 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. 2016); valley-wide monitoring (point counts) for birds and diurnally active small mammals (Goetz et al. 2010, Holmes 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 important top predators in the brown web, permitting comparisons with historical surveys that have become inactive (Burton 1976); and (4) estimates of % herbivory from samples of leaves examined shortly before abscission begins. To strengthen analyses of interannual patterns we will also incorporate data from the elevation gradient measurements of soil temperature, moisture and N cycling discussed in section 2.3.4.

2.4 Theme 3: Changing biota

2.4.1 Overview

The biota of Northeastern forests is always changing, but the magnitude and pace of change 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 research proposed in this section. First, the HBR forest is responding to multiple interacting drivers that alter its structure and species composition in complex ways. Introduced pests, climate change, natural successional dynamics, and N enrichment and base cation depletion due to chronic acid deposition are simultaneously affecting the dynamics of the forest. In the near future, two new introduced insects, emerald ash borer and hemlock woolly adelgid, are likely to have severe effects on white ash and eastern hemlock populations. In headwater streams, the decline of a top predator, the salamander *Gyrinophilus porphyriticus*, may restructure the stream food web. The studies proposed below address questions that arise from these trends. These changes demand new measurements and more encompassing models of forest ecosystem dynamics.

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

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 trees species, sugar maple and American beech,

replace themselves over time. However these expectations no longer hold. For example, we have documented a trend toward increased beech dominance (4% increase in relative abundance over the last 15 years) largely at the expense of sugar maple (2.3% decrease over the same time). Even more pronounced is the proportional increase in beech in the young adult size class (10-30 cm), which represents the canopy of the future (Fig. 9) (van Doorn 2014). Drivers of these changes likely include the depletion of soil Ca²⁺ 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 the biogeophysical template for other population, community and ecosystem processes. We propose a revision to our conceptual model that builds on the hierarchical-response framework (HRF) proposed by Smith et al. (2009) and accommodates transient as well as steady-state dynamics. Evidence from HBR suggests that directional change through time is characterized by multiple stepped responses (Fig. 17). 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) (e.g., Juice et al. 2006). 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., a wind storm or ice storm) could accelerate directional changes already underway, such as species immigrations (e.g., 17D).



Figure 17. A conceptual model of ecosystem dynamics in a novel disturbance regime. Adapted from hierarchical response framework of Smith et al. (2009) and informed by long-term observations at HBR. Chronic stress leads to a series of stepped vegetation responses that in turn influence ecosystem function. Episodic disturbances in addition to the chronic stress can speed the vegetation response.

Chronic Stressor (e.g., disease progression with time)

To understand the direction and rate of vegetation change, it is essential to quantify the patterns and processes of tree recruitment. Historically our sampling has emphasized established trees (≥ 2 cm in diameter at breast height or 1.37 m) because they dominate the contribution to carbon and nutrient budgets. However, 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 seedling survival (Cleavitt et al. 2008, 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 differ 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 HBR valley. Specifically, we will establish seedling transects in a stratified random subset of our permanent plot network, which covers the entire HBR landscape. 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 (e.g., van Doorn et al. 2011) and soil resource availability (Battles and Fahey 2015) in the permanent plots. 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 disturbance events, diseases, and immigration will test predictions from the HRF. For example, we will be able to test the HRF prediction that canopy openings caused by a windstorm should accelerate the establishment of species that are gradually expanding their range in a warming climate.

2.4.3 The incipient loss of <u>Fraxinus</u> from HBR (Contributes to synthesis question 3. Research team: Ayres, Battles, Lany, Lovett, Fahey.)

The emerald ash borer (*Agrilus planipennis*), an invasive insect that kills ash (*Fraxinus*) trees, was within 50 km of HBR as of November 2015. Based on patterns elsewhere, we expect that it will virtually eliminate ash from HBR and the surrounding region within the next 5-10 years (Herms and McCullough 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). Moreover, white ash (*F. americana*, the ash species present at HBR) is biogeochemically distinctive in that it has highly decomposable litter (Lovett et al. 2016a) and produces soil organic matter with low C:N ratios and high nitrification rates (Venterea et al. 2003), thus potentially creating hot spots for NO₃⁻ 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, 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 birds 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 by these co-dominants will affect C and N cycling in the ecosystem. In a selected set of ashdominant 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 manifest 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.

2.4.4 Changing stream food webs. (Contributes to synthesis question 4. Research team: Lowe, Rosi-Marshall, Likens.)

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 was 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 vs. 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 motivate 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 will continue intensive capture-mark-recapture studies of salamander populations (*G. porphyriticus* and *E. bislineata*) that were initiated in 2012 in three HBR streams. We will expand the study and assess the broader effects of changes in top-predator populations by sampling stream community variables (e.g., invertebrate diversity and abundance, salamander diet composition) in reaches that span gradients of salamander abundance and species composition.

2.5 Theme 4: The geophysical and historical 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) to develop a more detailed understanding of the spatial heterogeneity present across the entire HBR valley (3160 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. 18A) and N cycling, stream chemistry (Fig 18B), and animal populations (Fig. 18C).

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. 19) (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 the scale of the entire HBR valley. Our principal research question is:

• To what extent does the topographic model of hydropedology developed at the small watershed scale account for hydropedological variation at the valley-wide scale?

Approach. This will likely involve designation of one or more new hydropedologic units because as we scale up, more types of topography and soil parent materials are included. 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. Where the model fails to predict existing soil descriptions, new sampling strategies will be developed to characterize hydropedologic



conditions and the data will be used to improve the model (e.g., Gillin et al. 2015). Because of the strong influence of hydropedology on soil nutrient cycling, this work leads to a more comprehensive understanding of the continuum of soil solution, groundwater and streamwater. The improved model will help inform sampling strategies and interpretation of data from other research including Ca depletion (section 2.2.2), N cycling (2.2.3), and climate change (2.3), as well as the valley-wide stream sampling discussed in the next section.



Figure 19. Conceptual model showing the distribution of soil groups along a representative hillslope. Blue arrows show the direction of water flow. Horizon presence and thickness vary across the hillslope, and several different types of podzols are distinguished. From Bailey et al. (2014).

2.5.2 Characteristics of headwater and seasonal streams (Research team: Bailey, Likens, Bernhardt.)

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 HBR valley display a surprisingly high chemical diversity (e.g., Fig. 18B) (Likens and Buso 2006, McGuire et al. 2014) that drives variation in stream biota (Fierer et al. 2007). This same chemical diversity of streams may be 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 considerable 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 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). The key research questions are:

- What properties of the geophysical template lead to the initiation of seasonal streams and to the transition to perennial flow?
- Does the chemistry of downstream perennial reaches reflect the chemistry of their tributary seasonal streams?

<u>Approach.</u> We will undertake a new initiative to extend mapping of the complete stream network, including seasonal streams, to the entire HBR valley. This will entail 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 for the perennial portion of the stream network by Likens and Buso (2006). We will determine if spatial variability of seasonal streams at the fine scale is as great as it is in perennial streams across the valley, and if the chemistry of perennial streams reflects the sum of their tributary inputs.

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 (e.g., Fig. 18C) 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 spatial patterns set the stage for 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 investigate 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:

• What is the relative importance of abiotic and biotic variables in determining the distribution, abundance and dynamics of animals across the HBR valley?

<u>Approach.</u> To complement the ongoing surveys of birds, small mammals, Lepidoptera and salamanders (section 2.3.5), 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 geophysical and historical template. New surveys will include large mammal (moose, deer, bear, coyote, marten, beaver and bobcat) 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 (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 elevation transects within the HBR (from ~ 300 to 750 m elevation, 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 to identify all invertebrates to at least the level required to infer functional group, and to genera or species when possible.

2.6 Transforming the HBR 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 with specific criteria (e.g., stream samples from W6 in the 1980s with NO₃⁻ concentration > 2 mg/L) that will return a list of samples and corresponding metadata (e.g., barcode, physical sample location, volume/weight remaining, chemistry). These improvements will create a state-of-the-art resource which will pinpoint the most appropriate samples for

specific questions, expanding its value to researchers from around the world. (See the Data Management Plan for further discussion of the Archive.)

2.7. Related research and leveraging of LTER Funding

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: the weekly precipitation/stream chemistry measurements and the longterm study of breeding birds. These data sets complement our ongoing LTER research, and loss of these LTREB grants would diminish the spatial and temporal extent of our measurements in these areas..

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 hydrology 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. For example, we have recently begun two externally-funded experiments that augment our climate change research:

<u>Throughfall displacement experiment (TDE)</u>. To assess the response of the northern hardwood forest ecosystem to drought, a TDE was established at HBR in 2015 (primary funding from USDA, 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 forests.

<u>Ice storm experiment.</u> With funding from a NSF-DEB grant (C. Driscoll and L. Rustad, PIs), we have begun a new experiment to study the potential impacts of ice storms. During winter 2016 ice was generated using fire hoses in 8 experimental plots at varying intensity and frequency of ice damage. In addition, long-term responses to the severe 1998 ice storm at HBR will be evaluated from field data.

We are careful and selective about incorporating new projects into the longer-term LTER suite of measurements to avoid overcommitment of resources, while welcoming new investigators.

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 forests and streams at HBR have changed over time, and to make projections of ecosystem response to future change. We have produced a wide array of synthesis products ranging from books to monographs to analyses for policy makers (see section 1.5). Yet, synthesis and integration is a constant challenge for large, multidisciplinary long-term projects. Here we propose to focus on five synthesis questions to frame, focus and motivate synthesis and integration over the next six years. These questions will be addressed using the research described above, long-term data, and modeling. But more fundamentally they will be rallying points for group interaction and evaluation of progress. We have had recent success in using our quarterly group research meetings to launch synthesis efforts (Groffman et al. 2012, Fahey et al. 2015). Now we propose to use the questions below, and our quarterly meetings over the next six years to formalize this platform for synthesis and integration.

1. How will legacies of past air pollution, particularly depletion of available Ca and accumulation of organic matter, S and N in the soil, affect the future functioning of forest and stream ecosystems? (Organizer: Driscoll) Our long term data indicate that depletion of soil available 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 examine soil chemistry, hydrology, vegetation physiology and dynamics, and animal population studies to synthesize the accumulating knowledge on 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 N export in streamwater in the reference watershed to remain low despite continued N pollution and cessation of biomass accumulation in the watershed forest? (Organizer: Lovett). One of the most intriguing 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 C and N pools, microbial activity, hydrologic fluxes, climate, atmospheric deposition, and biomass trends to quantify the N sinks in our conceptual model (Fig. 11) 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. We will convene a workshop of watershed scientists to compare patterns of N deposition, retention, and export across Northeastern forested sites, an approach which we have used successfully in the past (e.g. Aber et al. 2003). 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 simulate longer time scales and include disturbances such as harvesting and climate change.
- 3. How will simultaneous and interactive effects of climate change, air pollution, plant succession, and invasive species alter the structure, function and biodiversity of forests of HBR? (Organizer: Battles). 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 such as 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 characterize and attribute disturbance impacts on 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. The flexible spatial resolution of the ED2 model is well suited to capture local plot-level changes within HBR and to analyze how local patterns scale up to regional changes in forest dynamics. By bridging spatial scales, the ED2 model will connect plot-level simulations with regional simulations from the PnET suite of models (Box 1). We have recruited an ecosystem data scientist (Matthes) to lead the ED2 model-data assimilation effort over the next cycle.
- 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? (Organizer: Groffman). 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 new 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 of 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? (Organizer: Ayres). 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 (Lepidoptera). We have also demonstrated that foliar N spatial patterns can be reliably estimated with high spectral resolution remote sensing (Fig. 18A) (Lepine et al. 2016). 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 fauna (Rodenhouse et al. 2009, Groffman et al. 2012). Over the next six years, we will integrate climate, biogeochemical, remote sensing, and biodiversity datasets using hierarchical statistical modeling to improve understanding of how changes in vegetation, invertebrates, bird, and mammals are linked to changes in climate and biogeochemistry, especially foliar N and soil N dynamics but also including P and Ca availability 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 identify the most efficient means to improve the precision and accuracy of our measurements, for example in calculations of forest biomass (Yanai et al. 2010) and nutrient export in streams (Yanai et al. 2015). These approaches have 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, our weekly sampling of streams appears to be unnecessarily frequent during base flow (summer time) but not frequent enough during snowmelt. To assess alternative monitoring strategies for these key aspects of the hydrologic budget, we plan to add more precipitation collectors and conduct dilution gauging during high flows. Our larger goal for this LTER cycle is to expand our focus and develop best practices for the collection, analysis, and curation of ecosystem data at HBR, which will be applicable to other LTER sites that share the challenges posed by the quantity and diversity of the data we collect and manage. By collaborating with colleagues in the LTER Network and in the QUEST Research Coordination Network (http://www.esf.edu/quest/), we will continue to develop and demonstrate tools for maximizing the efficiency of data collection and understanding the uncertainties associated with our measurements.

2.9 Education And Outreach (Coordinators: Outreach staff at the Hubbard Brook Research Foundation)

2.9.1 Schoolyard and outreach activities

We will continue our successful education and outreach programs, largely coordinated by The Hubbard Brook Research Foundation (HBRF), which serves as an interface organization between HBR researchers and schools and community stakeholder organizations in the region. We will continue to work with local teachers, including development of classroom curricula and other resources and 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. Policy-oriented activities that share cutting-edge research information with stakeholder organizations are organized around the Forest Science Dialogues Program, which uses facilitated roundtables and other activities to foster two-way conversations between HBR researchers and stakeholders, and the Science Links Program, which synthesizes policy-relevant research. HBR scientists also lead science synthesis and policy outreach programs within the Science Policy Exchange (SPE), a regional policy interface organization, a collaborative venture of regional universities and LTER sites. Science Links and SPE projects typically involve the production of a synthesis paper on a policy-relevant issue, coupled with a coordinated outreach effort to reach media, land managers, and policy makers (Driscoll et al. 2011).

In the term of this proposal we will:

- Maintain partnerships between HBRF and science education providers in NH and run teacher professional development programs, including the RET program.
- Maintain close working relationships with the five public K-12 schools closest to HBR, as well as with others who have requested our involvement.
- Create classroom lessons for middle- and high-school teachers based on studies and data from experimental forests and other research sites.
- Provide tours, assistance in data acquisition, and classroom usage, and interface with the research community as requested by other schools in the region.
- Expand the Forest Science Dialogues project beyond NH to other Northern Forest states.
- Develop two new Science Links projects on winter climate change and regional water issues
- Continue outreach activities for HBR-led SPE projects on forest pests, ecosystem and health impacts of coal combustion, and green infrastructure.

2.9.2 Supporting REU programs

HBR's Research Experience for Undergraduates (REU) program, organized in partnership with Plymouth State University, provides on-the-ground research opportunities for 8-10 students each year, allowing students to participate in the vibrant scientific community at HBR. Students present their work at the annual HBR Cooperators' Meeting and at a culminating annual REU conference. This effort has been 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.

2.9.3 Integration of art and science (Coordinator: Rustad)

There is a growing recognition within the LTER community and more broadly there is a need to revitalize relationships between the arts and sciences (A&S) (Swanson 2015). The HBR participates in the LTER Ecological Reflections program, an effort to combine the expertise of diverse disciplines to create a more unified approach to inter-related ecological and social issues. HBR has launched an A&S program in which ecosystem scientists collaborate with artists, musicians, neuroscientists, and teachers to explore environmental sensor data in creative ways. The flagship project, Waterviz, a water cycle visualization and sonification tool, has been featured at art shows, local science centers, and featured in online press releases, blogs and publications (see waterviz.org). We plan to grow our A&S program by continuing to develop Waterviz, by establishing an HBR artist-in-residence program around the theme of integrating art, technology and data, and by continuing to play a leadership role in the Ecological Reflections program and the new #ArtSciConverge community which spans LTERs, Field Stations and Biological Laboratories.

2.10 Cross-site and network activities

HBR scientists have been active participants in many LTER network activities and cross-site synthesis projects. HBR co-PI Peter Groffman is the chair of the LTER Science Council, and Groffman and co-PI Charles Driscoll are on the LTER Executive Board. HBR scientists have led or participated in numerous LTER Synthesis Working Groups, including: Pathways and Patterns of Litter Chemistry During Decomposition; Quantification of Structural Legacy Effects Via Synthesis of Long-Term Records And Eco-Hydrologic Modeling; The Disappearing Cryosphere; The Impacts of Within Season Rainfall Variability Across Ecosystems; Managing Sensor Networks and Data: Best Practices for LTER; Social and Ecological Responses to Climate Change and Land-use Effects on Water Availability; Extreme Climate Events Across Diverse Ecosystems; Engaging Arts/Humanities in Future Scenarios Work; Soil Biogeochemistry; Sensitivity of Ecosystem Properties to Winter Climate Anomalies; Exploring the Seasonal Synchrony of Catchment Nitrogen Dynamics; Quantifying Uncertainty in Ecosystem Studies; Quantifying Uncertainty in Wet Atmospheric Deposition; and Quantifying Uncertainty in Forest Nutrient Budgets.

HBR scientists have also taken a leadership role in regional research by developing the Northeastern Ecosystem Research Cooperative (<u>www.nercscience.org</u>), an organization of regional ecosystem scientists that convenes a very popular biennial conference and has produced many cross-site comparisons and other synthesis efforts (e.g., Aber et al. 2003, Pardo et al. 2006, Lovett et al. 2007, Mitchell et al. 2011). HBR PI Lovett chaired the NERC from its inception in 2000 until 2015, and many HBR scientists are active participants.

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Data Management Plan

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) development and maintenance of a website to share information on site history, current research, publications, photos, educational materials, etc. (4) maintaining a physical sample archive. The primary role of the HBR Information Manager is to support the HBR information management system (IM) and to provide expertise in data documentation, archiving and retrieval, for on and off-site scientists conducting research projects and data syntheses. Since 2012, the HBR Information Manager position has been held by Mary Martin, based at the University of New Hampshire in the Earth Systems Research Center (ESRC). The HBR Information Manager 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]), and has attended annual LTER Information Management Committee meetings (2012-2015), LTER Science Council meetings (2012, 2013), and the All-Scientists Meetings (2012, 2015).

Governance - Information management 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.

Information Technology (IT) Resources - IT support for HBR IM is provided through the UNH Research Computing Center (RCC) center. RCC 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 RCC (20+ years). See UNH facilities statement for additional details on available IT resources. In addition to general IT support, RCC also provides the personnel for as-needed project support. Key software and hardware features of the HBR Information Management system are described in Table 1.

| Feature | Details, software, resources |
|----------------------------------|---|
| Website: http://hubbardbrook.org | html, css, php, xslt, javascript, apache, piwigo |
| Bibliography | Zotero, MySQL, bibutils |
| Data Catalog | MySQL |
| Metadata | PostgreSQL, metabase2 (adopted from GCE/MCR/SBC), EML2.1.0 |
| Computer Hardware | Dell Poweredge R510, desktop and laptop linux systems. |
| Backup | BackupPC, rsnapshot, daily, weekly and monthly backups, on and off-site |
| Data management | R, GCE Toolbox, LibreOffice, QGIS |

Table 1. Features of HBR Information Management System

HBR Website - The HBR website (<u>http://hubbardbrook.org</u>) is the primary means by which HBR information is disseminated, with additional non-digital data (charts, maps, photographs) made available upon request. Online access to HBR information and data has been available since the early 1990s, with several major upgrades in the intervening years. The most recent HBR website redesign occurred 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 a webserver managed by RCC, housed in a temperature controlled environment with power backup. Website use is tracked using Google Analytics. From Jan. 1, 2015 to Dec. 31, 2015 the site had 24,891 visits, with over 8,000 visitors using the site more than once. In addition to the data catalog and publication database (described in separate sections below), the website provides access to:

<u>Personnel database</u> - A personnel database, including curricula vitae, is maintained on the HBR website. Individuals update their own vitae via a password-protected web form. Updates can be made any time and reminders are sent out twice annually to ensure that the information is current.

<u>Current Research</u> - A description of current research activities is available through the HBR website to inform the research community and public about research initiatives and preliminary findings. Updates reflect changes in the development and scope of current research.

<u>Photo archive</u> - 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. The online photo gallery was recently updated with the installation of Piwigo (http://piwigo.org) on the webserver. This full-featured, open source 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 general HBR use, and we are in the process of identifying additional historical slides and film from HBR research teams, to be added to the digital collection.

Education and Outreach Material – Educational materials are linked to the front page of the website through the 'For Students and Educators' link. These resources are on both the HBR website as well as that of the Hubbard Brook Research Foundation (HBRF). Funding has been obtained to improve the integration of education, outreach, and stakeholder material on the HBRF website with that of the HBR-LTER website, and this work will begin in early 2016.

<u>External links</u> - The website provides links to LTER resources and data, the US Forest Service website for the Hubbard Brook Experimental Forest, and the Hubbard Brook Research Foundation.

<u>Internal Website</u> - Password protected intranet access is available to the core HBR research teams. This was developed as a means of sharing and archiving ideas, information, and documents among the approximately 70 geographically dispersed members of the Committee of Scientists.

Publications - The publications from the Hubbard Brook Experimental Forest date back to 1955, and number more than 2,400 books, journal articles, conference presentations, and theses. A list of these publications is accessible in a searchable format on the HBR website. New 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 harvests citations, citation metrics, and associated pdf's through a browser, and exports to standard reference management file exchange formats. Early publications are archived in paper at the Cary Institute of Ecosystem Studies; publications since 2011 are archived in pdf format. The pre-2011 publications are being assembled in digital format by downloading pdfs from the publishers, and scanning original paper copies when a digital version is unavailable. Publications are now added to the list with a hyperlinked DOI to improve access to the documents. All HBR publications are uploaded to the ceneral LTER bibliography database at http://bibliography.lternet.edu.

Data catalog - The HBR data catalog is available on the HBR website as well through the LTER data portal. A complete inventory of data is available in a Supplemental Document. The data catalog contains 138 data sets ranging from single year studies to longterm data collections, with more than 20 data packages containing data collected for more than 50 years, and another 30 covering a timespan of more than 20 years. During this past funding cycle, we have appended to our core data sets and incorporated many new data sets. See 'data lifecycle' section for a description of steps being taken to improve our data tracking and submission rates. We have also restructured a number of data sets to better serve the user community. For example, a data series collected at 5 year intervals, packaged in different data sets, with varying formats, has been restructured in to a single data set with a common format. A number of other data sets will undergo similar restructuring to improve usability (vegetation inventory). For almost a decade, we have averaged 10 data downloads per day, and the downloads by user affiliation can be seen in Table 2.

<u>Data Access Policy</u> - HBR adheres to the LTER Network Data Access Policy. 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. 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 and users. Data sets accessed through the LTER-NIS are tracked through 'Data Package Access Reports'.

Table 2. Summary of data downloads by user affiliation. Records have been filtered for download testing and incomplete user identification.

| Type of Institution | 2013 | 2014 | 2015 | total | % of total |
|--------------------------|------|------|------|-------|------------|
| Academic Research | 612 | 1136 | 663 | 2411 | 22 |
| Education (K-12) | 408 | 508 | 444 | 1360 | 12 |
| Education Post-Secondary | 1443 | 1943 | 1102 | 4488 | 41 |
| Government | 82 | 217 | 143 | 442 | 4 |
| Hubbard Brook LTER | 454 | 399 | 308 | 1161 | 10 |
| Other LTER | 83 | 18 | 45 | 146 | 1 |
| Other | 319 | 543 | 204 | 1066 | 10 |

<u>Database</u> - Tabular data for all HBR data sets are stored in a MySQL database, and retrieved by website queries via php code. A development version of the website and underlying database is used to test and stage data sets for review and approval. All databases are backed up daily (on-site and off-site), and data are easily restored for the entire database, or for individual tables as necessary.

Metadata - HBR researchers have a long history of data sharing, and were among the first LTER sites to provide dial-up access to data sets, beginning in 1989. Within a year of LTER Ecological Metadata Language (EML) adoption (circa 2004), all HBR data were upgraded, and made available on-line with level 5 EML documentation (fully described attributes). 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 data sets were brought into compliance with EML Best Practices and EML 2.1, as demonstrated through their PASTA congruency, and availability in the LTER data catalog. In the process of updating these long-standing data sets, we also brought them into compliance with the LTER Controlled Vocabulary and LTER Network Unit Registry. The most important task ahead with regard to metadata, is completing the migration of our existing EML flat files into the Metabase Metadata Management System (MMS). Initially developed by the GCE LTER, and further modified by SBC and MCR LTER sites, this system uses a comprehensive suite of relational database tables to store metadata content. We have been able to leverage the postgreSQL schema from these other sites, as well as xsl transformation files to extract EML components from our existing files attributes, personnel, keywords, etc. The population of this database is in progress, and once complete, we will also leverage MCR/SBC code that generates EML from this database. Moving to a model in which HBR EML metadata are generated from the MMS will streamline data package development.

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, for the purpose of tracking project status. In the next RAC cycle (spring 2016), we will be implementing a number of changes that have been developed by the RAC chair and the Information Manager. These changes will improve our ability to track the status, progress, data, publications, and associated material, for all projects at HBR. Three important changes will be 1) the requirement for a data management plan that will be signed off on by both RAC and IM prior to the initiation of a project, 2) a formalized data policy that requires all researchers at HBR to contribute the data obtained in the study, and associated metadata, to the HBR Information Manager, and 3) a formalized annual reporting protocol, 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 IM interaction with HBR researchers over the data lifecycle, and will increase the number and quality of data sets 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, data backup) prior to submission to the centralized data catalog. The IM 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. Once data and

metadata have been provided, the IM reviews submissions (data formatting, QA/QC checks, LTER-PASTA congruency, etc.) prior to uploading data to the data catalog.

Environmental Sensors - HBR information management provides support for the environmental sensor network at the site; HBR sensors are located in 9 watersheds and at 10+ meteorological stations throughout HBR, and at a number research plots. Maintenance and operation of the core hydro- and meteorological sensors is done by Forest Service staff, and the HBR-IM works closely with that team on the implementation and operation of data processing and quality control. Data are processed through a workflow developed in the GCE Data Toolbox (developed by GCE-LTER) to provide quality controlled data products. The analysis of overlapping chart/sensor data (~2008-2012) established the baseline necessary for deriving core meteorological and hydrological, data sets from these digital sensors. A forthcoming USDA Forest Service General Technical Report will fully document this transition from paper chart to digital data, and upon publication, we anticipate more rapid updates of our current sensor-based data sets, and the addition of many more data sets from this sensor network. While we still maintain our traditional core daily data products, our GCE Data Toolbox workflow generates a web-based interface for access to near realtime data and graphs, and provides the underlying data for additional real-time interactive data portals. Realtime access to HBR data has enabled field teams to sample in response to current conditions, and to monitor instrumentation installed on the sensor network. Campbell, Rustad, and Martin from HBR, in addition to 5 other LTER Information Managers, co-authored the following paper based on our collective experiences in working with electronic sensor data: Campbell, JL, Rustad, LE, Porter, JH, Taylor, JR, Dereszynski, EW, Shanley, JB, Gries, C, Henshaw, DL, Martin, ME, Sheldon, WM, Boose, ER. 2013. Quantity is nothing without quality: automated QA/QC for streaming sensor networks. BioScience. 63(7): 574-585.

Sample Archive - More than 20 years ago, HBR made a commitment to the permanent storage of physical samples collected at the site (e.g., streamwater, precipitation, vegetation, soil). A dedicated building on-site serves as the archive facility, and now houses approximately 100,000 samples. Samples are preserved, barcoded, and cataloged with associated 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) maintain the chemical integrity of these samples; 2) preserve sample volume for future analysis; 3) to document the use of these samples, and any resulting changes; 4) inform principal investigators of interest in sample use; and 5) to acknowledge the appropriate funding sources for their original collection. Requests for analysis of these samples (e.g. isotopic analyses, heavy metals) are received regularly, and have resulted in at least 37 publications (soils n=8; water n=15; forest floor n=11; plant material n=3). During this current funding cycle, the establishment of the HBR Archive Committee and archive support from LTER supplemental funding, have improved our capability to move forward in cataloging and storing additional samples. We have been able to make extensive 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.

A subset of the 100,000 samples in the archive (n=25,000) have been barcoded, and are described in detail in the database. A shortcoming of the current system, is that the tables have not been keyed to enable queries that join physical samples with 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 those criteria, their location within the archive (room/shelf/bin), and the amount of sample remaining, and PI contact. This initial exercise has been informative – existing sample and analytical data were not prepared with this type of integrated 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 or similar program) who will work closely with the US Forest Service staff and HBR-IM during the summer(s).

Other HBR-IM Activities: 1) The HBR Information Manager receives funding to support to the US Forest Service Smart Forests initiative, led by Forest Service researchers at Hubbard Brook. 2) Recently, a NSF EAGER proposal entitled *Collaborative Research: The Confluence of Music, Art and Science at Long Term Ecological Research Sites* (\$300K), was awarded to three institutions: UNH (lead institution with HBR-IM as PI),

Dartmouth College and the Hubbard Brook Research Foundation. This project has since received both RET and REU supplements for summer 2016.

HBR Information Management Timeline:

Current Cycle:

- 2013 All metadata documents upgraded to EML 2.1. All data evaluated for PASTA congruency. Website redesigned – new style, wider use of Google Analytics and data download tracking, updates to existing content and addition of new content; Incorporation of GCE Toolbox into environmental sensor data workflow (used with core hydrological and meteorological sensors, and project-specific sensors)
- 2014 Initial content uploaded to the Metabase schema in PostgreSQL database. This schema was leveraged from work at other LTER sites (GCE/SBC/MCR), with customization for HBR. Initial scanning of paper charts from the Hubbard Brook Archive to facilitate access to legacy data.
- 2015 Data sets submitted to the LTER Provenance-Aware Synthesis Tracking Architecture (PASTA) system. Updates to online photo gallery (software and image content). Improvements to publication database.

Proposed Products and Milestones:

- **2016** Complete transfer of xml flat files to Metabase Metadata Management System and implement EML generation from this database. Implement new proposal and reporting requirements in the Research Approval Committee (RAC) process. Implement changes as necessary in response to establishment of new LTER data center.
 - **Deliverable:** EML generation from metabase database
 - Deliverable: Implementation of new RAC protocol (proposal and reporting forms).
- **2017** Improve website function by moving to database-driven content (dynamically linking projects, publications, people, and data). Complete full documentation of spatial data. Complete full cycle of new RAC reporting system. Archive intern program to barcode and catalog archive samples.
 - Deliverable: Database-driven web content.
 - **Deliverable:** GIS and image data available through web mapping services.
 - Deliverable: Generate first annual reports for RAC from data collected in new protocol.
- 2018 Improve the submission process for data/metadata through the use of a web-based tool developed by the NSF funded NH-EPSCoR Data Discovery Center (DDC).
 - Deliverable: Online data/metadata submission tools.
- **2019** Continue to build and/or leverage tools that enable and streamline website updates (for both IM and HBR community).

Deliverable: Integrated search capability available for archived samples and associated analytical data.

• **2020-2022** - Ongoing maintenance of HBR website, data catalog, and other resources. Periodic review of underlying technology in HBR IM system, and adaptation to new tools and technology as needed.

Postdoctoral Mentoring Plan

Cary Institute of Ecosystem Studies

Both the Cary Institute and the Hubbard Brook LTER project provide a collegial and productive environment for postdoctoral researchers. At the Cary Institute, new postdocs are encouraged to give either a formal academic or less formal lunchtime seminar within the first three months of arrival. Postdocs are encouraged to attend monthly Scientific Staff meetings, to serve on Institutional committees, as interested, and they actively participate in our weekly seminar program by inviting speakers (at Institute expense). Postdocs also participate in Institutional programs on Responsible Conduct in Research, which include online training modules, discussion groups and seminars. They are also invited to all Institute social events such as picnics and potlucks. The success of our mentoring program is evidenced by the numerous, ongoing collaborative relationships among Cary scientists and former postdoctoral researchers.

Special effort is made to define expectations for the position in a detailed appointment letter. Specific tasks that need to be accomplished are listed, but the position is structured so that the postdoc has the opportunity to design aspects of the research themselves and to publish it as principal author. Postdocs are provided travel funds to present papers at a conference, which allows practice in presentation skills as well as networking opportunities. Practice talks are reviewed and critiqued beforehand to provide instruction in how to give an effective presentation. Postdocs are also encouraged to co-mentor undergraduate students through either the Cary Institute or Hubbard Brook REU programs, which allows development of mentoring skills as well as a means of exploring new research directions. Postdocs may also contribute to mentoring of graduate students. Opportunities for collaborative proposal writing are explored throughout the postdoc's tenure.

This postdoc will have the additional opportunity of becoming part of the network of Hubbard Brook researchers, a large, diverse, and collegial group. The postdoc will be encouraged to attend the quarterly science meetings, to present his/her work to the HBR research community at the annual Cooperator's Meeting, and to attend the LTER All Scientists Meeting as well as other national meetings. Funds for travel to meetings, in addition to travel between the Cary Institute and HBR, will be provided.

Data Set Inventory

Hubbard Brook data sets can be found in both the site data catalog at <u>http://hubbardbrook.org</u>, and in the LTER Network Information System <u>https://portal.lternet.edu</u>. A complete inventory of these data is shown in Table 1. HBR signature datasets are shown in **bold**.

| Table 1. HBR datasets in the LTER Network Information System | | | | |
|--|---|-----------|--|--|
| Hydrometeorology | | | | |
| knb-lter-hbr.1 | Hubbard Brook Experimental Forest (USDA Forest Service): | 1956-2014 | | |
| | Instantaneous Streamflow by Watershed, 1956 - present | | | |
| knb-lter-hbr.2 | Hubbard Brook Experimental Forest (USDA Forest Service): Daily | 1956-2014 | | |
| | Streamflow by Watershed, 1956 - present | | | |
| knb-lter-hbr.13 | Hubbard Brook Experimental Forest (USDA Forest Service): Daily | 1956-2014 | | |
| | Precipitation Standard Rain Gage Measurements, 1956 - present | | | |
| knb-lter-hbr.14 | Hubbard Brook Experimental Forest (USDA Forest Service): Total | 1956-2014 | | |
| | Daily Precipitation by Watershed, 1956 - present | | | |
| knb-lter-hbr.27 | Hubbard Brook Experimental Forest (USDA Forest Service): Snow | 1955-2015 | | |
| | Depth Measurements, 1955 - present | | | |
| knb-lter-hbr.28 | Hubbard Brook Experimental Forest (USDA Forest Service): Snow | 1955-2015 | | |
| | Water Measurements, 1955 - present | | | |
| knb-lter-hbr.136 | Snow depth, soil frost depth and snow water content along an | 2010-2014 | | |
| | elevation gradient at the Hubbard Brook Experimental Forest. | | | |
| knb-lter-hbr.58 | Hubbard Brook Experimental Forest (USDA Forest Service): Daily | 1955-2014 | | |
| | Mean Temperature Data, 1955 - present | | | |
| knb-lter-hbr.59 | Hubbard Brook Experimental Forest (USDA Forest Service): Daily | 1955-2014 | | |
| | Maximum and Minimum Temperature Records, 1955 - present | | | |
| knb-lter-hbr.57 | Hubbard Brook Experimental Forest (USDA Forest Service): Vapor | 1966-2010 | | |
| | Pressure Measurements, 1966 - present | | | |
| knb-lter-hbr.56 | Hubbard Brook Experimental Forest (USDA Forest Service): Wind | 1965-2009 | | |
| | Speed and Wind Direction Measurements, 1965 - present | | | |
| <u>knb-lter-hbr.60</u> | Hubbard Brook Experimental Forest (USDA Forest Service): Daily | 1959-2009 | | |
| | Solar Radiation Measurements, 1959 - present | | | |
| knb-lter-hbr.68 | Hubbard Brook Experimental Forest (US Forest Service): Sediment | 1956-2000 | | |
| | Yield in Weir Basins | | | |
| knb-lter-hbr.83 | Hubbard Brook Experimental Forest: Mirror Lake Thermal Profiles | 1981-2011 | | |
| | 1981 - 2011 | | | |
| knb-lter-hbr.118 | Hubbard Brook Experimental Forest: Mirror Lake Ice Cover 1968 - 2011 | 1968-2011 | | |
| knb-lter-hbr.161 | Water level recordings from wells in Watershed 3 at the Hubbard | 2007-2013 | | |
| | Brook Experimental Forest, 2007 - present | | | |
| knb-lter-hbr.173 | The Effects of Climate Downscaling Technique and Observational Datase | t on | | |
| | Modeled Ecological Responses: Supporting Data Tables | | | |
| | Water Chemistry | 1 | | |
| knb-lter-hbr.15 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1963-2014 | | |
| | Forest, Watershed 1, 1963 - present | | | |
| knb-lter-hbr.16 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1963-2014 | | |
| | Forest, Watershed 2, 1963 - present | | | |

| knb-lter-hbr.17 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1963-2014 |
|---------------------------|--|-----------|
| | Forest, Watershed 3, 1963 - present | |
| knb-lter-hbr.18 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1963-2014 |
| | Forest, Watershed 4, 1963 - present | |
| knb-lter-hbr.19 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1963-2014 |
| | Forest, Watershed 5, 1963 - present | |
| knb-lter-hbr.20 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1963-2014 |
| | Forest, Watershed 6, 1963 - present | |
| knb-lter-hbr.21 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1995-2014 |
| | Forest, Watershed 7, 1995 - present | |
| knb-lter-hbr.22 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1995-2014 |
| | Forest, Watershed 8, 1995 - present | |
| knb-lter-hbr.23 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1995-2014 |
| | Forest, Watershed 9, 1995 - present | |
| knb-lter-hbr.24 | Chemistry of Bulk Precipitation at Hubbard Brook Experimental | 1969-2012 |
| | Forest, 1969 - present, Robert S. Pierce Ecosystem Laboratory Facility | |
| knb-lter-hbr.3 | Chemistry of Streamwater at the Hubbard Brook Experimental Forest, | 1963-2014 |
| | Watershed 1, 1963 - present | |
| <u>knb-lter-hbr.4</u> | Chemistry of Streamwater at the Hubbard Brook Experimental Forest, | 1963-2014 |
| | Watershed 2, 1963 - present | |
| <u>knb-lter-hbr.5</u> | Chemistry of Streamwater at the Hubbard Brook Experimental Forest, | 1963-2014 |
| | Watershed 3, 1963 - present | |
| <u>knb-lter-hbr.6</u> | Chemistry of Streamwater at the Hubbard Brook Experimental Forest, | 1963-2014 |
| | Watershed 4, 1963 - present | |
| knb-lter-hbr.7 | Chemistry of Streamwater at the Hubbard Brook Experimental Forest, | 1963-2014 |
| | Watershed 5, 1963 - present | |
| <u>knb-lter-hbr.8</u> | Chemistry of Streamwater at the Hubbard Brook Experimental Forest, | 1963-2014 |
| | Watershed 6, 1963 - present | |
| knb-lter-hbr.9 | Chemistry of Streamwater at the Hubbard Brook Experimental Forest, | 1995-2014 |
| | Watershed 7, 1995 - present | |
| knb-iter-nbr.10 | Chemistry of Streamwater at the Hubbard Brook Experimental Forest, | 1995-2014 |
| luch they block 14 | Watersned 8, 1995 - present | 1005 2014 |
| | Watershed 9, 1995 - present | 1995-2014 |
| kph-ltor-bbr 156 | Longitudinal Stream Chemistry at the Hubbard Brook Experimental | 1001-2014 |
| <u>KIID-ILEI-IIDI.130</u> | Forest Watershed 1 1991 - present | 1551-2014 |
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| | Brook Experimental Forest, 1997 - 2010 | |
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PROJECT MANAGEMENT PLAN

Governance of the Hubbard Brook Ecosystem Study

At the center of the governance structure of the Hubbard Brook Ecosystem Study (HBES) is the Committee of Scientists (COS), which consists of the active PI-level scientists working at the site (currently 67 members). The COS includes all of the LTER co-PIs and senior personnel, plus scientists who are active at the site but not part of the LTER. The 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 from the COS 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 are a key venue for project coordination and generally draw 30-40 attendees, including students and postdocs as well as lead scientists. Typically about 75% of the time at these meetings is spent on science topics (new initiatives, synthesis activities, etc.) and 25% on project business. The winter meeting spans two 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 scientists who participate in the project. The summer meeting is held at HBR. Science topics for these meetings are chosen by the SCC from suggestions made by the COS. We have been quite successful in using these meetings to launch new initiatives and synthesis activities. Each of the five synthesis questions in the proposal will be the subject of at least one quarterly meeting during this LTER cycle.

In addition to the quarterly meetings, the Hubbard Brook Cooperator's Meeting is held every year in early July at HBR, a tradition dating back to 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 with active research at HBR, including undergraduate and graduate students. The meeting is attended by many people who are not HBR researchers but who are interested in research 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 ~150 attendees.

Management, leadership and transition plans for the HBR-LTER project

While there are many research grants active at HBR, the LTER grant is central and acts as 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 HBES project structure (described above) in that one of the two LTER PIs 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, Timothy Fahey from Cornell University and Charles 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.

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.

The HBR-LTER team includes a diversity of disciplines, genders, and career stages. Of the 36 co-PIs and senior personnel, 16 (44%) are women and 9 (25%) have received their PhDs in the last 10 years. Thirteen of the co-PIs and senior personnel were not involved in previous cycles of the LTER, and were recruited to add gender, career stage, and disciplinary diversity to the project.

Decisions on allocation of the LTER funds in this proposal are made by PIs Lovett and Groffman in consultation with the previous LTER PIs and leaders of the various subprojects. The first priority is to support the continuation of the long-term core data sets (see supplemental document with the list of our datasets), data management, and the long-term experiments that are considered central to the LTER project. The second priority is to provide smaller amounts of funding for co-PIs with LTER-related research projects at the site. These funds might be used as seed money to initiate a project or for baseline data collection, but in general the co-PIs need to find external funding to run a full research program. With this model we have been very successful at leveraging the LTER funds by obtaining other research grants. Co-PIs are encouraged to use LTER funds to support students.

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 the sensor network, 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. Close collaboration between the USFS and the HBR-LTER project have been essential to the success of the site.

The Research Approval Committee (RAC) is advisory to the USFS Lead Scientist (currently Scott Bailey) who chairs the committee and bears ultimate responsibility for research activities at the HBR. 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 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 recommendation.