



## Project Summary

### Overview

The Hubbard Brook LTER (HBR) 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 a diverse community of students and teachers at levels from K-12 to graduate students and postdoctoral fellows.

### 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 project 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 biogeophysical template that includes variation across the landscape in topography, geology, soils, vegetation, and history of past disturbance. Within the ecosystem, the disturbances affect the interacting processes of hydrology, biogeochemistry, vegetation, and food web dynamics. The conceptual model is evolving to focus on “control points of change” in the landscape - specific places and times where significant changes will begin or accelerate. 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, as well as more recent reductions in atmospheric nitrogen deposition and how these interact with changing carbon and phosphorus cycles. Proposed climate change research is focused on causes of an observed marked increase in evapotranspiration at HBR, 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 how species additions and losses alter ecosystem, demographic, evolutionary processes, and energy flow. Proposed research on the biogeophysical template focuses on understanding how disturbance interacts with specific places and times that serve as control points for change in ecosystem dynamics. These control points may have a disproportionate influence on long-term patterns of important ecosystem characteristics such as carbon storage, low redox conditions, or biodiversity. Four overarching questions provide a nexus for synthesis and integration of the project across different disciplines of study and spatiotemporal scales.

### Broader Impacts

Broader impacts activities at HBR are driven by four goals: (1) establish long-term, trusting relationships with diverse community members and environmental decision-makers across the northern forest ecoregion; (2) recruit and train the next generation of ecosystem scientists and environmental leaders; (3) support diversity, equity, inclusion, and anti-racism (DEI&A) within the HBR and broader scientific communities; and 4) drive innovations in research, education, and outreach. To achieve these goals, five approaches are utilized; public and policy engagement programs, science education and training programs, an art-science program, development and maintenance of infrastructure for DEI&A, and use of the Critical Ecology approach to make the lens of HBR’s research more inclusive and holistic. The Critical Ecology framework merges critical theories of power, privilege, and human/environment interactions with existing frameworks for ecological perturbations. This new approach expands understanding of the societal roots of disturbances such as acid rain and climate change, addresses past, current, and future interests of Indigenous people in the northern hardwood forest, and increases diversity, equity, and inclusion in our research group.

## 1. RESULTS FROM PRIOR SUPPORT

The mission of the Hubbard Brook (HBR) LTER program is to improve understanding of the response of northern forest ecosystems to natural and anthropogenic disturbances. The conceptual model guiding our research envisions disturbance playing out on a biogeophysical template that influences the biogeochemistry, vegetation, hydrology, and food webs of the northern forest (Fig. 1). Our research focuses on three drivers of disturbance: (1) atmospheric chemistry change, (2) climate change, and (3) biotic change. These drivers interact with a biogeophysical template (i.e., topography, geology, soils, vegetation, disturbance history), producing spatial and temporal variation within our site and across the broader region.

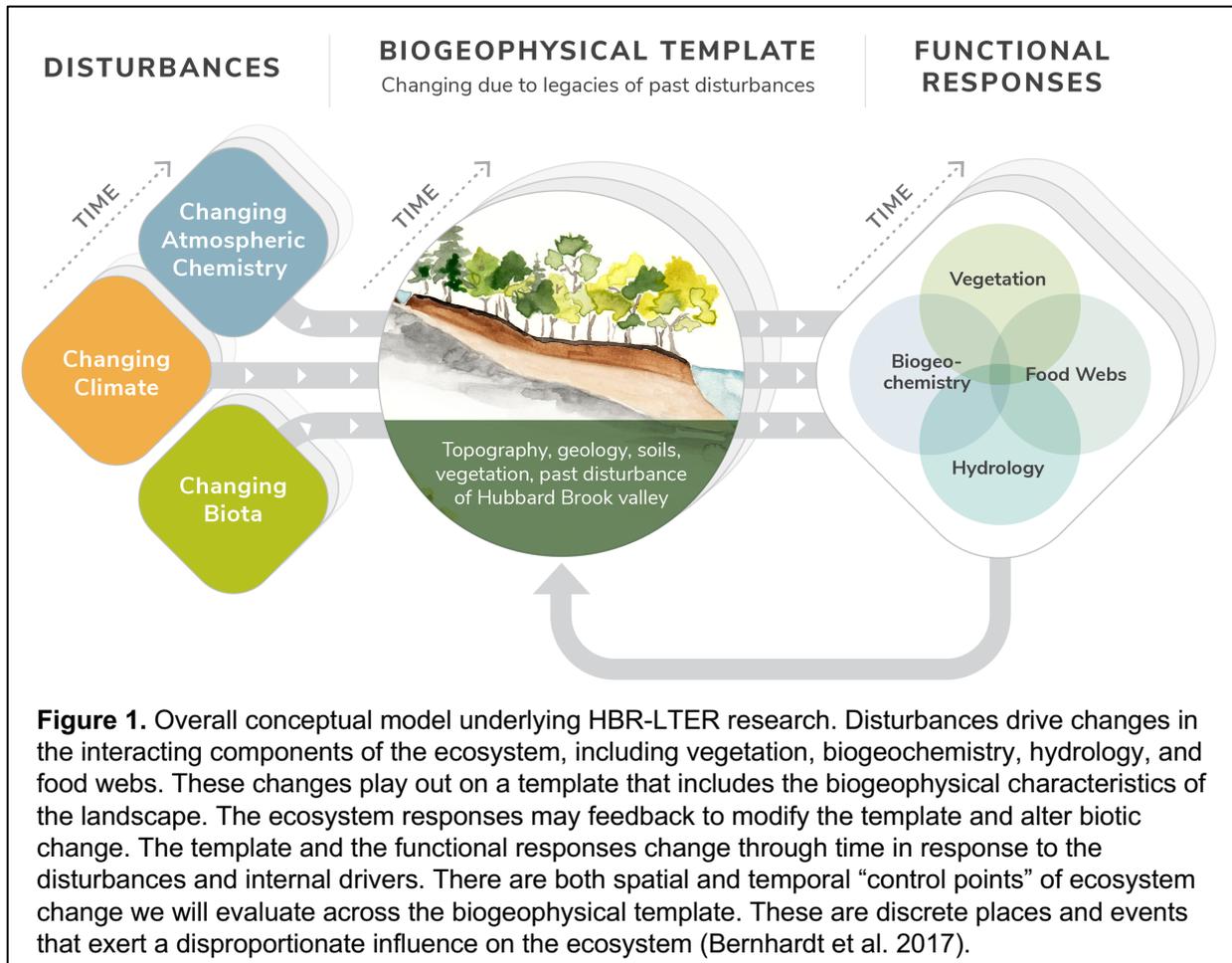
The intellectual evolution of the project is propelled by surprising results that emerge from long-term studies and require further long-term research to resolve. Many of these surprises emerge from interactions between drivers and the biogeophysical template and require interdisciplinary study to address. As our understanding of disturbance has matured, we are developing a new emphasis on spatial and temporal “control points of change” in the landscape – specific places and times where significant changes will begin or accelerate. Our approach to broader impacts has also evolved so that we now propose to incorporate a “critical ecology” framework which merges critical theories of power, privilege, and human/environment interactions with existing frameworks for ecological perturbations. This new approach will allow us to expand our understanding of the societal roots of disturbances such as acid rain and climate change, address past, current, and future interests of Indigenous people in the northern hardwood forest, and increase diversity, equity and inclusion in our research group.

Our proposed activities include: (1) collection, analysis and curation of long-term data sets encompassing the five core areas of LTER research (Table 1 in **Data Management Supplementary Document**); (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) just and equitable engagement with a diverse community of students, educators, natural resource managers, and policymakers. To focus synthesis and integration, we propose to use four “integrative questions” as the basis for cross-disciplinary synthesis efforts. Below, we review results from the past six years of research, organized by focal disturbances (air pollution, climate change, biotic change) and the underlying biogeophysical template, as well as advances in synthesis, education, and outreach. Ten significant publications resulting from the last six years of funding are listed in Table 1.

### 1.1 Atmospheric Chemistry Change

HBR has experienced elevated air pollution for decades, with clear improvements over time. Long-term measurements of sulfur (S), nitrogen (N), and mercury (Hg) deposition, and their effects on ecosystem structure and function have informed U.S. policies regulating emissions to the atmosphere (Sullivan et al. 2018, Likens et al. 2021). Our monitoring shows a continuous decline in S deposition since the early 1970s, a decline in nitrate ( $\text{NO}_3^-$ ) deposition starting in the early 2000s, and no significant change in ammonium deposition (Campbell et al. 2022), consistent with pollutant emission trends in the U.S (Fig. 2). Long-term stream chemistry measurements show decreases in sulfate concentrations that are consistent with decreases in S deposition (Campbell et al. 2021) and significant, but erratic, decreases in stream  $\text{NO}_3^-$  that preceded the decline in atmospheric N deposition (Fig. 3). These changes have resulted in a shift in the acid-base status of soil solutions and streamwater, with increases in pH and acid neutralizing capacity, and decreases in dissolved inorganic aluminum (Fuss et al. 2015). Streamwater at HBR is trending toward a chemical condition that last occurred prior to the Industrial Revolution (Likens et al. 2021), a surprising result that motivates further long-term study (**sections 2.2.3 and 2.2.5**).

In 1999, we initiated an experimental addition of wollastonite ( $\text{CaSiO}_3$ ) to watershed 1 (W1), to replace the calcium (Ca) that was lost from soils during the 20<sup>th</sup> century by acid deposition-induced 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 continue today. The Ca amendment reversed the forest decline that had previously been occurring in W1, supporting more leaf area, greater aboveground net primary



production (NPP), and decreased fine root biomass, compared to the untreated reference watershed (Battles et al. 2014, Cleavitt et al. 2021) (Fig. 4). Rates of 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, soil pools of available N also declined as tree N uptake was stimulated more than microbial N mineralization (Groffman and Fisk 2011). However, in recent years there have been unexpected increases in  $\text{NO}_3^-$  concentrations in soil solution and streamwater in the Ca-treated watershed (Fig. 3), indicating an oversupply of N relative to plant and microbial demand (Rosi-Marshall et al. 2016, Marinos et al. 2018). These surprising responses to “deacidification” are relevant to forests in many areas of the globe and warrant further long-term study (**section 2.2.5**).

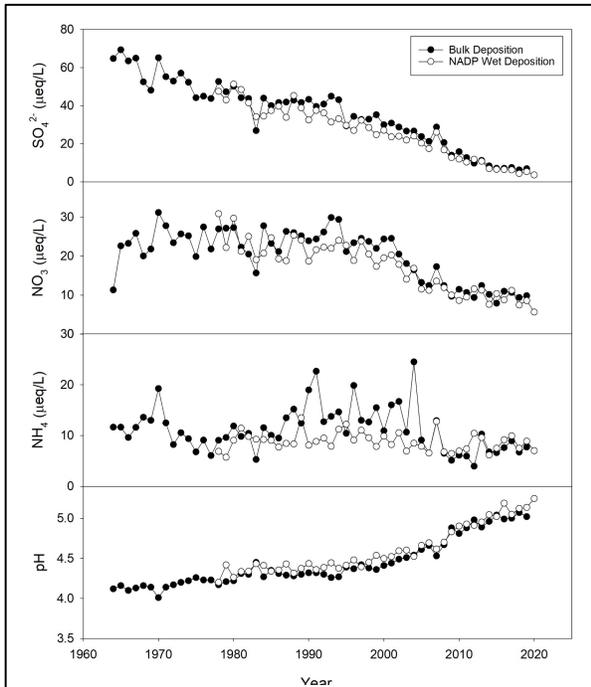
In contrast to the Ca-treated watershed, streamwater  $\text{NO}_3^-$  concentrations have generally remained low (with occasional brief spikes associated with ice storm or soil freezing events) for the last two decades in the reference watershed (W6, Fig. 3) and elsewhere at HBR (Campbell et al. 2021, Likens et al. 2021). These low  $\text{NO}_3^-$  concentrations are unexpected given that the forests at HBR are no longer aggrading biomass (Fig. 4) (Lovett et al. 2018, Cleavitt et al. 2021) and experienced elevated atmospheric N deposition for decades. Under these conditions, longstanding ecological theories predict high rates of N loss (Yanai et al. 2013, Lovett et al. 2018). Hypotheses (**sections 2.2.2 and 2.2.3**) for these unexpected patterns center on ideas about N “oligotrophication” or a decline in soil N supply relative to biotic demand. These declines may be driven by increases in N uptake by trees and microbes induced by greater carbon (C) fixation associated with atmospheric  $\text{CO}_2$  fertilization, an increase in growing season length and temperature, and changes in soil organic matter dynamics associated with recovery from acid deposition, i.e., deacidification (McLauchlan et al. 2017, Groffman et al. 2018, Mason et al. 2022). i.e., deacidification (McLauchlan et al. 2017, Groffman et al. 2018, Mason et al. 2022).

<b>Table 1. Ten significant publications resulting from the last six years of funding</b>
Cleavitt, N.L., Battles, J.J., Fahey, T.J., and N.S. van Doorn. 2021. Disruption of the competitive balance between foundational tree species by interacting stressors in a temperate deciduous forest. <i>Journal of Ecology</i> 109:2754-2768.
Cowles, J., L. Templeton, J. J. Battles, P. J. Edmunds, R. C. Carpenter, S. R. Carpenter, M. Paul Nelson, N. L. Cleavitt, T. J. Fahey, P. M. Groffman, J. H. Sullivan, M. C. Neel, G. J. A. Hansen, S. Hobbie, S. J. Holbrook, C. E. Kazanski, E. W. Seabloom, R. J. Schmitt, E. H. Stanley, A. J. Tepley, N. S. Doorn, and J. M. Vander Zanden. 2021. Resilience: insights from the U.S. LongTerm Ecological Research Network. <i>Ecosphere</i> 12:ecs2.3434.
Goswami, S., M. C. Fisk, M. A. Vadeboncoeur, M. Garrison-Johnston, R. D. Yanai, and T. J. Fahey. 2018. Phosphorus limitation of aboveground production in northern hardwood forests. <i>Ecology</i> 99:438-449.
Harris, J. E., N. L. Rodenhouse, and R. T. Holmes. 2019. Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. <i>Biological Conservation</i> 240.
Harrison J.L., R. Sanders-DeMott, A.B. Reinmann, P. Sorensen, and P.H. Templer. 2020. Growing season warming and winter soil freeze/thaw cycles increase transpiration in a northern hardwood forest. <i>Ecology</i> 101:e03173.
Lowe, W. H., L. K. Swartz, B. R. Addis, and G. E. Likens. 2019. Hydrologic variability contributes to reduced survival through metamorphosis in a stream salamander. <i>Proceedings of the National Academy of Sciences</i> 116:19563 - 19570.
Marinos, R. E., J. L. Campbell, C. T. Driscoll, G. E. Likens, W. H. McDowell, E. J. Rosi, L. E. Rustad, and E. S. Bernhardt. 2018. Give and take: A watershed acid rain mitigation experiment increases baseflow nitrogen retention but increases stormflow nitrogen export. <i>Environmental Science &amp; Technology</i> 52:13155 - 13165.
Mason, R. E., J. M. Craine, N. K. Lany, M. Jonard, S. V. Ollinger, P. M. Groffman, R. W. Fulweiler, J. Angerer, Q. D. Read, P. B. Reich, P. H. Templer, and A. J. Elmore. 2022. Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. <i>Science</i> . In press.
Ni, X., and P. M. Groffman. 2018. Declines in methane uptake in forest soils. <i>Proceedings of the National Academy of Sciences</i> 115:8587-8590.
Reinmann, A. B., J. R. Susser, E. M. C. Demaria, and P. H. Templer. 2019. Declines in northern forest tree growth following snowpack decline and soil freezing. <i>Global Change Biology</i> 25:420-430.

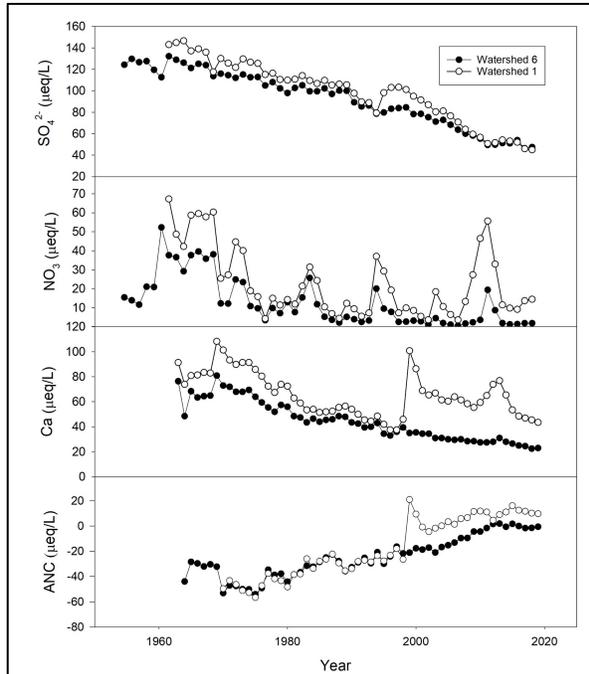
Even as N availability has decreased in recent decades, the legacy of ecosystem N enrichment from elevated N deposition over the 20<sup>th</sup> century has raised important questions about shifting patterns of nutrient limitation of plants and microbes. These questions are being tested in a N x P fertilization experiment conducted across a wide gradient of soil fertility at HBR and other sites in the region. Results to date indicate that aboveground forest productivity in mid-successional and mature forests is limited by primarily by P, whereas early-successional productivity is N-limited (Goswami et al. 2018). Belowground, limitation of root growth by N in mature forests and co-limitation by N-P in young forests indicate that above-belowground interactions mediate co-limitation of total primary productivity (Shan et al. 2018, 2022). Consistent with a suggestion from our mid-term review, these studies will be continued, with increased emphasis on the importance of P in the face of a dynamically changing N cycle (**section 2.2.4**).

## 1.2 Climate Change

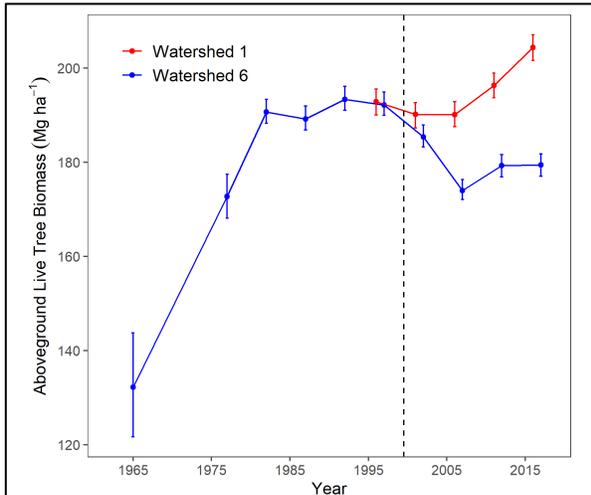
Records from HBR show clear changes in climate since the inception of monitoring in the mid-1950s. Mean annual air temperature has increased by 0.25 °C decade<sup>-1</sup> (Campbell et al. 2022). During the growing season (15 Mar – 15 Oct), the increase in temperature conducive for biological activity (i.e., days >4 °C) over the last 50 years is equivalent to a 250 m decrease in elevation (Fig. 5). Deciduous tree leaf out is occurring earlier in spring and leaf senescence is occurring later in fall (Melaas et al. 2016). Precipitation has also increased substantially (~50 mm decade<sup>-1</sup>, ~15% total) over the monitoring period



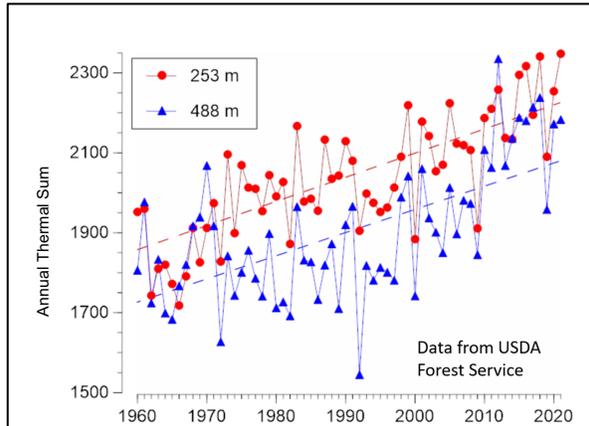
**Figure 2.** Trends in chemistry of wet deposition from the National Atmospheric Deposition Program (NADP) site at HBR (open circles), and bulk deposition from reference watershed 6 (filled circles) at HBR. Decreases in  $\text{SO}_4^{2-}$  and  $\text{NO}_3^-$  and increases in pH reflect national reductions in emissions of S and N oxides.



**Figure 3.** Trends in stream chemistry for the biogeochemical reference (Watershed 6) and Ca-treated (Watershed 1) watersheds at HBR. Declines in  $\text{SO}_4^{2-}$  and  $\text{Ca}^{2+}$  and increases in acid neutralizing capacity (ANC) reflect declines in acid deposition. Increases in Ca and ANC in W1 reflect the Ca treatment in 1999.



**Figure 4.** Trends in aboveground live tree biomass for the reference (Watershed 6) and Ca-treated (Watershed 1) watersheds. Values are watershed means with plot-level standard errors. The gray vertical line indicates timing of the calcium addition in Oct 1999. Modified from Battles et al. (2014).



**Figure 5.** Trends in annual thermal sums (degree days greater than  $4\text{ }^\circ\text{C}$ ) at HBR. Data from USDA Forest Service

(Campbell et al. 2022). Greater precipitation has caused an increase in the high streamflow events (i.e., >90<sup>th</sup> percentile). Summer base flows (i.e., <10<sup>th</sup> percentile) have also increased, indicating that hydrologic droughts are becoming less frequent (Campbell et al. 2021). Snowpack has declined, with 19 fewer days of snow cover per winter, and the maximum annual snow depth has decreased by 270 mm (Contosta et al. 2019). Reductions in snowpack depth increase the likelihood of soil freezing in winter, advance the timing of rapid soil warmup in spring, and affect soil temperature throughout the growing season (Harrison et al. 2020, Wilson et al. 2020).

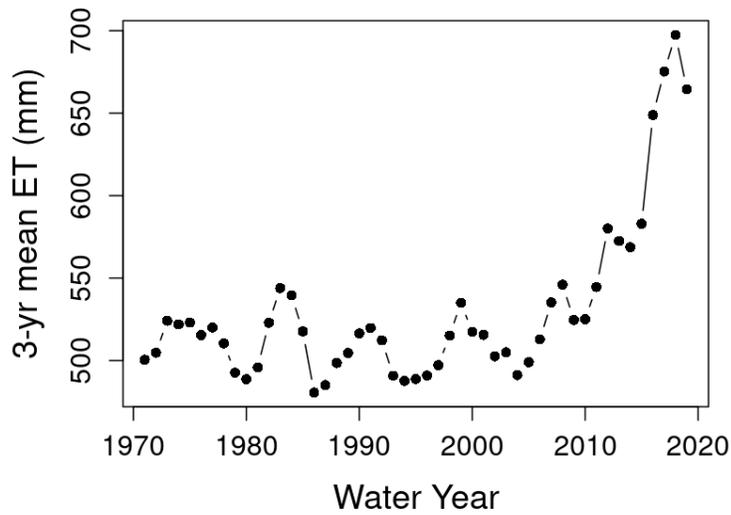
One of the most surprising changes in the hydrologic cycle at HBR is a recent marked increase (30%) in evapotranspiration (ET) (Fig. 6) (Vadeboncoeur et al. 2018, Green et al. 2021). Preliminary analyses of this increase point to changes in both climate and vegetation as the cause (Green et al. 2021) and warrant further long-term study (**section 2.3.2**).

In addition to long-term changes in mean climate, there is also evidence of increasing climate variability at HBR. For example, records of ice in and ice out dates on Mirror Lake at HBR show that the duration of ice cover has decreased, and also become more variable over time (Likens 2019). Climate change is also increasing the frequency and magnitude of weather whiplash events, defined as a rapid back-and-forth change between two conditions. At HBR, these events include freezing conditions in spring after trees leaf out, snow early in fall when leaves are still on tree canopies, rain-on-snow events, and winter heat waves (Casson et al. 2019). Weather events have been used as opportunities for analysis of ecosystem response to disturbance, e.g., effects of a recent microburst windstorm on the forest (Battles et al. 2017), and analysis of how streamflow variability affects stream salamander populations (Lowe et al. 2019).

Because extreme weather events are rare, they are impractical to study by natural occurrence. Consequently, we have used manipulative plot-scale experiments to simulate extreme events that have occurred, including a regional ice storm in 1998, a regional drought in the 1960s, and several winters (1989, 2006) with little snow. To study ice storm impacts, water was sprayed over the forest canopy during subfreezing conditions in the 2015/2016 winter to mimic freezing rain (Campbell et al. 2020, Rustad et al. 2020). Damage to the forest canopy was commensurate with the amount of ice applied (Fahey et al. 2020), but responses were often surprising. Ice damage caused an increase in abundance of insectivorous birds (Leuenberger et al. 2021), but had little effect on N losses (Weitzman et al. 2020). The surprisingly muted effect on N losses may be linked to N oligotrophication (Groffman et al. 2018). A drought simulation experiment (2015-2019) removed throughfall with troughs installed beneath the forest canopy (Asbjornsen et al. 2018). Extreme (100%) removal caused an increase in tree water-use efficiency and decreases in fine root production and soil respiration. The Climate Change Across Seasons Experiment (CCASE) has used buried heating cables and snow removal since 2012 to simulate interactive effects of warmer soils in the growing season and increased frequency of soil freeze-thaw cycles in winter (Templer et al. 2017). The combined effects of these treatments increased transpiration (Harrison et al. 2020), but reduced soil microbial biomass, enzyme activity, soil respiration (Sorensen et al. 2018), N uptake by tree roots (Sanders-DeMott et al. 2018a), and stem herbivory in winter (Sanders-DeMott et al. 2018b). We propose to build on these long-term experiments and observations with new research that addresses how ongoing changes in seasonality will affect HBR forests (**section 2.3.3**).

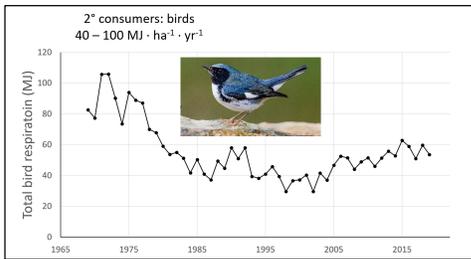
### 1.3 Biotic Change

Plant and animal communities at HBR are in a dynamic transitional period that will shape the future of the northern hardwood forest ecosystem, whether by setting a new steady state or marking the start of an era of disequilibrium. While annual leaf production and input to both green (grazing) and brown (detrital) food webs has been relatively stable over the last 30 years, there have been surprising changes in trees, birds, insects, and vertebrates (Fig. 7). Long-term data, new sampling over the last six years, and model predictions show remarkable changes in abundance of individual species, the arrival of new species, and shifts in the composition of tree, vertebrate, and invertebrate communities (Fig. 8). We have monitored changes in the foundational species that define the mature northern hardwood forest (sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) (Fig. 8a) and the two most likely climate migrants (red oak (*Quercus rubra*) and white pine (*Pinus strobus*) (Sharma et al. 2022). However, changes in trees have been much more complex than expected, driven by a multitude of factors interacting with climate

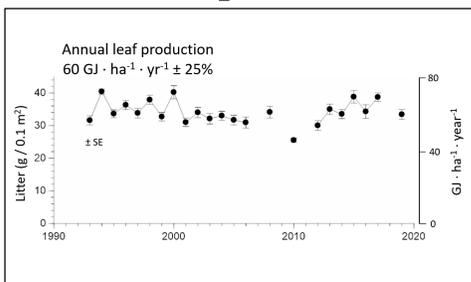
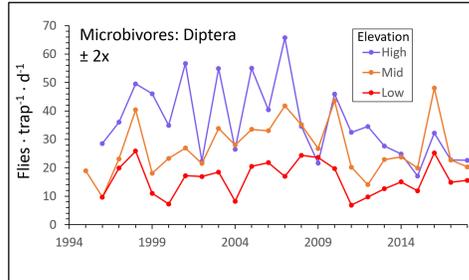
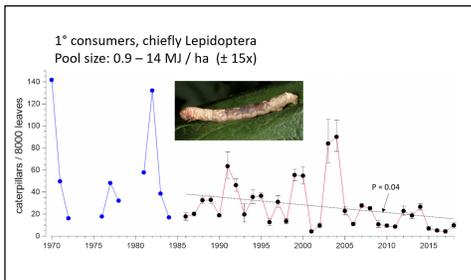
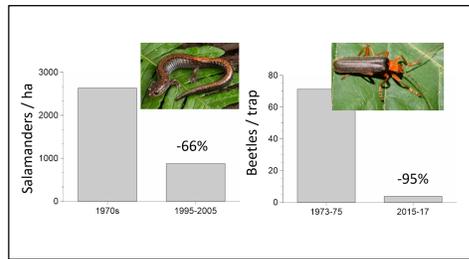


**Figure 6.** Time-series of evapotranspiration in four reference watersheds at HBR. Evapotranspiration is calculated as the difference between precipitation and streamflow on a water-year basis.

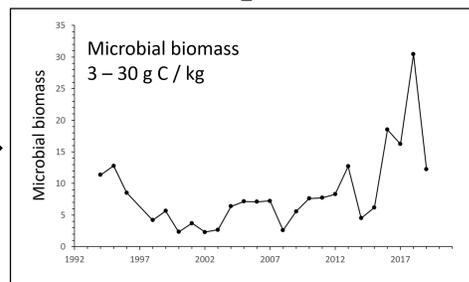
### Green Food Web



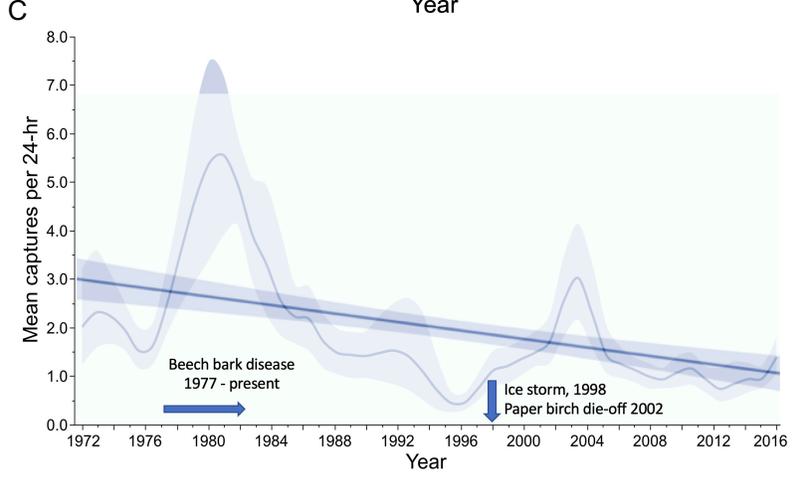
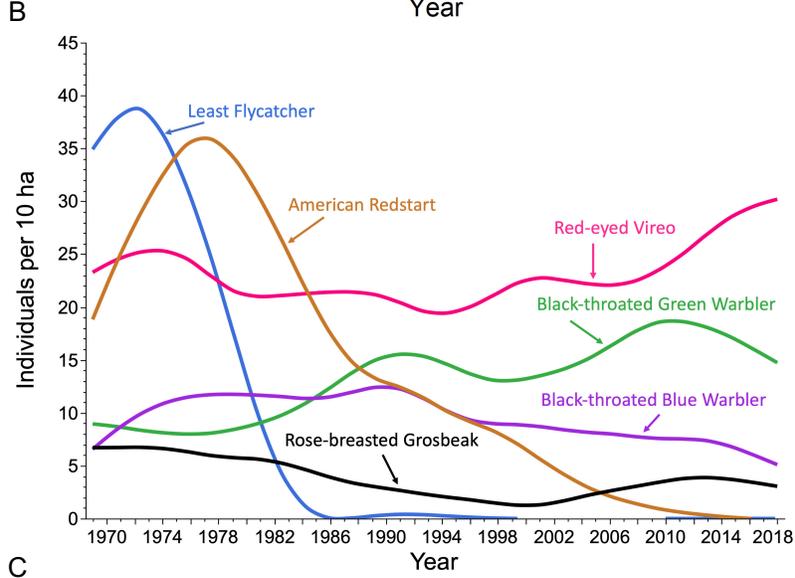
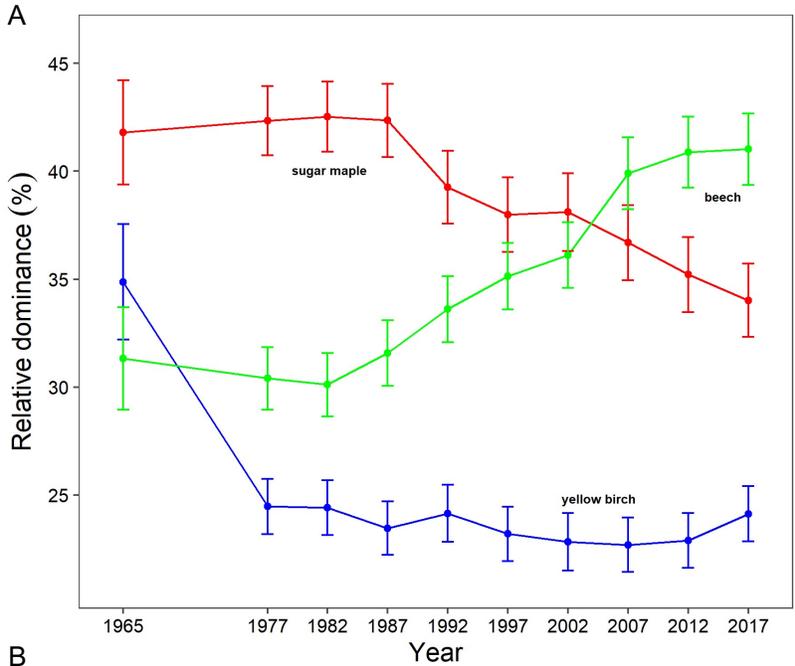
### Brown Food Web



Dead Organic Matter



**Figure 7.** Trends in pool sizes within the green and brown food webs at HBR from ca. 1970 to present, as the age of canopy trees went from about 60 to 110 years.



**Figure 8.** Trends in changing biota at HBR. (A) Changes in relative abundance of the canopy tree species in the reference watershed; points represent the means and the error bars represent standard errors. (B) Changes in population density for leaf foraging birds in the long-term demography study area; colored lines represent smoothed fits. (C) Changes in the abundance of beetles in the malaise trap network; blue trace with grey-blue shading is the smoothed fit with 95% confidence intervals; dark blue line with light blue shading is the linear fit with 95% confidence intervals.

(Kosiba et al. 2017). For example, a whole-tree harvest experiment initiated in 1985 showed that biomass removal by harvest interacts with the depletion of soil Ca due to acid deposition to cause marked (four-fold) declines in sugar maple compared to American beech (Cleavitt et al. 2018). In contrast, the progression of beech bark disease (Fig. 8c) favors beech seedlings and sprouts and inhibits maple regeneration (Cleavitt et al. 2021). Other factors affecting the tree community include interactions of climate and logging (Valipour et al. 2018, 2021), windstorms (Battles et al. 2017), ice storms (Sanders-DeMott et al. 2018b), soil freezing (Reinmann et al. 2019), changing phenology (Duveneck and Thompson 2017), air pollution (Kosiba et al. 2018, Belyazid et al. 2019), Ca addition (Fahey et al. 2016), and spatiotemporal patterns in tree seed production (Cleavitt and Fahey 2017, Clark et al. 2021). These changes impact the demography of orchids (Cleavitt et al. 2017, Berry and Cleavitt 2021), epiphytes (Cleavitt et al. 2019, Clyne et al. 2019), stream ecosystem processes (Bechtold et al. 2016), and soil respiration (Lang et al. 2019). We propose both detailed work on the specific factors influencing the productivity, composition, and structure of the forests at HBR (**section 2.4.2**), as well as integration and synthesis activities to facilitate prediction of future forest structure and function (**section 2.7**).

The HBR forest, like many north temperate forests globally, is being challenged by a rising tide of new pests due to range expansions and introductions of nonnative species (Ayres and Lombardero 2018). As expected, emerald ash borer (EAB) has become established in the HBR forest during the present LTER grant. We anticipate that nearly all of the ~26,000 canopy ash (*Fraxinus americana*) trees within HBR will be killed by EAB within 5 - 10 years. In anticipation of the arrival of EAB, we established 60 study plots that we propose to study in the next six years (**section 2.4.2**).

The long-term records of insect abundances at HBR are relevant to widely noted debates on the possibility of a global insect apocalypse (McDermott 2021, Welti et al. 2021). We repeated window-trap sampling of Coleoptera with the same protocols and locations as had been used in 1973-77 and found dramatic declines in beetle abundance (95%) and diversity (39%), with 19 beetle families disappearing entirely (Harris et al. 2019). Declines may be linked to reduced snow cover, which exposes fauna of the brown food web to inclement winter temperatures (Christenson et al. 2017). Other studies investigated the role of invertebrates in mercury bioaccumulation (Rodenhouse et al. 2019), and C and N cycling (Crowley et al. 2016). Our surveys resulted in the discovery of a new insect species (Chandler and Hamilton 2017). New proposed work on insects is described in **section 2.4.3**.

We have continued our 50-year record of the forest bird community and the environmental conditions that sustain migratory birds at HBR (Doser et al. 2021). We have used the black-throated blue warbler (*Setophaga caerulea*) as a model for examining behavioral and demographic responses of migratory birds to forecasted environmental change including changes in spring leaf out, the timing of breeding, mating and parental effort, annual fecundity, annual recruitment, and population growth (Lany et al. 2016, Townsend et al. 2016, Kaiser et al. 2017). Longitudinal studies on the behavior and demography of individuals within the black-throated blue warbler population have also enabled us to study evolutionary questions. These include the selective consequences of variation in breeding strategies (Kaiser et al. 2017), opportunity for selection in a monogamous bird (Germain et al. 2021), sexual selection on male behavioral and morphological traits (Cramer et al. 2017, Cramer et al. 2020a, 2020b), and thermal adaptations of nests (Smith et al. 2018). New bird work is described in **section 2.4.4**.

In the last five years, stream salamanders have been a valuable model for understanding (1) the demographic effects of changing stream hydrology, (2) the causes and consequences of dispersal, and (3) species interactions within headwater food webs (Davenport and Lowe 2018, Lowe et al. 2018, Addis et al. 2019, Lowe and Addis 2019, Lowe et al. 2019, Addis and Lowe 2020, Bayer and Lowe 2021, Bayer et al. 2021, Lowe et al. 2021). These results provide a strong platform for new research on ecological and evolutionary drivers of change in HBR communities (**section 2.4.7**).

In 2015 we established the first systematic collection of bioacoustic data from HBR. Via ultrasonic recording we expanded the list of known bat species from 1 to 8. Passive acoustic recording for birds began in 2016 and has since expanded, allowing for collection of bird data during the pandemic year of 2020. The recordings analyzed by Symes et al. (2022) contained >127,000 songs representing 45 species, with an average of 31 recognizable songs per recorded minute. This resulted in the first posting

of bioacoustic data to the Environmental Data Initiative (EDI) data portal (Symes et al. 2021). A network of 30 motion-detecting camera stations for monitoring wildlife was installed across the valley in 2018. We propose to continue these novel measurements in our long-term study (**section 2.4.5**).

#### **1.4 Biogeophysical template**

A major advance for HBR over the past 15 years has been to conceptualize forest ecosystem dynamics within a biogeophysical template that controls spatial variation in the response of ecosystem structure and function to disturbance (Figs. 1 and 12). This approach characterizes distinct soil types with predictable spatial distribution (Bailey et al. 2014, Gillin et al. 2015, Bailey et al. 2019), driven by variation in groundwater saturation frequency (Gannon et al. 2014) and lateral water flux (Gannon et al. 2017). The template also encompasses legacies of past disturbance that interact with soils, topography, and hydrological factors. This functional soil classification is a powerful tool to explain spatial and temporal patterns in microbial C and N cycle processes (Morse et al. 2014, Wexler et al. 2014), dissolved organic matter (DOM) composition and export (Gannon et al. 2015, LoRusso et al. 2021), soil C storage (Bailey 2020, Possinger et al. 2020), and stabilization of organometallic complexes (Bourgault et al. 2017).

Spatial patterns in soil properties and processes influence the chemistry of both surface water and groundwater, causing predictable patterns in stream chemistry (Zimmer et al. 2013, Benettin et al. 2015, Gannon et al. 2017, Bailey et al. 2019) that affect forest dynamics (Cleavitt et al. 2018). We have demonstrated that the biogeophysical template is spatially predictable and driven by topography (Gillin et al. 2015) and the areal extent of bedrock outcrops and shallow soils at HBR (Bailey et al. 2019, Fraser et al. 2020). We have also shown that topography controls how water accumulates and forms streams, including ephemeral streams (Jensen et al. 2017, 2018, Prancevic and Kirchner 2019) that ultimately follow predictable wetting sequences throughout the stream network (Botter et al. 2021). One unexpected finding shows the roles that shallow-to-bedrock regions and soil saturation frequency play in connecting distal parts of the watershed to the stream network, especially intermittent streams and source areas for DOM and  $\text{NO}_3^-$  export (Pardo et al. 2022). This spatial structuring provides opportunities for new research (**section 2.5.2**) on how the biogeophysical template creates control points for change in other ecosystem components such as vegetation and food web dynamics, and animal populations.

#### **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) (updated 2013) and vegetation dynamics (Bormann and Likens 1979), and a series of monographs on individual elements (Likens et al. 1994, 1998, 2002, Fahey et al. 2005, Lovett et al. 2005, Yanai et al. 2013). A recent synthesis book highlights major findings from the HBR ecosystem over the 50+ year study, and suggests likely future changes (Holmes and Likens 2016). An online book, accessible from the HBR website, provides a concise synthesis of the research in a “living” format, updated as new results emerge. Long-term changes in precipitation chemistry have also recently been synthesized in a broader historical and geographic context (Likens et al. 2021).

In our last proposal, we posed a series of integrative questions that served as an intellectual nexus for project synthesis efforts. This effort resulted in synthesis papers on atmospheric deposition (Crowley and Lovett 2017, Sullivan et al. 2018, Gilliam et al. 2019), changing seasonality (Melaas et al. 2016, Contosta et al. 2017, Grogan et al. 2020), N oligotrophication (Groffman et al. 2018, Gilliam et al. 2019, Mason et al. 2022), and nutrient retention (Lovett et al. 2018). Long-term data and models from HBR have been used in regional and global scale analyses including estimating changes in precipitation over time (Sahu et al. 2020), simulation of long-term effects of forest harvesting with changing climate (Valipour et al. 2018, 2021), assessing relationships between soils, plant diversity, and climate (Belyazid et al. 2019), determining relationships between climate and temperate forest vegetation (McDonnell et al. 2018) and photosynthesis and foliar N (Madison 2018), ecohydrology of northeastern U.S. watersheds (Pourmokhtarian et al. 2016), constraining the effects of climate on tree phenology and C budgets (Duvencek and Thompson 2017), testing the N cycle dynamics of the Community Land Model (CLM-CN5.0) (Nevison et al. 2022), examining long-term effects of pest-induced changes in forest composition (Crowley et al. 2016), and synthesis of soil organic matter data (Harms et al. 2021, Wieder et al. 2021).

Long-term data from HBR have also been used to characterize and quantify uncertainty associated with ecosystem measurements and models (Yanai et al. 2018), including measures of annual runoff (See et al. 2020), litterfall (Yang et al. 2017), and the hydrologic flux of Ca (Campbell et al. 2016). Results from HBR have informed policies related to air quality, climate change, and invasive species (Lovett et al. 2016b, Templer et al. 2016, Lovett et al. 2019).

A new synthesis effort used long-term data to evaluate changes in the ability of ecosystems to maintain function while experiencing perturbation by evaluating “early warning signals” in ecological time series (Contosta et al. 2022). Results suggest declining resilience in watershed nutrient retention and tree, bird, and insect populations. Changes in early warning signals were correlated with precipitation chemistry and temperature, suggesting that acid deposition and climate change have reduced ecosystem resilience and compromised biological and biogeochemical functioning of the northern hardwood forest ecosystem.

### **1.6 Publication and leveraging research funding**

In the current LTER grant cycle, we have produced 195 peer-reviewed papers that have been cited a total of 2330 times; with an H-index of ~26, as computed by the Institute of Scientific Information Web of Science. The complete list of HBR datasets published in the EDI repository is shown in the Table in the **Data Management Supplementary Document**. In this table, datasets associated with the papers in Table 1 and other publications from the past 6 years are highlighted.

HBR investigators have used LTER funding to generate synergies with other funded research from NSF and other agencies including projects on nitrogen oligotrophication (NSF DEB), weathering gradients (NSF EAR), ice-storm effects (NSF-DEB), salamanders (NSF PCE), CCASE (NSF DEB), denitrification (NSF DEB), water-use efficiency (NSF EAR), stakeholder interactions (NSF AISL), linking roots and microbes to watershed biogeochemistry (DOE), evaluating NEON and AmeriFlux data streams (NSF MSB), and testing a novel, automated soil frost sensor (USDA NIFA). Two Long Term Research in Environmental Biology (LTREB) grants augment long-term studies of precipitation and stream chemistry, and bird populations.

### **1.7 Broader impacts: Education, outreach and diversity, equity inclusion and anti-racism (DEI&A)**

The Hubbard Brook Research Foundation (HBRF) connects diverse groups of HBR researchers, K-12 schools, policymakers, and other stakeholder groups in the region. HBRF's Roundtables and Science Links programs bring scientists and stakeholders together to share knowledge and perspectives about socio-scientific issues, resulting in scientific synthesis papers and stakeholder reports, live briefings with decision-makers, and media outreach (Swanson et al. 2021). Recent successes include a synthesis of winter climate change in the northern forest (Contosta et al. 2019), a synthesis of social and ecological resilience in New Hampshire (Rogers and Garlick 2021), and a series of stakeholder dialogues related to invasive forest pests, ice storms, and sugar maple regeneration. Proposed new engagement work is described in **section 2.8.1**.

HBRF integrates social science research with its engagement programs to advance both fundamental knowledge and innovative practices for the science communication and learning fields (Besley et al. 2021, Peterman et al. 2021, Garlick and Lambert 2022). This work was facilitated by an award from NSF's Advancing Informal STEM Learning program with collaborators at the Harvard Forest (HFR) LTER site in 2017-2021. A pending proposal would expand these efforts to other LTER sites (**section 2.8.1**).

HBRF has recently initiated innovative professional development programs for young scientists (**section 2.8.2**). Young Voices of Science (YVoS) began in 2020 and follows a participant-centered cohort model that pairs a semester-long series of online, skills-based seminars with one-on-one mentorship for outreach projects and policy engagements. YVoS serves a diverse community of undergraduate and graduate students (53% participants of color or gender nonconforming). HBRF also leads events for engaging early-career scientists with national policy-makers, clean energy pioneers, and corporate sustainability and non-governmental organization leaders, including a 2020 Youth Climate and Clean Energy Town Hall with U.S. presidential candidates in February 2020, a Climate and Clean Energy Forum

with members of U.S. Congress and the Biden/Harris Administration in March 2021, and a Road to COP26 virtual conference with the British Consul General to New England in October 2021.

HBRF's Schoolyard LTER program includes partnerships with K-12 schools, including "Zoom-a-Scientist" activities that bring HBR scientists virtually into classrooms, and educational field trips and tours. These activities have engaged 1,700 students from 74 towns across New Hampshire over the past 5 years. HBRF partnered with the USDA Forest Service (USFS) to advance HBR's Art-Science program, including its flagship project, Waterviz, a water cycle visualization and sonification, powered by near-real-time sensor data from HBR. Recent successes include the development of classroom materials that bring Waterviz into middle school classrooms, with a focus on serving students with visual impairments and other seen and unseen disabilities. Proposed plans related to Schoolyard LTER and Art-Science programs are described in **sections 2.8.2** and **2.8.3**.

The HBR community has initiated a suite of activities to address diversity, equity, inclusion and anti-racism (DEI&A) and scientific culture. The HBR DEI&A Committee, with 16 active members, grew out of a community-wide brainstorming session in July 2020 led by Linda Pardo (USFS) and Clara Chaisson (HBRF), members of the LTER Network DEI group. Activities have included programs on implicit bias and bystander intervention, surveys to assess meeting dynamics during each quarterly HBR project meeting, development of a Code of Conduct and an anonymous complaints procedure, an Indigenous Knowledge and Networking sub-committee, and outreach to students from the City University of New York (CUNY), a minority serving institution. A chapter of Strategies for Ecology Education, Diversity and Sustainability (SEEDS) has been established at CUNY Hunter College. HBR plans to host the next National SEEDS field trip. We propose to expand these DEI&A activities in the next LTER cycle (**sections 2.8.4-5**).

### **1.8 Response to mid-term review**

The HBR mid-term review took place in June 2019. As noted in the cover letter from the NSF program officer, "*all aspects of the project appear to be on track [and] the panel felt that the project research was strong with provocative findings on many fronts. Further, they were extremely impressed and excited about the governance structures that the project has in place and, in particular, the approaches being taken to expand the participation of young scientists, including those from outside the LTER network. A noteworthy aspect of this structure, are the within site synthesis activities.*" The review panel made a primary recommendation to engage in further investigation of the role of P limitation. We have embraced this recommendation by continuing the Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE) project, a long-term fertilization experiment evaluating the relative importance of N and P in HBR forests (**section 2.2.4**) and adding a new P focus to our detailed research on ecosystem recovery from acid deposition (**section 2.2.5**) and responses to climate change (**section 2.3.3**).

## **2. PROPOSED RESEARCH**

### **2.1 Introduction**

#### *2.1.1 Background*

The need for long-term research on forest ecosystems has accelerated markedly in recent years. Traditional interests in provision of wood products and clean water for drinking and recreation have expanded to include climate mitigation, biodiversity conservation, and the ecological and social resilience of landscapes and regions (Cowles et al. 2021). Forests are complex ecosystems, dominated by long-lived organisms, and are highly connected to adjacent ecosystems at local, regional, and global scales (Trumbore et al. 2015). Long-term studies have made unique contributions to understanding the structure, function, and services of forests over the 50–100 year time frames that are essential for ecosystem assessment and management (Nelson and Groffman 2021).

Since the establishment of the Hubbard Brook Experimental Forest (HBEF) by the USFS in 1955, research at HBR has focused on the ecology and management of northern hardwood forests. The Hubbard Brook Ecosystem Study, founded in 1963, developed the small watershed approach to provide a quantitative understanding of forest ecosystems and to advance the use of whole-ecosystem manipulations to quantify their response to disturbance. From the beginning, HBR has sought to bring

research results to policy and management. Research from the site has influenced national discussions on air pollution, climate change, and forest management (Holmes and Likens 2016, Likens et al. 2021).

Since joining the LTER network in 1988, HBR research has focused on understanding the role of disturbance in the functioning of forest ecosystems. Our conceptual model and research program have continually evolved as unexpected observations emerge from our long-term studies, raising questions that can only be addressed with continued long-term research. Recent surprises include:

1. *The elevational distribution of some tree species shifted upward, as expected in response to climate warming. However, other species have surprisingly migrated downward in response to succession, recovery from acid deposition (i.e., deacidification), and pests and pathogens.* Interacting responses to multiple environmental changes complicate predictions of future community structure and function.
2. *Rates of evapotranspiration abruptly increased by about 30% over the past 10 years (Fig. 6).* The drivers of this fundamental change in ecosystem function involve complex interactions among climate, biota, and atmospheric chemistry.
3. *Exports of N from the reference watershed (W6) continue to decline (since the 1970s), contrary to established theory that the opposite should be occurring in these aging forests.* An N oligotrophication process, driven by declines in atmospheric N deposition, increases in atmospheric CO<sub>2</sub> concentrations and growing season length and temperature, and decreases in acid deposition may be driving these declines. This process may affect ecosystem recovery from disturbance, and drive declines in insect and bird populations, NPP, and C sequestration.
4. *We observed significant declines in birds, salamanders, caterpillars, and beetles since the 1970s, but not all species have declined in all places.* This variation may be linked to factors as diverse as forest maturation, deacidification, regional species declines, and changes in seasonality and snow cover.
5. *Analysis of long-term (>50 year) biology and biogeochemistry data from HBR for early warning signals of state change suggest declining resilience in watershed nutrient retention and tree, bird, and insect populations.* Changes in early warning signals were correlated with precipitation chemistry and temperature, suggesting that acid deposition and climate change have reduced ecosystem resilience and compromised biological and biogeochemical functioning of the ecosystems at HBR.

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

### 2.1.2 Research themes, conceptual model, theory

The overarching research theme of this proposal is the **response of ecosystem structure, composition, and function to disturbance**. While the disturbance theme retains continuity with previous HBR-LTER proposals, our ideas about disturbance continue to evolve. In this proposal, we begin to focus on how disturbance interacts with “control points” of change on the biogeophysical template.

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 1985, Danneyrolles et al. 2019). 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 (Campbell et al. 2021). Others are acute and episodic, such as ice storms, wind storms, and insect outbreaks (Rustad et al. 2020, Weitzman et al. 2020). Further, these disturbances play out on a landscape-level biogeophysical 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 legacies of land use and past natural disturbances (Fraser et al. 2020). Thus, predicting the response of an ecosystem to disturbance requires knowledge not only of its current functioning, but also its spatial context and temporal trajectories. We will advance our analyses of disturbance by developing an ability to identify and predict specific places and times where significant changes will begin or accelerate. We consider **control points** as “areas of the landscape or periods of time that exert disproportionate influence on the behavior of the ecosystem under study (Bernhardt et al. 2017).” Control points have both spatial and temporal

(e.g., periods of recurring saturation/anoxia, seasonal transitions) components, and a quantitative basis (e.g., higher rates, or different dominant processes from the surrounding matrix or time periods).

Our conceptual model (Fig. 1) focuses on, and our research plan is organized around, three drivers of change in the HBR ecosystem: changing atmospheric chemistry, changing climate, and changing biota. These changes are intertwined, but they provide a useful structure for grouping the broad range of HBR research into themes. Our model illustrates that these drivers of change cause perturbations in the interacting ecosystem processes of biogeochemistry, hydrology, vegetation dynamics, and food webs, and that responses vary across the landscape because of the characteristics of the biogeophysical template. 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.

Improvements in our ability to characterize this template and to track spatial and temporal variation in responses (Torresan et al. 2021) motivated our goal to identify particular places and times likely to catalyze, or be vulnerable to significant change in ecosystem structure, function, and services. Examples of control points include forest stands dominated by ash on particular soil types that will undergo significant mortality as EAB spreads, forest stands dominated by beech undergoing structural change due to the ongoing effects of beech bark disease, riparian areas destabilized by increased streamflow or beavers, and high elevation areas dominated by conifers (spruce/fir forests) on shallow soils likely to be strongly affected by climate warming. These areas may become focal points for colonization by invasive species, be vulnerable to physical, chemical and biological degradation, or be hotspots of demographic or evolutionary responses that shape the future of species, populations, or communities. In this cycle of LTER research, we propose to explore the utility of control points in our long-term studies. We do not posit that control points will be relevant across the entire study. Rather we will explore the idea in specific places and times that we hypothesize function as control points, and consider if this idea should be a fundamental component of our conceptual model in future research.

Our focus on control points is based on the concept of disproportionality which has theoretical roots in several disciplines including the shifting mosaic concept of ecosystem development developed at HBR Brook (Bormann and Likens 1979), variable source area theory from hydrology (Hewlett and Hibbert 1967, McGuire and Likens 2011), and hot spot/hot moment ideas in biogeochemistry (McClain et al. 2003, Bernhardt et al. 2017). Other theories guiding the research at HBR include co-limitation theory (Harpole et al. 2011, Borer et al. 2014), hierarchy response theory (Whittaker et al. 2001, Smith et al. 2009), and resilience and state change theory (Holling 1973, Groffman et al. 2006). Integrating theory with long-term data collection, quantitative analysis, and modeling is critical for the development of a predictive capacity for complex ecological systems (Campbell et al. 2021, Valipour et al. 2021).

Our research encompasses the five LTER core areas: primary production, population studies, movement of organic matter, movement of inorganic matter, and disturbance patterns (**Table in Data Management Supplementary Document**). Of the 263 HBR datasets in the EDI LTER data portal, there are 160 relevant to the core area of disturbance, 86 on organic matter, 111 on inorganic matter, 54 on primary production, and 62 on population studies. Of our 78 signature datasets, there are 45 on disturbance, 20 on organic matter, 34 on inorganic matter, 27 on primary production, and 27 on population studies.

### *2.1.3. Synthesis and integration*

Many of the surprising results that drive the evolution of our long-term research emerge from interactions between drivers and the biogeophysical template, and require multidisciplinary integration to address. In recent HBR research cycles, “integrative questions” have been used as focal points for project synthesis and integration efforts. Here we propose four new integrative questions that will frame, focus, and motivate our proposed synthesis and integration for the next LTER cycle:

1. Are there specific locations in the HBR landscape that are potential control points for ecosystem change, i.e., are there places where a physical disturbance might unleash a cascade of changes from soil processes to vegetation, to organic matter quality, to biodiversity? Are these control points driven by physical (e.g., bedrock constrictions), chemical (e.g., low redox), and/or biological (e.g., species

loss/gains) phenomena? How do these spatial patterns interact with temporal events? Should control points be a fundamental component of the conceptual model guiding HBR research?

2. How will the interactions among climate change, air pollution, and biotic change alter the composition and structure of the forests at HBR? How will these changes affect ecosystem function?
3. How are increases in atmospheric CO<sub>2</sub> and a longer and warmer growing season affecting NPP, nutrient uptake by trees, and soil C, N, and P availability? How are these effects mediated by recovery from acid deposition, mycorrhizal associations, and spatial variation in soil properties?
4. How will complex changes in the water cycle, including increases in the quantity and variability of precipitation, loss of snowpack, variability in growing season droughts, and changes in ET alter the structure and function of the ecosystem?

Answering these questions (**section 2.7.1**) will challenge us to span (1) disciplines from hydrology and soil chemistry to vegetation dynamics and food web structure, (2) levels of organization from genes and organisms to populations to landscapes, and (3) fields of study from ecology to evolution.

#### 2.1.4 Research sites

The HBR LTER project is located primarily at the HBEF (43°56'N, 71°45'W), a 3160-hectare site operated by the USFS 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 our studies encompass the whole HBEF, which includes the wider HBR valley.

The HBR-LTER also includes other forested sites in the region that provide further context for our research (Fahey et al. 2015). For example, we conduct complementary research at the USFS Bartlett Experimental Forest (BEF), located about 30 km east of the HBEF, where silvicultural treatment of forests on sites with similar soils and tree species composition provides a valuable resource for experimental work. Eddy flux towers (Ameriflux and NEON) at BEF provide valuable context for the eddy flux tower that was established at HBR in 2015. 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	Aspect	Size (ha)	Measurements began	Experimental Watershed Treatment
1	S	11.8	1956	CaSiO <sub>3</sub> (wollastonite) addition 1999.
2	S	15.6	1957	Clear felled in winter 1965-66; no products removed. Herbicide 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 and removal, 1983-1984.
6	S	13.2	1963	None; biogeochemical reference watershed.
7	N	76.4	1965	None
8	N	59.4	1969	None
9	N	68.2	1986	None

## 2.2 Theme 1: Changing atmospheric chemistry

### 2.2.1 Overview

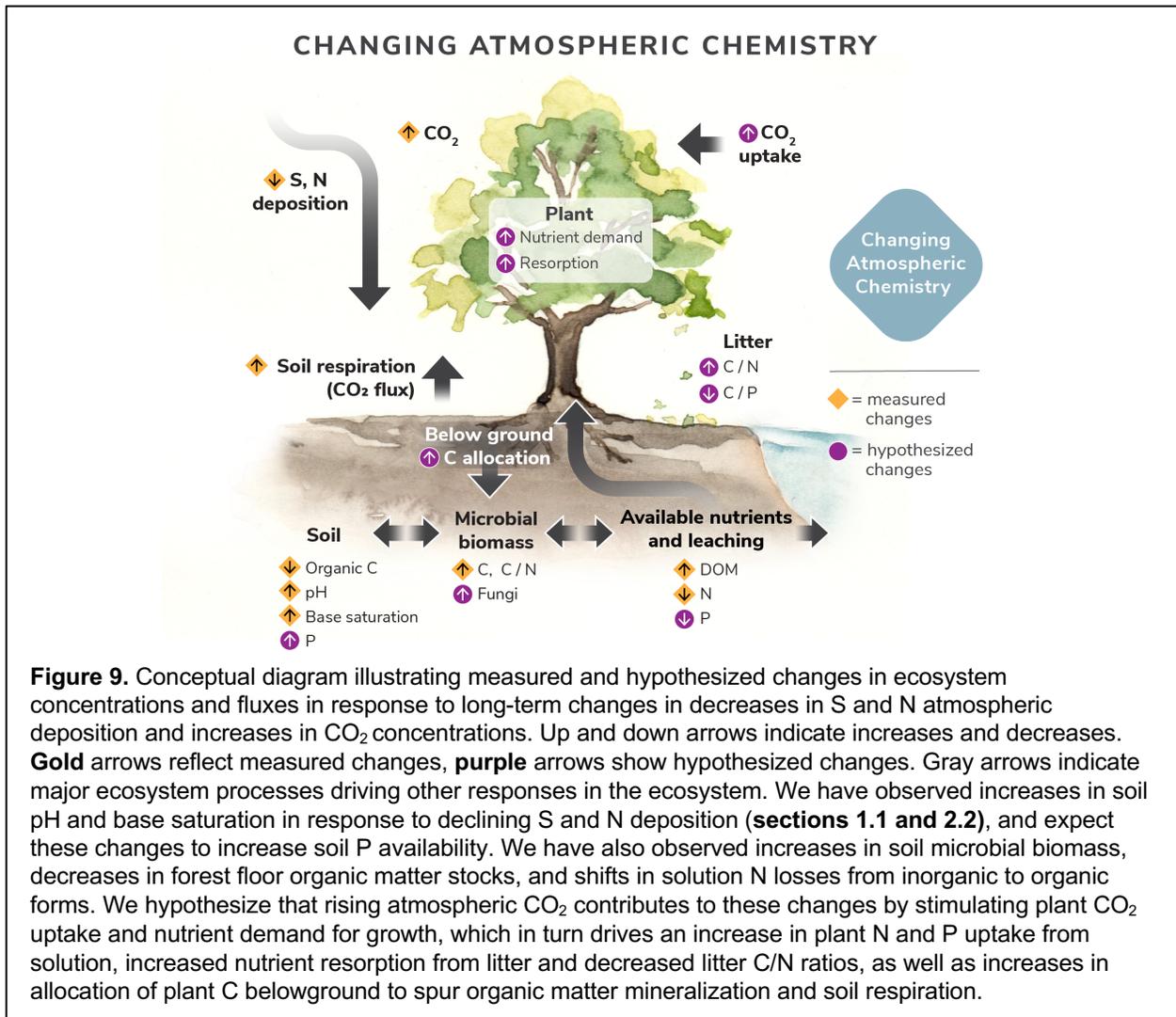
Atmospheric chemistry has changed continuously over the past 60 years of study at HBR. Atmospheric deposition of N and S have decreased markedly since the 1970s, and this “deacidification” is having complex effects on soils and vegetation (Fig. 2) (Bernal et al. 2012, Yanai et al. 2013, Groffman et al. 2018, Lovett et al. 2019). Atmospheric CO<sub>2</sub> concentrations have risen steeply (Friedlingstein et al. 2020), but effects on the forest ecosystems at HBR have been difficult to detect due to complex terrain, and interactions among element cycles (Kou et al. 2020, Walker et al. 2021). We hypothesize that declines in atmospheric N deposition coupled with increases in atmospheric CO<sub>2</sub> are interacting with a longer, wetter, and warmer growing season to decrease the availability of soil N and P (Fig. 9). This oligotrophication process could increase N limitation of plant growth, reduce nutrient exports and flow through food chains, and alter ecosystem response to disturbance (Jonard et al. 2015, Elmore et al. 2016, Sabo et al. 2016, McLauchlan et al. 2017, Craine et al. 2018, Groffman et al. 2018, Gilliam et al. 2019, Mason et al. 2022).

We propose to address the effects of these surprising changes by maintaining key long-term data streams that track these trends, and adding new measurements, modeling, and synthesis activities to understand and predict their effects. These data streams include continuation of a suite of regular measurements (described briefly below) at the watershed and plot scales, a decade-long N x P addition experiment, and a 20-yr watershed Ca-addition experiment. In response to our mid-term NSF review, we have intensified measurements of P in atmospheric deposition, vegetation, soil, soil solutions, and streamwater. New measurements will also include analysis of changes in soil C dynamics and storage with <sup>14</sup>C-dating approaches, and a new <sup>15</sup>N tracer experiment.

Our proposed research on ecosystem responses to changing atmospheric chemistry will address the overarching question: *How do changes in atmospheric chemistry (increasing CO<sub>2</sub> concentration and decreasing N, S, and acid deposition) alter plant growth, soil C dynamics, and nutrient limitation and losses?* In this section, we describe new and continuing research on four main topics: Changing soil C dynamics and storage (**section 2.2.2**), changing N losses and fate (**section 2.2.3**), multiple element limitation in northern hardwood ecosystems (**section 2.2.4**), and natural and accelerated ecosystem recovery from acidification (**section 2.2.5**).

The proposed research is platformed on long-term monitoring of forests, soils, and streams at HBR:

- Watershed-scale measurements. The USFS has collected data on streamflow from 9 gauged watersheds (Table 1) and precipitation data on >20 stations across the HBR valley since the 1950s. Precipitation and stream chemistry are analyzed as part of an LTREB-funded project.
- Primary production, including eddy covariance and measurements of aboveground wood and foliage production are described in the “Changing Biota” (**section 2.4**) below.
- Soil microbial biomass C and N content, potential net N mineralization and nitrification, microbial respiration, and denitrification potential have been measured at least annually since 1994 adjacent to the reference watershed (W6), and since 1998 in the Ca-treated watershed (W1) (Bohlen et al. 2001).
- Soil fluxes of CO<sub>2</sub>, nitrous oxide (N<sub>2</sub>O), and methane (CH<sub>4</sub>) have been measured monthly during the growing season since 2001 in W6 and W1 using static chambers (Ni and Groffman 2018).
- Soil solutions and longitudinal streamwater samples have been collected approximately monthly from W6 since the early 1980s, and from W1 since the mid-1990s. These collections are analyzed for concentrations of major solutes (anions, cations, organic C and N). More recent measurements characterize dissolved organic matter (DOM) fractions and select trace elements (P, As, Co, Cd, Fe, Ni, Pb, Se, Sr, Zn) (Fuss et al. 2015, LoRusso et al. 2021).
- Surface soils are quantitatively sampled every 4-5 years across W6 and W1. Samples are collected from combined Oi+Oe horizons, the Oa horizon, and the top 10 cm of underlying mineral soil using the pin-block method. Samples are measured for total mass, C, N, P, base cations and metals, pH, total acidity and extractable Al (Johnson et al. 2014).



### 2.2.2. Changing soil C dynamics and storage

We propose to combine new measurements with our existing long-term data streams described above to determine how changes in the belowground C cycle may be contributing to N and P oligotrophication processes at HBR. Questions addressing potential C cycle changes include:

- *How are soil respiration ( $R_{soil}$ ) and its components (heterotrophs, autotrophic) changing over time? Are observed increases in  $R_{soil}$  since 2011 linked to the oligotrophication process (Fig. 9)?*
- *Do changes in the amount and partitioning of soil C among fractions (adsorbed, particulate, occluded particulate, mineral-associated fractions) suggest that soil C cycling rates have changed over time?*

**Changing Soil Respiration:** Long-term measurements of soil CO<sub>2</sub> fluxes adjacent to W6 indicate that rates of  $R_{soil}$  have increased over the last two decades (Groffman 2019). We will continue these low-frequency, but long-term, measurements while incorporating continuous automatic chamber measurements established with EPSCOR funding at the base of W3 to more fully characterize annual patterns of soil C gaseous losses. We will also incorporate ongoing measurements of  $R_{soil}$  from the combined growing season soil warming and snow removal CCASE experiment (**section 2.3.3**) (Templer et al. 2017), the N and P MELNHE fertilization experiment (**section 2.2.4**) (Bae et al. 2015), and the flux tower (**section 2.3**) into a comprehensive database. We will examine drivers of  $R_{soil}$  trends (e.g., oligotrophication, warming, deacidification) by evaluating spatial and interannual patterns of  $R_{soil}$  with concurrent measurements of

soil temperature, litter inputs, N and P availability, microbial biomass, and soil solution chemistry.

Changing Soil C Fractions, Age, and Transit Time: New measurements of soil organic matter fractions, radiocarbon, and organo-mineral associations of archived samples, and new collections will allow assessment of how soil C storage and cycling has changed over the past half a century, with a focus on particulate (free and occluded POM) and mineral-associated (MAOM) organic matter pools. Archived mineral soil samples are available back to 1976 from near W6 (reference), from 1983 for W5 (harvested 1989), and from 1998 for W1 (Ca-amended in 1999). We will fractionate selected archived soils by density, measure the C, N, and  $^{14}\text{C}$  of each fraction, and characterize organo-mineral associations (poorly crystalline iron and aluminum oxides and organo-mineral complexes). By fitting three-pool soil C models to time series of the  $^{14}\text{C}$  data, we will estimate how C cycling, including decomposition constants, system ages, and transit times have changed over time (Sierra et al. 2017).

### 2.2.3. Changing N losses and fate

The long-term measurements of N fluxes described above and detailed mechanistic studies (funded by NSF DEB Ecosystem Studies grants) provide a strong platform for investigating the dynamics of the N oligotrophication process. We also propose a new ecosystem-scale tracer  $^{15}\text{N}$  tracer study to partition the fate of N across the biogeophysical template. Together, these measurements will enable us to address the following questions over the next six years:

- *How have plant- and microbial N cycling changed over the long-term HBR record? How do these patterns inform net N input/output budgets and responses of aboveground NPP and soil C fluxes?*
- *How do seasonal patterns of plant and microbial N uptake and hydrology (soil saturation and connectivity with streams) drive ecosystem retention or loss of N?*
- *How do landscape variations in soil saturation frequency govern N cycling and the fate of added  $^{15}\text{N}$ ?*

We will address these questions in two ways:

Long-term and seasonal nitrogen budgets: Building on the analysis of Yanai et al. (2013), we will assemble and synthesize long-term seasonal and annual pool and flux measurements from the reference watershed (W6) to elucidate major plant, microbial, and hydrologic drivers of N retention and loss. Linking these measurements with parallel measurements of NPP and other C fluxes will help constrain the C-N coupling of these fluxes and trade-offs of plant C cost for nutrient acquisition. The model PnET-CN/BGC is being revised and re-parameterized based on these measurements for use as a research tool in the evaluation of mechanisms driving N oligotrophication.

Tracing N retention and loss: Recent work to characterize N gas losses and N retention in mineral soil at HBR show that these two N fates remain difficult to measure (Morse et al. 2015a, 2015b, Lovett et al. 2018, Fuss et al. 2019, Darby et al. 2020, Weitzman et al. 2020) and model (Cheng et al. 2019, Nevison et al. 2022). Field-scale  $^{15}\text{N}$  tracers provide an alternative approach to quantifying these fluxes (Templer et al. 2012, Goodale 2017). We propose a set of ecosystem-scale  $^{15}\text{N}$  tracer experiments in three pairs of 12 m<sup>2</sup> plots located at two points on the biogeophysical template (periodically versus rarely or never saturated soils) to examine the importance of soil water saturation frequency in controlling the seasonal and annual fate of newly added  $^{15}\text{N}$  into organic and mineral soil, microbial biomass, and plant tissues.

### 2.2.4. Multiple Element Limitation in Northern Hardwood Ecosystems (MELNHE)

Ecosystem theory predicts N limitation of NPP in temperate forests (Vitousek and Howarth 1991), and ongoing N oligotrophication suggests that this should be intensifying over time (Mason et al. 2022). However, the MELNHE N and P- addition experiments at HBR and two nearby sites (BEF, Jeffers Brook) showed that tree diameter growth responded more to P than N addition over the first four years of treatment (2011 – 2015), with only young stands responding more to N than P (Goswami et al. 2018). Trees with arbuscular mycorrhizal associations showed enhanced growth with N and P addition but those with ectomycorrhizal associations did not. Later measurements (2015-2019) show significant growth response to N addition instead of P.

We propose to continue the long-term N and P fertilizations across 13 northern hardwood stands at HBR, BEF, and Jeffers Brook that span a range of forest age classes and site fertility. Each stand contains four plots (0.25 ha in older stands, 0.16 ha in younger stands) assigned to one of four treatments: control, N addition (30 kg N ha<sup>-1</sup> yr<sup>-1</sup> as NH<sub>4</sub>NO<sub>3</sub>), P addition (10 kg P ha<sup>-1</sup> yr<sup>-1</sup> as NaH<sub>2</sub>PO<sub>4</sub>), and both N and P addition, applied annually since 2011. This experiment is the longest-running full-factorial N x P manipulation experiment in a temperate forest. Questions we will address over the next six years include:

- *Is aboveground growth limited by N, P, or both nutrients over decadal timescales?*
- *Is belowground production of fine roots and mycorrhizae limited by the same element as aboveground production? If not, why?*
- *How does the soil mycorrhizal and decomposer community regulate nutrient acquisition and growth responses, e.g., between arbuscular and ectomycorrhizal associations?*

We propose to measure aboveground growth again in 2023 to test for (1) persistence of N limitation following a transient P limitation; (2) a return of P limitation or (3) N-P co-limitation, in which the response to N+P is greater than the sum of the main effects of N or P alone.

In response to a mid-term NSF review recommendation, we also propose a set of experiments to test effects of N, P, and N+P on mycorrhizal responses in concert with those of roots. Species composition and growth of roots and mycorrhizal hyphae will be quantified in ingrowth cores to examine root-mycorrhizal tradeoffs. Effects on P acquisition will be inferred from enzyme activities and nutrient dynamics in paired root and root-fungal ingrowth cores. Nutrient enrichment feedbacks to recycling will be quantified in ongoing measures of litterfall nutrient flux, enzyme stoichiometry, and soil nutrient availability. The effects on belowground C inputs of root and mycorrhizal treatment responses will be tested using <sup>13</sup>C-labeled organic C tracers in subsets of ingrowth cores.

#### *2.2.5. Natural and accelerated ecosystem recovery from acid deposition*

The W1 experiment, where in 1999 an amount of Ca corresponding to historical loss by acid rain was replaced by an experimental CaSiO<sub>3</sub> addition, continues to produce valuable insights. The Ca addition increased tree biomass accumulation and leaf area (Battles et al. 2014), seedling establishment and mycorrhizal infection (Juice et al. 2006), late-stage litter decomposition (Lovett et al. 2016a), and ET (Green et al. 2013), and decreased root biomass (Fahey et al. 2016). More recently, we have seen loss of soil C and N from the Oa horizon (Johnson et al. 2014) and increased NO<sub>3</sub><sup>-</sup> losses in soil solutions and streamwater (Rosi-Marshall et al. 2016, Marinos et al. 2018). These observations motivate the following questions:

- *Why did soil C and N pools decline in the Ca-treated watershed (W1), and have those declines persisted? What are the mechanisms behind these changes?*
- *Do long-term patterns of soil C and N in the reference watershed (W6) reflect the same patterns in recovery from acid deposition as observed experimentally in W1?*
- *How has soil and solution C:N:P stoichiometry changed over time and with Ca addition?*

We will address these questions with quantitative soil sampling and chemistry (described below), and with repeated inventories of tree biomass and foliar chemistry, and measurements of microbial biomass and activity, greenhouse gas fluxes, and soil solution and stream chemistry (described above). Synthesis will be supported and informed by simulations of changes in ecosystem acid-base status using PnET-BGC.

Soil sampling will be repeated at five-year intervals (2023, 2028) and will include forest floor and upper mineral soil samples at 100 locations (each) on W1 and W6. This sampling would extend our records to 32 and 52 years, respectively, and allow assessment of whether large losses of Oa material observed in 2013-14 persist through the next decade. We will also make new measurements to characterize P availability using soil solutions and ion exchange resins in W1 and W6, and C, N, and P concentrations in different density fractions.

## 2.3 Theme 2: Changing Climate

### 2.3.1 Overview

The clear climate shifts observed at HBR raise important questions about how ecosystems will respond physically, chemically, and biologically over time. The ecosystem response to climate change at HBR is neither simple nor linear, but arises from cumulative responses to climate dynamics operating at multiple time scales. *The overarching goal of our climate change work is to produce new understanding of ecosystem response to climate change at multiple time scales, in the context of other sources of variation and disturbance, and to explore implications for organisms and ecosystem processes in the forest and streams at HBR.* Specific questions that we propose to address over the next six years include:

- *What is the relative impact of atmospheric humidity versus tree physiological processes on the recent 10-year increase in ET? How does the warming and lengthening growing season impact annual ET?*
- *Are there dominant synoptic meteorological modes (weather systems) associated with the largest forest water and C fluxes? If so, which atmospheric factors (e.g., net radiation, vapor pressure deficit (VPD), wind) change the most with these different synoptic conditions?*
- *How do stream fluxes of solutes during (increasingly intense) storm events influence catchment element budgets? How do these fluxes vary with landscape position, Ca treatment, and forest age?*
- *Has the combination of increased ET and precipitation intensity changed streamflow generation pathways in the experimental (gauged) catchments?*
- *Do shorter, milder winters, earlier springs, and a longer vernal window period decrease foliar N, C assimilation, and forest productivity by reducing soil moisture and shifting the balance between soil microbes and trees in the competition for nutrients during the winter-spring transition?*
- *How does climate change across the growing season and winter alter net C storage and trophic interactions in the northern hardwood forest?*

The proposed research is platformed on extensive long-term monitoring of climate variables at HBR:

- The USFS has collected data on streamflow from nine gauged watersheds, and temperature and precipitation data at >20 stations across the HBR valley since the 1950s (Campbell et al. 2007, 2021). Event sampling provides information on the importance of storm events (Fuss et al. 2016).
- The USFS has collected data on snow cover, soil frost, solar radiation, windspeed and direction, and humidity on one or more of the nine watersheds since the 1950s (Bailey et al. 2003).
- Measurements of water stable isotopes ( $^2\text{H}$  and  $^{18}\text{O}$ ) date to 2005 and provide information on streamflow generation pathways, ET partitioning, and watershed travel times (Benettin et al. 2015, Green et al. 2015).
- Sub-hourly eddy flux tower measurements began in 2016 and provide data on forest phenology, days of high/low ET and C-uptake, and annual C, energy and ET budgets. A forest biomass inventory in the flux tower footprint occurred in 2018 and will continue every 5 years. Soil temperature, moisture, tension and heat flux, snowpack thermal profile, and air temperature/humidity sensors are collocated near the base of the tower.
- An elevation/aspect gradient was established in 2012 with an NSF Ecosystem Studies program grant and adopted by the LTER in 2016 to support long-term monitoring of snowpack (depth, density, water content), soil frost, temperature, and moisture (Wilson et al. 2020).
- The CCASE buried heating cables and snow removal have simulated effects of warmer growing season soils and increased frequency of soil freeze-thaw cycles since 2012 (Templer et al. 2017).

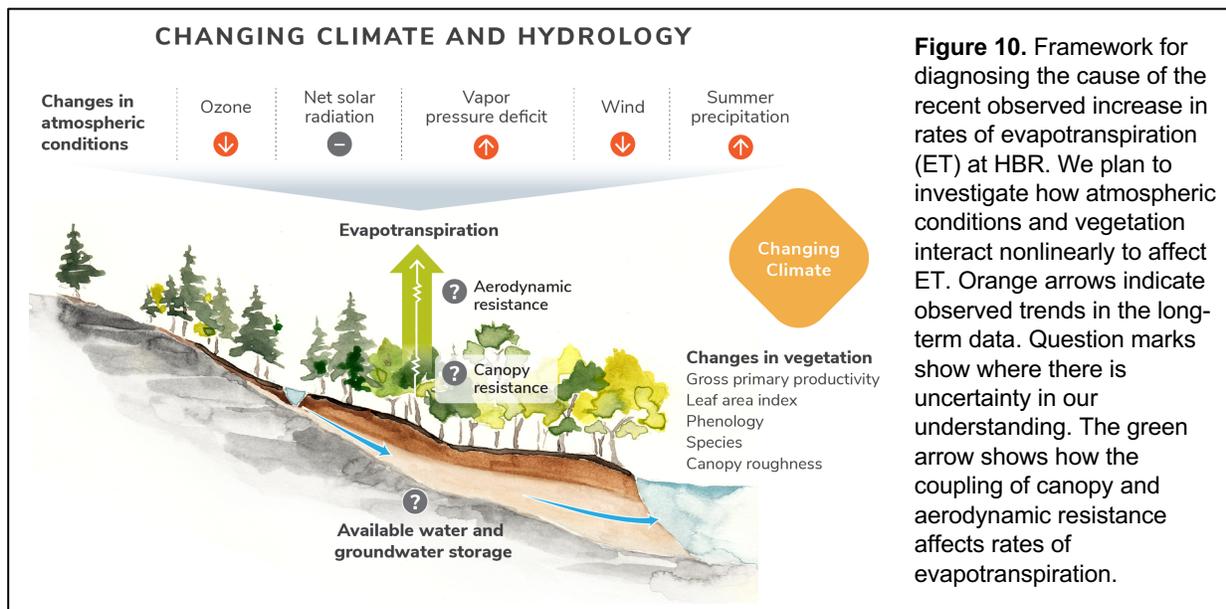
### 2.3.2 Diagnosing Causes of Increasing ET

The HBR catchments have experienced an approximately 30% increase in apparent ET over the past decade (Fig. 6) (Green et al. 2021). Hypothesized mechanisms we will investigate include threshold responses to changes in the instantaneous drivers of ET (e.g. VPD, net solar radiation, vapor pressure deficit, wind, precipitation), stomatal acclimation, extension of the growing season, and plant physiological changes in response to rising atmospheric  $\text{CO}_2$  and declining  $\text{O}_3$  concentrations (Fig. 10).

We will measure ET in three complementary ways: (1) with catchment water budgets for all nine gauged

watersheds, (2) with eddy covariance towers at HBR and BEF, and (3) by monitoring sapflow at five newly established plots using the heat-ratio method (Burgess et al. 2001, Hernandez-Santana et al. 2015). Measuring ET and sapflow at these different spatial scales and at high temporal resolution provides insight on how the timing of tree-scale transpiration is manifested at the forest stand scale (eddy covariance) and how these processes affect interannual variation in water budgets (catchment scale). The eddy covariance and sap flow data will also allow us to characterize the impact of warmer and extended growing seasons on annual ET.

We will also follow up on preliminary analyses indicating that synoptic weather patterns that produce warm, dry weather may contribute to the increase in ET at HBR. We therefore propose to determine if there are dominant synoptic meteorological modes (weather systems) associated with the largest forest water and C fluxes. The eddy covariance towers at HBR and BEF provide independent measures of C flux and ET. Machine learning methods will be optimized to identify the synoptic patterns associated with high ET and CO<sub>2</sub> uptake using atmospheric gridded reanalysis data that extend back to the 1940s.



**Figure 10.** Framework for diagnosing the cause of the recent observed increase in rates of evapotranspiration (ET) at HBR. We plan to investigate how atmospheric conditions and vegetation interact nonlinearly to affect ET. Orange arrows indicate observed trends in the long-term data. Question marks show where there is uncertainty in our understanding. The green arrow shows how the coupling of canopy and aerodynamic resistance affects rates of evapotranspiration.

### 2.3.3. Changing Ecosystem Seasonality

Climate warming has lengthened growing seasons and reduced the amount and duration of snow cover at HBR, which has altered ecosystem productivity, biogeochemistry, and animal movement (Ouimette et al. 2018, Contosta et al. 2019). Winter climate change has resulted in a longer vernal window - the period between snowpack melting and deciduous tree leaf-out - which impacts growing season ecosystem processes (Ouimette et al. 2018, Wilson et al. 2020). We propose to continue the CCASE combined growing season soil warming and winter snow manipulation experiment that investigates how these changes in climate across seasons alter forest ecosystem processes, from primary production to changes in microbial and insect composition (Templer et al. 2017). We will also continue monitoring of snowpack, soil frost, temperature, and moisture along the elevation/aspect gradient established in 2012. In addition, we will incorporate a new site with high resolution sensor measurements established as part of an EPSCOR funded state-wide terrestrial sensor network (Mulukutla et al. 2015, Contosta et al. 2017).

CCASE: We will continue measurements at CCASE to analyze relationships between climate change across seasons, C uptake and net sequestration by hardwood trees, and soil and stem respiration. We will continue the CCASE treatments that use buried heating cables and snow removal to simulate interactive effects of warmer soils in the growing season and increased frequency of soil freeze-thaw cycles in winter. Measurements include soil N cycling (i.e. mineralization, nitrification, denitrification, and N leaching), shifts in soil microbial communities (Garcia et al. 2020), tree N uptake (Campbell et al. 2014),

root health, transpiration (using the Granier method), C uptake and net sequestration (using dendrometer bands and litterfall baskets), and rates of soil and aboveground respiration (using soil and tree stem collars) throughout the year. Component soil respiration fluxes will be quantified by installing new microtrenches (Reinmann and Templer 2018). We will measure arthropod abundance and diversity in the forest floor, as well as herbivore effects on saplings. We have initiated studies of P response to the CCASE treatments including foliar (Blagden et al. 2022) and soil solution P and soil microbial exoenzymes, including acid phosphatase. Together, these measurements will inform how warmer growing seasons and smaller winter snowpack alter C storage and trophic interactions in the HBR forest.

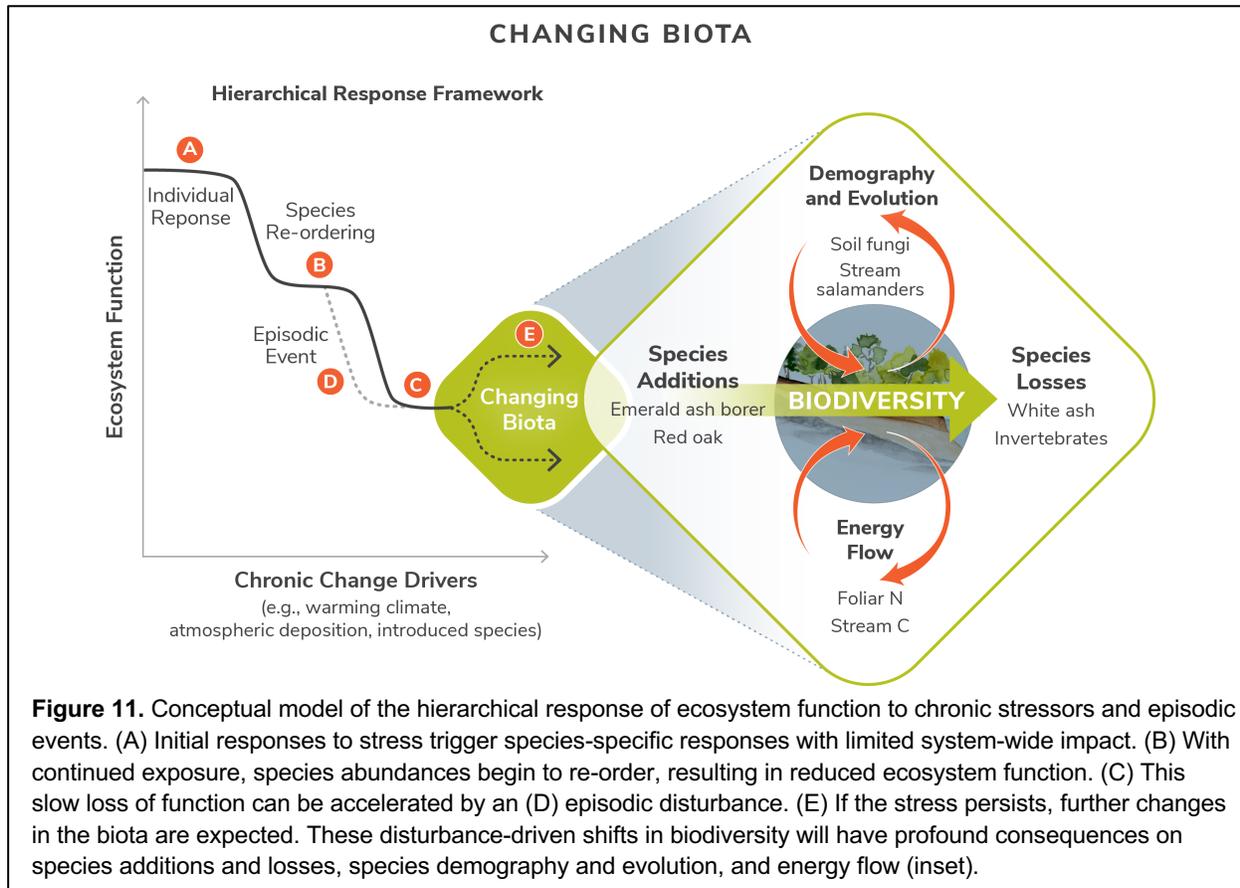
Elevation/aspect gradient: We will continue monitoring of snowpack, soil frost, temperature, and moisture that has been ongoing since 2012 at 14 plots along an elevation/ aspect gradient spanning a 2 °C annual mean temperature range. In addition, we will incorporate a site with high resolution sensor measurements to improve assessment of how changing winter and spring conditions impact N cycling, foliar N and P concentrations, and ecosystem C balances. This EPSCOR-funded site has been operating at the base of W3 since 2014 (Contosta et al. 2017). We will combine ongoing *in situ* observations of microclimate, forest growth, phenology, foliar chemistry (%N and  $\delta^{15}\text{N}$ ), soil biogeochemistry, and tower-based C flux estimates with the PnET-CN and PnET-SOM ecosystem models. Additional measurements of soil oxygen, net N mineralization and nitrification, denitrification, and leaching will be added to continuous soil respiration monitoring at this site. The PnET-CN and PnET-SOM models will be modified to: (1) improve representation of snowpack dynamics, (2) simulate the relationship between snowpack and soil microclimate by adding a soil frost module, and (3) allow soil temperature rather than air temperature to drive soil processes (e.g., N cycling, decomposition). We will assess how these model improvements alter simulated ecosystem C and N fluxes under past conditions and a range of future climate scenarios. Model validation will make use of forest productivity and GPP estimates from inventory plots and the eddy covariance towers at HBR and BEF. Consistent with the N oligotrophication work discussed above, these measurements will determine if shorter, milder winters, earlier springs, and a longer vernal window period lead to decreases in foliar N and P, C assimilation, and forest productivity by reducing soil moisture and shifting the competition for nutrients between microbes and trees during the winter-spring transition.

## 2.4 Theme 3: Changing biota

### 2.4.1 Overview

We conceptualize changes in ecosystem structure as a hierarchical progression, where the initial responses of individual species to a chronic stressor (e.g., warming climate, atmospheric deposition, introduced species) have a limited system-wide impact (Fig. 11a). With continued exposure, species abundances begin to re-order, resulting in reduced ecosystem function (Fig. 11b). This slow loss of function (Fig. 11c) can be accelerated by an episodic event (Fig. 11d). If the stress persists, further changes in biota are expected (Fig. 11e), including species additions and losses, changes in species demography and evolution, and changes in energy flow. These disturbance-driven shifts in biodiversity will have profound consequences on species additions and losses, species demography and evolution, and energy flow (Fig 11 inset). Thus, we expect that the most significant ecosystem effects will occur in those communities where changes in biodiversity create interactions with strong cascading effects (spatial control points) and where chronic stress increases species susceptibility to episodic disturbance (temporal control points). *The overarching question driving our research on biotic change is “how do species losses and gains alter ecosystem, demographic and evolutionary processes? Specific questions include:*

- *How are NPP and foliar N and P affected by shifts in tree species dominance compared to changes in canopy structural traits, such as through the loss of ash trees caused by EAB?*
- *What controls the abundance and diversity of insects and vertebrates (birds, mammals, salamanders) in northern hardwood forests, how do these relate to NPP and foliar N and P?*
- *Will breeding bird abundance return to levels of 50 years ago with continued maturation of the forest and how will their populations be impacted by changing atmospheric chemistry and climate?*
- *How does streamflow variability during metamorphosis influence demography, phenotypic adaptation, and life history evolution of salamanders?*



We propose to continue long-term data collection on trees, insects, birds, salamanders, bats, and large mammals. We will also add new research on the demography and evolution of stream salamanders, and on the effects of the imminent loss of a major tree species (ash) due to an invasive pest.

The proposed research is platformed on extensive long-term monitoring at HBR:

- **Vegetation:**
  - Tree demography and diameter at breast height of all trees > 10 cm for reference (W6) and Ca-treated (W1) watersheds have been measured at 5-year intervals since 1996/97.
  - Tree and sapling inventories of forest composition, structure, and productivity on reference and experimental watersheds, starting in 1965 on W6.
  - Inventories of 371 plots established in 1995 across the entire HBR valley every 10 years, with a subsample of 30 plots sampled more intensively every 5 years.
  - The growth and survival of more than 5,000 tagged trees in a 10-ha area that is the focus of long-term bird studies have been tracked biannually since 1991.
  - Annual “sentinel surveys” of climate migrant seedlings, e.g., red oak, white pine.
  - Annual surveys of foliar chemistry along elevation gradients in W6 and W1.
- **Insects:**
  - Caterpillar surveys since 1986 and malaise trap sampling for flying insects since 1996.
  - Cameras, sensors and sticky traps for aquatic insects in W1 – 6 and 9 since 2018.
- **Birds:**
  - Annual censuses and territory mapping since 1969 of all birds breeding in a 10-ha study plot.
  - Detailed demographic studies of black-throated blue warblers since 1986.
  - Spatially extensive breeding season point counts throughout HBR since 1999 (>19,000 point counts that include > 100 species).
  - Acoustic sampling since 2016.

- Bats: Acoustic sampling since 2015.
- Other Mammals (wildlife): Motion detecting cameras since 2018.
- Salamanders: Intensive capture-recapture surveys of *Gyrinophilus porphyriticus* populations in three HBR streams since 2012.

#### 2.4.2 Trees

The tree species composition and NPP of the northern hardwood forest at HBR is in a state of flux. Contrary to expectations, conifers from higher elevations are moving downslope into the hardwood forest. At the same time, red oaks and white pine are invading at lower elevations. We will continue to monitor these species transitions with our network of tagged-tree inventories. We will also maintain our “sentinel monitoring” designed to quantify climate-driven changes in species survival and growth at low elevation.

We expect the ongoing shift in tree species dominance (more beech dominated) (Figs.7, 8a) with a less complex canopy structure) to reduce rates of NPP. To understand the effects of changes in tree species dominance and NPP on biodiversity “up” the food chain, we will focus on changes in canopy structure, which affect light capture, and therefore NPP, and foliar N and P concentration and content. Foliar N is frequently limiting to primary consumers due to nutritional stoichiometry (Gonzales and Yanai 2019). Concentrations of foliar N, which vary with season, year, and elevation at HBR, may be decreasing due to oligotrophication (**section 2.2.3**). Foliar N could thus be a fundamental control on the abundance of primary consumers, and therefore the flow of energy and matter from plants to top order consumers in the green food web (including birds, bats, and wasps). We will intensify foliar N and P sampling to characterize details of the natural annual decline from spring to summer in leaf N, as well as changes due to oligotrophication. These measurements will be concentrated in the area of existing long-term studies of birds and caterpillars to facilitate tests of how foliar N influences Lepidoptera and insectivorous birds. We also plan to intensify the temporal resolution of our measurements of tree growth from every 5-years to annually and add three-dimensional characterizations of canopy structure using Terrestrial Laser Scanning (TLS) (Atkins et al. 2020). Annual measures of wood increment and aboveground NPP will be measured with new dendrometer bands on 30 trees in long-term litterfall collection areas to get empirically based, site-specific, measures of annual tree growth and productivity.

In the next 10 years, we expect the rapid death of > 90% of ~26,000 canopy ash trees at HBR due to the arrival of EAB. We will continue studies of understory flora, brown web invertebrates, and soil microbes below ash and other canopy tree species in study plots established during the last five years. We will measure responses of the bird community to (1) the pulse of dead wood and xylophagous insects, and (2) increases in understory foliage corresponding to death of the canopy trees. These studies will be complemented by a new manipulation experiment in which we will protect ash trees (with emamectin benzoate) in 20-30 experimental plots (20 m diameter).

#### 2.4.3 Insects and other invertebrates

Insects are the most important link between primary production and higher order consumers (birds, bats, salamanders, and wasps). Our overarching long-term question related to insects is: “What controls the abundance and diversity of insects in northern hardwood forests, how are these related to NPP and foliar N and P, and how do they in turn influence bird populations? We will continue caterpillar surveys and malaise sampling for flying insects and will add (1) blacklight sampling for nocturnally active insects (chiefly moths but also *Tipulidae* and other taxa) and (2) Lindgren funnel traps for wood and bark-boring insects. The protocol of blacklight sampling (developed and validated in 2021) will employ time lapse cameras that permit enumeration of many taxa from the resulting images. Sampling will continue in the area of long-term bird studies and be augmented by matched sampling in W1 (Ca treatment) and in W2 and W4 that were cut about 50 years ago and now match the age of the bird plots when studies began in the late 1960s. Funnel trapping will be designed to record the expected surge and subsequent decline of bark and woodboring insects associated with invasion by EAB.

Other new efforts include: (1) document the arrival and establishment of deer ticks (*Ixodes scapularis*). This vector of Lyme disease is expected to become common in HBR during this funding period, (2) monitor for new mosquito species, (3) survey for hemlock woolly adelgid and other forest pests, and (4)

map the occurrence and spread of non-native earthworms (now present in some parts of the valley).

For aquatic insects, we propose to continue the headwater stream sampling initiative that began in 2018 that has the objective of determining how long-term changes in water chemistry influence aquatic organisms and ecological processes. We established sampling platforms, cameras, sensors and sticky traps in W1 – 6 and 9 to capture fine scale stream ecosystem, aquatic insect and canopy dynamics. These nascent, aquatic ecology records have already revealed substantial variation in primary producer and aquatic insect biomass across streams and across years. Additional data will allow for time series modeling to identify how interannual variation in hydrology, temperature, and solar energy collectively determine these core aquatic ecosystem processes.

We will continue to use the StreamLight model (Savoy et al. 2021) coupled with MODIS datasets as input to estimate daily light availability to streams for all HBR watersheds. These “stream climate” datasets (dating back to 2001) document substantially colder spring water temperatures, highly variable timing of canopy budburst and closure, and remarkable interannual variation in the total annual solar energy reaching the stream channel. Our ultimate objective is to build a time series dataset for weekly stream algal biomass, rates of instream decomposition, organic matter standing stocks in the stream channel, and numbers and identity of emerging aquatic insects. We will link these biological measurements to long-term stream chemistry datasets.

#### 2.4.4 Birds

Specific questions that have emerged from the long-term bird studies include: Why has total bird biomass supported by the forest declined and then partially returned over the last 50 years (Fig. 8b)? Will breeding bird abundance return to levels of 50 years ago with continued maturation of the forest? Which species will respond to advances in spring leaf-out and delays in autumnal leaf senescence? How will a lengthening green season affect foliar N and the flow of energy through trophic levels? Which species of birds will respond most dramatically to the death of up to 26,000 canopy ash trees over the next decade?

We will (1) continue annual censuses and territory mapping of breeding birds following the protocol began in 1969; (2) transition from sampling valley-wide breeding birds via only point counts to increasing use of passive acoustic recorders (Symes et al. 2022); and (3) add demographic studies of ovenbird (*Seiurus aurocapilla*) (primarily a brown food web forager) to complement continuing studies of the black-throated blue warbler (a green food web forager). Territory mapping will transition from hand drawn maps to a GPS-based system. TLS measurements of forest structure will improve habitat assessment in the main long-term bird monitoring plot. The transition to increased use of acoustic recorders for occupancy analysis will be accompanied by the development of new analyses, including statistical comparisons of point count and acoustic data. We will work to adapt BirdNET (a computational platform from the Cornell Lab of Ornithology) for the semiautomated quantification from acoustic data of species-specific vocalizations during the dawn chorus. The addition of demographic studies of ovenbirds will provide leverage in understanding general effects of changing phenology in both spring and fall on migrant songbirds. To better resolve the trophic structure of green and brown food webs, we will include measurements of stable isotopes ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) in leaves, litter, insect herbivores, brown web insects, and secondary consumers (wasps, beetles, spiders, and birds) tissues.

#### 2.4.5 Bats

Analysis of the diversity and abundance of bats is important given their roles in seed dispersal, pollination and insect consumption (Ramirez-Francel et al. 2021, Russo et al. 2021). Continuation of novel acoustic sampling that began in 2015 will allow us to document the recovery (or not) of bat species that have been decimated by white-nose syndrome, and to assess their importance in the northern hardwood forest.

#### 2.4.6 Other mammals

To better understand the integrated forest and climate influences on wildlife species, we will continue to use a network of 30 motion-detecting camera stations installed across the valley in 2018. Natural history observations of every animal image collected will be assessed for individual animal general health condition, species interactions including herbivory, carnivory and parasitism, and evidence of reproductive

status, including offspring detection, antler development, and reproductive behaviors. We will use image data to validate a spatial habitat model of suitable habitat conditions for moose during both summer and winter seasons and perform occupancy modeling for all species identified with the camera monitoring.

#### 2.4.7 Salamanders

We propose to build on our salamander studies to address questions about how demography and evolution mediate population and community-level changes, and to identify key temporal and spatial controls on those population-level effects. We will test the hypothesis that metamorphosis is a key temporal control point in the demography and evolution of salamanders at HBR. Most animals undergo some form of metamorphosis, a stage when abrupt developmental changes can make individuals vulnerable to environmental stressors (Wilbur 1980, Lowe et al. 2021). At HBR, streamflow is becoming more variable with climate change (Hayhoe et al. 2008, Campbell et al. 2011). We have discovered that increasing streamflow variability reduces survival during metamorphosis in the stream salamander *G. porphyriticus* (Lowe et al. 2019). Ultimately, these climatic effects may lead to widespread population declines, but it is also possible that local phenotypic or life history adaptations will buffer populations from the negative effects of changing hydrology. We will test these alternative predictions by combining long-term mark-recapture data with new genomic analyses.

*We propose to answer two new questions: (1) Do phenotypic traits affect individual survival and performance during metamorphosis, and (2) How does streamflow variability during metamorphosis influence demography, phenotypic adaptation and life history evolution?* We will answer question 1 by conducting intensive capture-recapture surveys and phenotype sampling throughout the period when metamorphosis occurs (June – October) in four study streams at HBR. We will answer question 2 by combining phenotypic and demographic data with genotypes of 2000 individuals from our three primary study streams. Specifically, we will use single-nucleotide polymorphisms (SNPs) already developed for *G. porphyriticus* and genomic clustering analyses to determine whether individuals that share the same phenotypic and life history traits are genetically related (Stelkens et al. 2012). With these methods, we will test for a genetic basis of phenotypic and life history traits, and for local adaptation by comparing the SNP signatures of trait-associated clusters across the four study streams (Forester et al. 2018).

### 2.5 Theme 4: The biogeophysical template and control points of ecosystem change

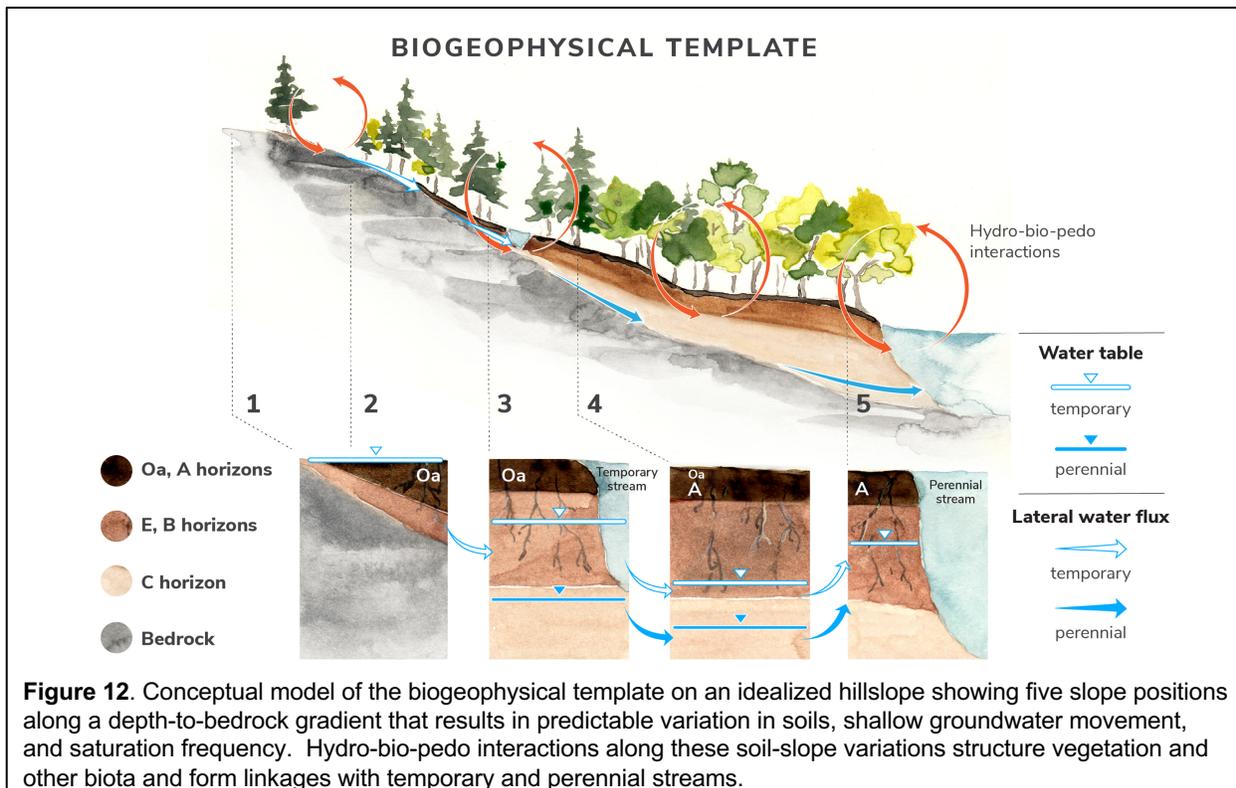
#### 2.5.1 Overview

Forests are always changing, whether it is a gradual shift in community composition or a response to a disturbance (e.g., timber harvest, windstorm). In either case, the response may be spatially dependent on particular combinations of biogeophysical factors such as soil and vegetation type, site history, slope position, and hydrologic regime that we refer to as the biogeophysical template. While some geophysical aspects of the template are essentially fixed on ecological time scales (e.g., parent materials and topography), many biological aspects (e.g., species composition or nutrient cycling) can vary in response to disturbances or disturbance history. Additionally, biological changes such as shifts in forest structure and composition can produce feedbacks that alter the template (e.g., changes to soil organic matter or soil moisture) and affect other population, community, and ecosystem processes.

We conceptualize the biogeophysical template as a set of spatial ecosystem properties resulting from interactions among geological, pedological, biological, and hydrological processes (Fig. 12). At HBR, slope position, topography and depth to bedrock control shallow groundwater movement and saturation frequency, which exert a dominant role in soil development. Shallow-to-bedrock areas (slope positions 1-3; Fig. 12) frequently connect hydrologically to ephemeral streams, which expand and contract with storm events and snowmelt (Jensen et al. 2017, 2018). These connections facilitate solute export or translocation to downstream settings such as near-stream soils that can serve as a sink for C, metals, and nutrients (position 5) (Bourgault et al. 2017, Gannon et al. 2017). Spruce, fir, and paper birch dominate areas where soils are shallow-to-bedrock and wet (positions 1-2, Fig. 12). This zone then transitions to position 4, where soils are deeper and well-drained with northern hardwood tree species.

The question driving our research on the biogeophysical template is: *Can we identify specific places and*

times that serve as control points for change in ecosystem dynamics and long-term patterns of important ecosystem characteristics such as C storage, low redox conditions, or biodiversity? Drivers and disturbances clearly play out differently across the template. The identification of control points or “areas of the landscape that exert disproportionate influence on the behavior of the ecosystem under study” (Bernhardt et al. 2017) will greatly advance our understanding and ability to predict the effects of disturbance on the forests at HBR. Control points have both spatial and temporal dimensions and should have a quantitative basis, e.g., higher rates, or different dominant processes from the surrounding matrix. For example, dynamic soil saturation and the hydrologic connectivity of different regions of the landscape can lead to thresholds in the fluvial export of constituents from the watershed. These dynamics in soil wetting and drying can in turn enhance processes such as denitrification or C stabilization (Zimmer et al. 2013, Morse et al. 2014, Jensen et al. 2017, Bailey et al. 2019, Pardo et al. 2022), and drive landscape variation in response to climate stresses such as heat or drought.



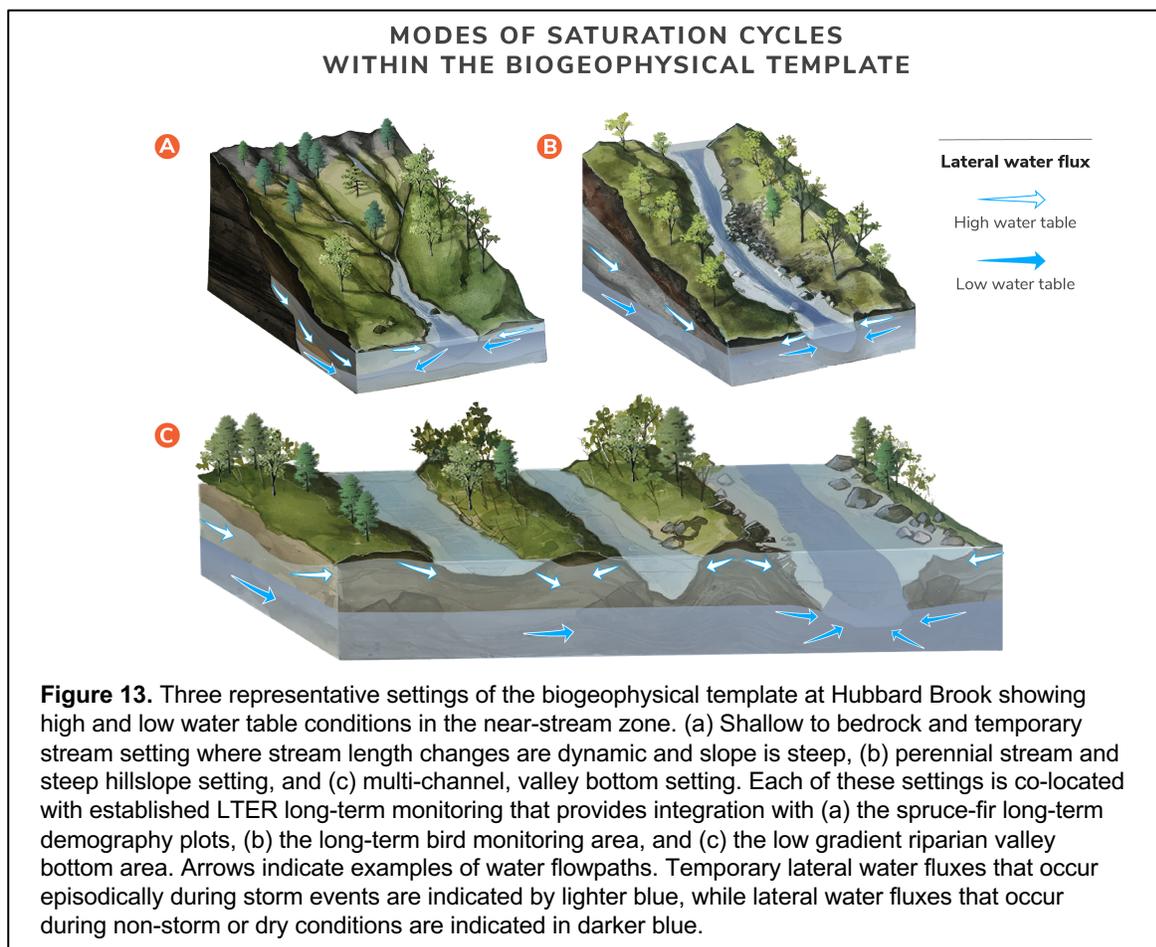
### 2.5.2. The biogeophysical template as a framework to understand control points of change

Most of our work to date has focused on describing spatial patterns of the biogeophysical template in terms of the interactions between hydrological processes and soil development (i.e., hypedology) in a few areas (e.g., W3, W9) (Gillin et al. 2015, Bailey et al. 2019). However, to broaden understanding of how long-term changes influence ecosystem properties and processes, or how disturbance effects differ among components of the template, long-term measurements of saturation dynamics and groundwater chemistry are needed in other parts of the landscape. Therefore, we propose new soil and groundwater observations from settings that are more common lower in the HBR valley and that overlap with other ongoing HBR long-term studies (e.g., long term vegetation, food web, and nutrient cycling work).

We will establish a new long-term hypedological monitoring network in three hypothesized control points where saturation dynamics are a key feature of the biogeophysical template (Fig. 13). This new work will expand the monitoring network beyond W3 and contribute to a dataset initiated in 2006. Each setting is co-located with established LTER long term monitoring: **(a)** spruce-fir zone long-term demography plots near shallow-to-bedrock areas that are the source areas of headwater intermittent and ephemeral headwater streams (Fig. 13a); **(b)** the long-term bird monitoring area, which also has forest

inventory and seedling demography plots, and where ash is common in riparian areas and will soon be lost to EAB (Fig. 13b); and (c) the low gradient riparian valley bottom area where a maturing forest and the regional return of beavers are increasing prevalence of dams, increasing riparian interactions, and renewing activity on fossil multithreaded stream channels (Fig. 13c).

Monitoring wells for measuring shallow groundwater levels and for sampling water chemistry will be installed in each of the three sites in areas where groundwater dynamics represent conditions shown in Fig. 13. Groundwater data and soil morphological/mineralogical and organic matter analyses will be used to characterize the saturation regime and provide baseline data to detect long-term change in the biogeophysical template as climatic drivers and disturbance proceed. In addition to soil and vegetation parameters, measurements of microbial biomass and activity, greenhouse gas fluxes, and soil C cycle processes described above (section 2.2.1) will be made in each of the locations in Fig. 13. This framework provides opportunities to study organic matter source/sink dynamics from shallow-to-bedrock source areas to depositional riparian areas along perennial streams, changes in vegetation such as the increasing dominance of conifers in high elevation zones, N cycling dynamics, the role of increasing wood inputs in aging forests, the return of beavers in the valley bottom, and variation in response to climate stress, e.g., heat, drought. Data will be analyzed using the criteria presented in Bernhardt et al (2017) to quantitatively assess control points.



## 2.6. 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 USFS maintains and runs the HBEF, our principal research site. USFS maintains the site infrastructure (roads, weather stations, weirs, sensor network, etc.), collects the basic hydrological and meteorological data, maintains the sample archive, and provides intellectual collaboration through its

team of project scientists. Two NSF-LTREB grants that support the weekly precipitation and stream chemistry measurements, and the long-term studies of breeding birds.

The long-term data from the HBR-LTER have been leveraged to obtain short-term research grants on many of the topics presented here. Recent grants related to the research proposed for the next six years include research on nitrogen oligotrophication (NSF DEB), ice storm dynamics (NSF DEB) weathering gradients (NSF EAR), salamanders (NSF PCE), CCASE (NSF DEB), denitrification (NSF DEB), water-use efficiency (NSF EAR), public engagement with science (NSF AISL), linking root and soil microbial stress metabolism to watershed biogeochemistry (DOE), evaluating the continuity of NEON and AmeriFlux data streams (NSF MSB), and testing a novel, automated soil frost sensor (USDA NIFA).

## **2.7 Synthesis, integration, and prediction**

### *2.7.1 Challenges for synthesis and prediction*

We propose to focus on four 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, experiments, and modeling. More fundamentally they will be rallying points for group interaction and evaluation of progress over the next six years:

1. *Are there specific locations in the HBR landscape that are potential control points for ecosystem change, and should control points be a fundamental component of the conceptual model guiding HBR research? Are there places where a physical disturbance might unleash a cascade of changes from soil conditions to vegetation, to organic matter quality, to biodiversity? Are these control points driven by physical (e.g., bedrock constrictions), chemical (e.g., low redox), or biological (e.g., debris or beaver dams) phenomena? How do these spatial patterns interact with temporal events?*
2. *How will the interactions among climate change, air pollution and biotic change alter the composition and structure of the forests at HBR? How will these changes affect ecosystem function? Here the need for synthesis and integration has great practical implications because our partners in the USFS and state and local management agencies have a great need to predict changes in forest communities over the next 20 years. This topic provides unique opportunities for engaging with stakeholders and for comparison of observations at HBR with results from other sites in the region.*
3. *How are increases in atmospheric CO<sub>2</sub> and a longer and warmer growing season affecting NPP, nutrient uptake by trees, and soil C, N and P availability? How are these effects mediated by recovery from acid deposition, mycorrhizal associations, and spatial variation in soil properties? We plan to re-focus some of our long-term data streams (e.g., soil C pools, soil respiration, flux towers) and to add new measurements (soil<sup>14</sup>C) to determine if and how the C cycle is changing at HBR. Modeling and comparison with other sites and experiments will be important for this effort.*
4. *How will complex changes in the water cycle, including increases in the quantity and variability in precipitation, loss of snowpack, variability in growing season droughts, and changes in ET alter the structure and function of the ecosystem? We will integrate data from multiple sources (e.g., flux towers, soil moisture sensors) and locations (e.g., north versus south facing watersheds) to determine how changes in the amount and variability of precipitation affect ecosystem functions.*

Each of these integrative questions, and many of our specific research questions, are inherently predictive. Our analyses will produce predictions of which trees, insects, birds, and other vertebrates will dominate the forests at HBR and the northern forest region, the quantity and quality of the water that will drain from these forests, soil C storage, and many other variables of interest to science and society. We will make predictions of places and times (control points) that should be closely watched for signs of change. Our capacity for prediction is actualized by combining data with heuristic, mechanistic, and statistical models to generate system-level insights that scale across time and space.

### *2.7.2 Tools and models for synthesis, integration and prediction*

#### *2.7.2.1 New data tools*

The long-term data record at HBR provides the framework for understanding ecosystem dynamics in response to drivers of change, including air pollution, climate change, and biotic disturbances. New data

tools help us to evaluate emerging trends that are superimposed on long-term trends. For example, high-resolution stream water quality sensors have created a new perspective on the foundational stream chemistry data record at HBR, and soil moisture and oxygen sensors show surprising periods of saturation and anoxia in HBR “well-drained soils”. Advances in unmanned aerial vehicles and laser scanning technology have improved assessment of the timing of key phenological events, mapping of imperiled white ash trees, and measurement of canopy structure. Since 2015 an eddy covariance tower has provided new understanding of water and carbon cycling and the impact of synoptic meteorology on ecophysiology at sub-daily temporal scales. Dendrometer bands will continue to capture and characterize annual and seasonal changes in tree growth and ecophysiology. Passive acoustic sensors and wildlife camera traps provide critical information about the seasonality of animal behavior like migration and movement patterns for critical species in response to environmental change. Next-generation genomic approaches are being used to assess whether and how evolution buffers populations from functional and demographic change. Together with the long-term record, these tools will help test key hypotheses at finer temporal and spatial scales and refine our mechanistic understanding of ecosystem change.

#### *2.7.2.2 Models and prediction*

The core datasets collected by HBR enable multiple forms of modeling that span hydrology, biogeochemistry, animal populations, and food web dynamics. Physical models, including HydroGeoSphere, use intensive spatial data to describe the biogeophysical template, and will be used to quantitatively address our integrative question about control points on this template. Many models applied at HBR integrate observational chemistry and vegetation data with mechanistic processes. The PnET family of models (PnET-CN, PnET-BGC, PnET-SOM) (Valipour et al. 2021) will be used to address our integrative questions about changing water and element cycles, as well as questions about changing seasonality. The SoilR package will be used to model soil organic matter decomposition and estimate system ages and transit times of pool-based models using inverse parameter estimation constrained with radiocarbon data (Sierra et al. 2014). The Spe-CN model (Crowley et al. 2016) and the Ecosystem Demography model will be used to address our integrative question about forest community change. The Multiple Element Limitation Model (Rastetter et al. 2013) is used as a driver of the MELNHE experiments. Application of the Community Land Model (CLM) at HBR allows testing of this global model's C-N dynamics (Nevison et al. 2022). Population and food web transfer models will be used to synthesize long-term trends in animal abundance and responses to disturbance.

#### *2.7.2.3 Data science*

Synthesis efforts at HBR have long integrated data with models to gain novel system-level insights into ecosystem processes across time and space. New research efforts build on this legacy to formalize the characterization of uncertainty within field data, statistically align disparate datasets for synthesis, and develop machine learning methods for analysis of complex data and gain predictive insight into ecosystems. Formal uncertainty analysis has quantified uncertainty of field datasets in ways that have informed decisions to increase or decrease future collection efforts (Yang et al. 2017). Data alignment of disparate datasets has helped to prepare input and observation files for model parameterization, application and testing by a broader community of researchers (Valipour et al. 2018, 2021). Machine learning algorithms based on statistical models to fit long-term data are emerging as an important tool for description or prediction. For example, ongoing work at HBR uses machine learning to investigate an unexpected pulse of stream  $\text{NO}_3^-$  in 2015 (Campbell et al. 2021). Machine learning is also being used with acoustic monitoring sensors to identify the calls of bird and bat species. We will continue efforts using statistical analysis of “early warning signals” in multiple ecological time series to evaluate changes in the ability of ecosystems to maintain function while experiencing perturbation (Contosta et al. 2022).

#### *2.7.2.4 Data-model synthesis*

Closely integrating data with models in a feedback loop will provide insight into several of our integrative questions. The models that we use span different components of the ecosystem by depicting simultaneous and interactive processes that bridge the biogeophysical template, including the atmosphere, vegetation, soils, and animals. Several of the integrative questions address processes at

sub-seasonal timescales, where high-resolution sensor data help inform mechanisms that drive the phenology of plants and animals, tree ecophysiology, stream dynamics, and the rapid evolution of organisms. This approach will also facilitate the identification and characterization of control points in ecosystem processes across both time and space at HBR.

## **Broader Impacts**

### **2.8 Education, outreach and diversity, equity, inclusion, and anti-racism (DEI&A)**

Broader impacts activities at HBR are driven by four goals: (1) establish long-term, trusting relationships with diverse community members and environmental decision-makers across the northern forest ecoregion; (2) recruit and train the next generation of ecosystem scientists and environmental leaders; (3) support DEI&A within the HBR and broader scientific communities; and 4) drive innovations in research, education, and outreach. To achieve these goals, we propose five approaches (**sections 2.8.1 – 5**)

#### *2.8.1 Public and policy engagement programs*

Our public and policy engagement programs focus on relationship-building, scientific synthesis, and integrating social science to advance effective practices. In this 6-year cycle we will:

- Facilitate two-way briefings (2-3/year) with state and federal policymakers and managers, including the NH congressional delegation and the White Mountain National Forest, with roundtable events and tailored translational materials like fact sheets and research briefs that directly link science and policy about winter climate change, forest management, changing biota, and air pollution.
- Build intentional and respectful relationships with members of Tribal Nations in the region. This entails work with Tribal liaisons, listening and learning to understand how HBR science relates to Tribal priorities, and building collaborations to advance Indigenous forest research and scholarship. The Indigenous Knowledge & Networking Sub-committee of our DEI&A Committee is leading efforts to build a network and document the history of Indigenous peoples in the region via a series of workshops. We have budgeted \$5K/year for the activities of this sub-committee.
- Continue to broker partnerships between HBR researchers and natural resource managers that lead to the co-production of actionable environmental knowledge. Recent partnerships include work with the Society for the Protection of New Hampshire Forests and the Nature Conservancy. Continue to work with the LTER Network Office (via proposals to the NSF AISL program) to leverage HBR and other LTER sites for advancing fundamental understanding about public engagement with science and the role of public engagement in scientific programs (Besley 2020, Besley et al. 2021).

#### *2.8.2 Science education and training programs*

HBR leads a suite of programs focused on innovative science learning and the recruitment and training of the next generation of ecosystem scientists and environmental leaders. In this 6-year cycle we will:

- Expand youth events and the Young Voices of Science (YVoS) program, including recruitment of alumni for high-impact outreach and policy engagements, and sharing the YVoS model with other LTER sites. Current YVoS workshops include how to write an op-ed, engage with policymakers, and share science using rhetoric, empathy, and storytelling. YVoS will engage 40 or more students/year.
- Strengthen our long-term partnerships with K-12 schools via our Schoolyard LTER program, including in the urban, racially and culturally diverse regions of southern NH and the rural, economically under-resourced schools of northern NH. This work entails expanding our “Zoom-a-Scientist” programs that bring HBR scientists into classrooms, data lessons that incorporate HBR data into core science curricula, and “Hubbard Brook-in-a-Box” kits that allow educators to adapt the tools and approaches of long-term ecological research into schoolyard investigations. These programs engaged 1,700 students over the past 5 years.
- Continue our LTER REU program, which supports 2-3 students per summer. These students may work on-site in a field research setting or beyond the HBEF on a “translational science” project co-mentored by an academic partner affiliated with HBR and a management or industry partner.
- Expand curriculum-based research opportunities within undergraduate classrooms, enabling more

students and more diverse students to participate in LTER research. Students at Virginia Tech will work with HBR data in two classes (~20 students/year) as part of semester-long research experiences, including a course for Environmental Informatics where students develop web-apps that visualize and analyze HBR data. CUNY undergraduates (4/year) are developing research projects associated with the N oligotrophication project using remote sensing, field and/or laboratory data.

### *2.8.3 Art-Science program*

HBR's Art-Science program integrates art and science to advance environmental knowledge, empathy, and action. We will support (~\$4K/year) an artist-in-residency program each year, engage Art-Sci REU students, continue to support the WaterViz project (long-term data visualization and sonification), and provide logistical support for a series of transdisciplinary workshops exploring the role of art and science in today's society. Our objectives are to: (1) work across disciplines to understand pattern and process in increasingly large, complex environmental data sets; (2) foster creativity, innovation, and new discoveries; and (3) communicate and translate HBR science for a broader audience.

### *2.8.4 Develop and maintain infrastructure for DEI&A at HBR*

We are committed to increasing participation by people from underrepresented groups in HBR. To accomplish this, we will: (1) use a Critical Ecology approach (described below) to make the lens of our research more inclusive and holistic; and (2) fund a series of activities under the direction of the HBR DEI&A Committee to make our site and community more inclusive. Our goal is to create a safe, comfortable, supportive atmosphere, where the flow of ideas and knowledge across disciplines and research groups is collegial and communal. We will accomplish this by creating intentional structures that empower all participants to envision and create a research environment where each member can thrive. These structures include a comprehensive feedback and complaints procedure that will allow anonymous complaints (when desired), a designated ombudsperson to address general site-level feedback, and the possibility of mediation for interpersonal issues. We will continue to provide anti-racism and bystander intervention training, and encourage participants to interrupt offensive or exclusionary behavior as it occurs. An onsite community relations staff person will organize orientations, social events, and activities for the entire on-site research community. We will participate in the Ecological Society of America's (ESA) SEEDs Partnership for Undergraduate Research Program, which provides a summer REU followed by two workshops and a presentation at ESA. We have budgeted ~\$25K/year to support the development and maintenance of DEI&A infrastructure at HBR.

### *2.8.5 Use a Critical Ecology approach to make the lens of our research more inclusive and holistic*

HBR has been a seminal site for the investigation of biogeochemical and ecological responses of northern hardwood forest watersheds to physical disturbances. In the areas of atmospheric chemistry and climate change, our work has extended to include regional-scale links between emissions, deposition, and ecological effects, policies, and programs to reduce these effects, and links to energy generation and use (Driscoll et al. 2001, 2003, 2011, 2012, 2015). Now we propose to use these long-term efforts as a platform to address social processes as explicit drivers of focal disturbances. While established theories of the relationships among societal ideologies, value systems, natural resource use, and environmental problems have come from the social sciences, biogeochemistry and ecology have been slow to address these relationships (Bianchi et al. 2021). We propose to address this gap and develop a "Critical Ecology" framework for the long-term research at HBR that will expand our understanding of the societal and social roots of disturbances such as acid rain and climate change. This work will be designed to address past, current, and future interests of Indigenous peoples and increase diversity, equity, and inclusion in our research group. To do so, we will partner with the Critical Ecology Lab (CEL), a nonprofit research organization founded by HBR alum Suzanne Pierre to integrate ecosystem science and critical social theory. CEL is an organization founded and organized entirely by Earth scientists who identify as female, nonbinary, queer, trans, Black, Asian, and Indigenous.

Working with CEL, we propose a series of virtual and in-person meetings at HBR that will take the format of symposia and theme-based working groups. This effort will build on our long experience of dialogue-based engagement with diverse stakeholders in the region. The initial goal of these convenings will be to

generate a shared framework drawing from leading global change and social equity theory, HBR research, and diverse community interests and concerns, including from Tribal liaisons and Indigenous scholars. The subsequent goal is to translate concepts and methods across disciplines to build shared capacity to address consensus-derived questions that emerge from the framework. Working groups will be led by critical ecology experts associated with CEL and will use HBR long-term data and historical information (e.g., atmospheric deposition, climate, biota) to build cross-disciplinary bridges. These working groups will produce collaborative publications for academic and broader audiences. Finally, these convenings will be fertile spaces for building new collaborations that will be sustained beyond the lifetime of the convening series at HBR, and should help attract a diverse group of scholars to HBR. We have budgeted \$25K/year to support CEL as well as \$10K/year for summer research fellowships available to student, faculty and/or community partners to develop activities that emerge from the workshops.

### **Cross-site and network activities**

HBR scientists have been active participants in many LTER network activities and cross-site synthesis projects. HBR scientists have contributed to efforts to document the history of the LTER network (Alber et al. 2021, Swanson et al. 2021, Zimmerman and Groffman 2021) and interactions between the LTER and other environmental research networks (Baatz et al. 2018, Richter et al. 2018, Weintraub et al. 2019, Clark et al. 2021, Jones et al. 2021). We have been active in network syntheses of the five core areas of LTER research (Gaiser et al. 2020, Bahlai et al. 2021, 2021, Cowles et al. 2021, Harms et al. 2021, Iwaniec et al. 2021, Rastetter et al. 2021, Sonti et al. 2021, Zinnert et al. 2021, Campbell et al. 2022).

Over the next six years we plan to play leadership roles in LTER network synthesis activities related to climate change (Campbell, Driscoll), advances in informal science learning (Garlick), interaction with the NEON and CZO networks (Groffman, Matthes), art/science interactions (Rustad), watershed studies (Green), and DEI&A (Pardo). HBR scientists have also taken a leadership role in regional research through the Northeastern States Research Cooperative (NSRC), a competitive grant program for northern forest research, jointly directed through the USFS, the HBRF, and public Universities in Vermont, New Hampshire, Maine, and New York.

### **3.0 Synthesis and Final Thoughts**

Understanding the interacting effects of atmospheric, climate, and biotic change on forest ecosystems is one of the greatest challenges in ecosystem science. Long-term research at HBR provides unique opportunities to address this challenge. Our long-term data have characterized surprising changes that have driven the development of the new theories, questions, experimental approaches, and methods described in this proposal. Results from the proposed work will advance basic science, and produce results relevant to important societal problems. We also propose to use the long-term data, and the impact of our science as a platform to diversify the context, participants, and beneficiaries of our science.

As is appropriate for an LTER program, the questions that we propose to address emerge from long-term data that we have collected, and require continued long-term data collection to address. Moreover, our project is evolving, with new ideas about control points that reflect our increasing understanding of how disturbance influences the northern hardwood forest, new tools for data collection, analysis, modeling and synthesis, and four new overarching questions to drive synthesis and integration. This evolution is improving our ability to make predictions of what trees, microbes, insects, birds and other animals will dominate the forests at HBR and the northern forest region, and how these forests will function to influence water, air, and soil across the region.

The long-term nature of our program has allowed us to build deep relationships with stakeholders. This is also evolving, and we now propose to diversify these relationships to increase the participation of underrepresented groups in our project by making the lens of our research more inclusive and more holistic, and by making our site and community more diverse. Our objective is address unique and important inherently long-term questions to provide important information for science and society, and to foster the development of an equitable and effective scientific community to ensure continued success in these endeavors.

## References cited

- Addis, B. R., and W. H. Lowe. 2020. Long-term survival probability, not current habitat quality, predicts dispersal distance in a stream salamander. *Ecology* 101:e02982.
- Addis, B. R., B. W. Tobalske, J. M. Davenport, and W. H. Lowe. 2019. A distance-performance trade-off in the phenotypic basis of dispersal. *Ecology and Evolution* 9:10644-10653.
- Alber, M., J. Blair, C. T. Driscoll, H. Ducklow, T. Fahey, W. R. Fraser, J. E. Hobbie, D. M. Karl, S. E. Kingsland, A. Knapp, E. B. Rastetter, T. Seastedt, G. R. Shaver, and R. B. Waide. 2021. Sustaining Long-Term Ecological Research: Perspectives from Inside the LTER Program. Pages 81 - 116 in R. B. Waide and S. E. Kingsland, editors. *The Challenges of Long Term Ecological Research: A Historical Analysis*. Springer International Publishing, Cham, Switzerland.
- Asbjornsen, H., J. L. Campbell, K. A. Jennings, M. A. Vadeboncoeur, C. McIntire, P. H. Templer, R. P. Phillips, T. L. Bauerle, M. C. Dietze, S. D. Frey, P. M. Groffman, R. Guerrieri, P. J. Hanson, E. P. Kelsey, A. K. Knapp, N. G. McDowell, P. Meir, K. A. Novick, S. V. Ollinger, W. T. Pockman, P. G. Schaberg, S. D. Wullschleger, M. D. Smith, and L. E. Rustad. 2018. Guidelines and considerations for designing field experiments simulating precipitation extremes in forest ecosystems. *Methods in Ecology and Evolution* 9:2310-2325.
- Atkins, J. W., B. Bond-Lamberty, R. T. Fahey, L. T. Haber, E. Stuart-Haëntjens, B. S. Hardiman, E. LaRue, B. E. McNeil, D. A. Orwig, A. E. Stovall, and J. M. Tallant. 2020. Application of multidimensional structural characterization to detect and describe moderate forest disturbance. *Ecosphere* 11:e03156.
- Ayres, M. P., and M. J. Lombardero. 2018. Forest pests and their management in the Anthropocene. *Canadian Journal of Forest Research* 48:292-301.
- Baatz, R., P. L. Sullivan, L. Li, S. R. Weintraub, H. W. Loescher, M. Mirtl, P. M. Groffman, D. H. Wall, M. Young, T. White, H. Wen, S. Zacharias, I. Kühn, J. Tang, J. Gaillardet, I. Braud, A. N. Flores, P. Kumar, H. Lin, T. Ghezzehei, J. Jones, H. L. Gholz, H. Vereecken, and K. Van Looy. 2018. Steering operational synergies in terrestrial observation networks: opportunity for advancing Earth system dynamics modelling. *Earth Systems Dynamics* 9:593-609.
- Bae, K., T. J. Fahey, R. D. Yanai, and M. Fisk. 2015. Soil nitrogen availability affects belowground carbon allocation and soil respiration in northern hardwood forests of New Hampshire. *Ecosystems* 18:1179-1191.
- Bahlai, C. A., C. Hart, M. T. Kavanaugh, J. D. White, R. W. Ruess, T. J. Brinkman, H. W. Ducklow, D. R. Foster, W. R. Fraser, H. Genet, P. M. Groffman, S. K. Hamilton, J. F. Johnstone, K. Kielland, D. A. Landis, M. C. Mack, O. Sarnelle, and J. R. Thompson. 2021. Cascading effects: insights from the U.S. Long Term Ecological Research Network. *Ecosphere* 12:ecs2.3430.
- Bailey, A. S., J. W. Hornbeck, J. L. Campbell, and C. Eagar. 2003. Hydrometeorological database for Hubbard Brook Experimental Forest: 1955-2000. General Technical Report NE-305. U.S. Department of Agriculture, Forest Service, Newtown Square, PA.
- Bailey, S. W. 2020. Tracking the fate of plagioclase weathering products: pedogenic and human influences. Pages 151-162 in K. Dontsova, Z. Balogh-Brunstad, and G. Le Roux, editors. *Biogeochemical Cycles: Ecological Drivers and Environmental Impact*. American Geophysical Union/John Wiley & Sons, Hoboken, NJ.
- Bailey, S. W., P. A. Brousseau, K. J. McGuire, and D. S. Ross. 2014. Influence of landscape position and transient water table on soil development and carbon distribution in a steep, headwater catchment. *Geoderma* 226:279-289.
- Bailey, S. W., K. J. McGuire, D. S. Ross, M. B. Green, and O. L. Fraser. 2019. Mineral weathering and podzolization control acid neutralization and streamwater chemistry gradients in upland glaciated catchments, northeastern United States. *Frontiers in Earth Science* 7:2296-6463.

- Battles, J. J., N. L. Cleavitt, D. S. Saah, B. T. Poling, and T. J. Fahey. 2017. Ecological impact of a microburst windstorm in a northern hardwood forest. *Canadian Journal of Forest Research* 47:1695-1701.
- Battles, J. J., T. J. Fahey, C. T. Driscoll, Jr., J. D. Blum, and C. E. Johnson. 2014. Restoring soil calcium reverses forest decline. *Environmental Science & Technology Letters* 1:15-19.
- Bayer, M. O., and W. H. Lowe. 2021. Top-down effects of salamanders on macroinvertebrates in fishless headwater streams. *Herpetologica* 77:111-120.
- Bayer, M. O., L. K. Swartz, and W. H. Lowe. 2021. Predictors of biofilm biomass in oligotrophic headwater streams. *Northeastern Naturalist* 28:28-48.
- Bechtold, H. A., E. J. Rosi, D. R. Warren, and W. S. Keeton. 2016. Forest age influences in-stream ecosystem processes in northeastern US. *Ecosystems* 20:1058-1071.
- Belyazid, S., J. Phelan, B. Nihlgård, H. Sverdrup, C. Driscoll, I. Fernandez, J. Aherne, L. M. Teeling-Adams, S. Bailey, M. Arsenault, N. Cleavitt, B. Engstrom, R. Dennis, D. Sperduto, D. Werier, and C. Clark. 2019. Assessing the effects of climate change and air pollution on soil properties and plant diversity in northeastern U.S. hardwood forests: Model setup and evaluation. *Water, Air, & Soil Pollution* 230:106.
- Benettin, P., S. W. Bailey, J. L. Campbell, M. B. Green, A. Rinaldo, G. E. Likens, K. J. McGuire, and G. Botter. 2015. Linking water age and solute dynamics in streamflow at the Hubbard Brook Experimental Forest, NH, USA. *Water Resources Research* 51:9256-9272.
- Bernal, S., L. O. Hedin, G. E. Likens, S. Gerber, and D. C. Buso. 2012. Complex response of the forest nitrogen cycle to climate change. *Proceedings of the National Academy of Sciences* 109:3406-3411.
- Bernhardt, E. S., J. R. Blaszczak, C. D. Ficken, M. L. Fork, K. E. Kaiser, and E. C. Seybold. 2017. Control points in ecosystems: Moving beyond the hot spot hot moment concept. *Ecosystems* 20:665-682.
- Berry, E. J., and N. L. Cleavitt. 2021. Population dynamics and comparative demographics in sympatric populations of the round-leaved orchids *Platanthera macrophylla* and *P. orbiculata*. *Population Ecology* 63:274-289.
- Besley, J. C. 2020. Five thoughts about improving science communication as an organizational activity. *Journal of Communication Management* 24:155-161.
- Besley, J. C., S. Garlick, K. Fallon Lambert, and L. A. Tiffany. 2021. The role of communication professionals in fostering a culture of public engagement. *International Journal of Science Education, Part B* 11:225-241.
- Bianchi, T. S., M. Anand, C. T. Bauch, D. E. Canfield, L. De Meester, K. Fennel, P. M. Groffman, M. L. Pace, M. Saito, and M. J. Simpson. 2021. Ideas and perspectives: Biogeochemistry – some key foci for the future. *Biogeosciences* 18:3005-3013.
- Blagden, M., J. L. Harrison, R. Minocha, R. Sanders-DeMott, S. Long, and P. H. Templer. 2022. Climate change influences foliar nutrition and metabolism of red maple (*Acer rubrum*) trees in a northern hardwood forest. *Ecosphere* 13:e03859.
- Bohlen, P. J., P. M. Groffman, C. T. Driscoll, T. J. Fahey, and T. G. Siccama. 2001. Plant-soil-microbial interactions in a northern hardwood forest. *Ecology* 82:965-978.
- Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, P. B. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, L. Biederman, D. Blumenthal, C. S. Brown, L. A. Brudvig, Y. M. Buckley, M. Cadotte, C. Chu, E. E. Cleland, M. J. Crawley, P. Daleo, E. I. Damschen, K. F. Davies, N. M. DeCrappeo, G. Du, J. Firn, Y. Hautier, R. W. Heckman, A. Hector, J. HilleRisLambers, O. Iribarne, J. A. Klein, J. M. H. Knops, K. J. La Pierre, A. D. B. Leakey, W. Li, A. S. MacDougall, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, B. Mortensen, L. R. O'Halloran, J. L. Orrock, J. Pascual, S. M. Prober, D. A. Pyke, A. C. Risch, M. Schuetz, M. D. Smith, C. J. Stevens, L. L. Sullivan, R. J. Williams, P. D. Wragg, J. P. Wright, and L. H. Yang. 2014. Herbivores and nutrients control grassland plant diversity

via light limitation. *Nature* 508:517-520.

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

Botter, G., F. Vingiani, A. Senatore, C. Jensen, M. Weiler, K. McGuire, G. Mendicino, and N. Durighetto. 2021. Hierarchical climate-driven dynamics of the active channel length in temporary streams. *Scientific Reports* 11:21503.

Bourgault, R. R., D. S. Ross, S. W. Bailey, T. D. Bullen, K. J. McGuire, and J. P. Gannon. 2017. Redistribution of soil metals and organic carbon via lateral flowpaths at the catchment scale in a glaciated upland setting. *Geoderma* 307:238-252.

Burgess, S. S. O., M. A. Adams, N. C. Turner, C. R. Beverly, C. K. Ong, A. A. H. Khan, and T. M. Bleby. 2001. An improved heat pulse method to measure low and reverse rates of sap flow in woody plants†. *Tree Physiology* 21:589-598.

Campbell, J. L., E. Boose, C. T. Driscoll, H. A. Dugan, P. M. Groffman, C. R. Jackson, J. B. Jones, J. A. Jones, G. P. Juday, N. R. Lottig, B. E. Penaluna, R. W. Ruess, K. N. Suding, J. R. Thompson, and J. K. Zimmerman. 2022. Forests and freshwater ecosystem responses to climate change and variability at US LTER sites. *BioScience* In press.

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

Campbell, J. L., C. T. Driscoll, A. Pourmokhtarian, and K. Hayhoe. 2011. Streamflow responses to past and projected future changes in climate at the Hubbard Brook Experimental Forest, New Hampshire, United States. *Water Resources Research* 47: W02514.

Campbell, J. L., L. E. Rustad, S. W. Bailey, E. S. Bernhardt, C. T. Driscoll, M. B. Green, P. M. Groffman, G. M. Lovett, W. H. McDowell, K. J. McGuire, and E. J. Rosi. 2021. Watershed studies at the Hubbard Brook Experimental Forest: Building on a long legacy of research with new approaches and sources of data. *Hydrological Processes* e14016.

Campbell, J. L., L. E. Rustad, C. T. Driscoll, I. Halm, T. J. Fahey, H. Fakhraei, P. M. Groffman, G. J. Hawley, W. Leuenberger, and P. G. Schaberg. 2020. Simulating Impacts of Ice Storms on Forest Ecosystems. *Journal of Visualized Experiments (JOVE)* 160:e61492.

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

Campbell, J. L., R. D. Yanai, M. B. Green, G. E. Likens, C. R. See, A. S. Bailey, D. C. Buso, and D. Yang. 2016. Uncertainty in the net hydrologic flux of calcium in a paired-watershed harvesting study. *Ecosphere* 7:e01299.

Casson, N. J., A. R. Contosta, E. A. Burakowski, J. L. Campbell, M. S. Crandall, I. F. Creed, M. C. Eimers, S. Garlick, D. A. Lutz, M. Q. Morison, A. T. Morzillo, and S. J. Nelson. 2019. Winter weather whiplash: Impacts of meteorological events misaligned with natural and human systems in seasonally snow-covered regions. *Earth's Future* 7:1434-1450.

Chandler, D. S., and K. A. Hamilton. 2017. Biodiversity and ecology of the leafhoppers (Hemiptera: Cicadellidae) of New Hampshire. *Transactions of the American Entomological Society* 143.

Cheng, S. J., P. G. Hess, W. R. Wieder, R. Q. Thomas, K. J. Nadelhoffer, J. Vira, D. L. Lombardozzi, P. Gundersen, I. J. Fernandez, P. Schleppi, M. C. Gruselle, F. Moldan, and C. L. Goodale. 2019. Decadal fates and impacts of nitrogen additions on temperate forest carbon storage: a data-model comparison. *Biogeosciences* 16:2771-2793.

Cho, Y., C. T. Driscoll, C. E. Johnson, J. D. Blum, and T. J. Fahey. 2012. Watershed-level responses to

calcium silicate treatment in a northern hardwood forest. *Ecosystems* 15:416-434.

Christenson, L., H. Clark, L. Livingston, E. Heffernan, J. Campbell, C. Driscoll, P. Groffman, T. Fahey, M. Fisk, M. Mitchell, and P. H. Templer. 2017. Winter climate change influences on soil faunal distribution and abundance: implications for decomposition in the northern forest. *Northeastern Naturalist* 24.

Clark, J. S., R. Andrus, M. Aubry-Kientz, Y. Bergeron, M. Bogdziewicz, D. C. Bragg, D. Brockway, N. L. Cleavitt, S. Cohen, B. Courbaud, R. Daley, A. J. Das, M. Dietze, T. J. Fahey, I. Fer, J. F. Franklin, C. A. Gehring, G. S. Gilbert, C. H. Greenberg, Q. Guo, J. Hillerislambers, I. Ibanez, J. Johnstone, C. L. Kilner, J. Knops, W. D. Koenig, G. Kunstler, J. M. Lamontagne, K. L. Legg, J. Luongo, J. A. Lutz, D. Macias, E. J. B. McIntire, Y. Messaoud, C. M. Moore, E. Moran, J. A. Myers, O. B. Myers, C. Nunez, R. Parmenter, S. Pearse, S. Pearson, R. Poulton-Kamakura, E. Ready, M. D. Redmond, C. D. Reid, K. C. Rodman, C. L. Scher, W. H. Schlesinger, A. M. Schwantes, E. Shanahan, S. Sharma, M. A. Steele, N. L. Stephenson, S. Sutton, J. J. Swenson, M. Swift, T. T. Veblen, A. V. Whipple, T. G. Whitham, A. P. Wion, K. Zhu, and R. Zlotin. 2021. Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications* 12:1242.

Cleavitt, N. L., J. J. Battles, T. J. Fahey, and N. S. Doorn. 2021. Disruption of the competitive balance between foundational tree species by interacting stressors in a temperate deciduous forest. *Journal of Ecology* 109:2754-2768.

Cleavitt, N. L., J. J. Battles, C. E. Johnson, and T. J. Fahey. 2018. Long-term decline of sugar maple following forest harvest, Hubbard Brook Experimental Forest, New Hampshire. *Canadian Journal of Forest Research* 48:23-31.

Cleavitt, N. L., E. J. Berry, J. Hautaniemi, and T. J. Fahey. 2017. Life stages, demographic rates, and leaf damage for the round-leaved orchids, *Platanthera orbiculata* (Pursh.) Lindley and *P. macrophylla* (Goldie) P.M. Brown in a northern hardwood forest in New Hampshire, USA. *Botany* 95:61-71.

Cleavitt, N. L., A. B. Clyne, and T. J. Fahey. 2019. Epiphytic macrolichen patterns along an elevation gradient in the White Mountain National Forest, New Hampshire. *The Journal of the Torrey Botanical Society* 146:8-17.

Cleavitt, N. L., and T. J. Fahey. 2017. Seed production of sugar maple and American beech in northern hardwood forests, New Hampshire, USA. *Canadian Journal of Forest Research* 47:985-990.

Clyne, A. B., N. L. Cleavitt, and T. J. Fahey. 2019. Terrestrial gastropod grazing on macrolichens in a northern broadleaf-conifer forest. *Northeastern Naturalist* 26.

Contosta, A. R., A. Adolph, D. Burchsted, E. Burakowski, M. Green, D. Guerra, M. Albert, J. Dibb, M. Martin, W. H. McDowell, M. Routhier, C. Wake, R. Whitaker, and W. Wollheim. 2017. A longer vernal window: the role of winter coldness and snowpack in driving spring transitions and lags. *Global Change Biology* 23:1610-1625.

Contosta, A. R., J. J. Battles, J. L. Campbell, C. T. Driscoll, S. R. Garlick, M. B. Green, R. T. Holmes, G. E. Likens, N. L. Rodenhouse, S. Rogers, P. H. Templer, M. A. Vadeboncoeur, and P. M. Groffman. 2022. Early warning signals of change suggest declining resilience in the biology and biogeochemistry of a northern hardwood forest. *Nature Communications* In revision.

Contosta, A. R., N. J. Casson, S. Garlick, S. J. Nelson, M. P. Ayres, E. A. Burakowski, J. Campbell, I. Creed, C. Eimers, C. Evans, I. Fernandez, C. Fuss, T. Huntington, K. Patel, R. Sanders-DeMott, K. Son, P. Templer, and C. Thornbrugh. 2019. Northern forest winters have lost cold, snowy conditions that are important for ecosystems and human communities. *Ecological Applications* 29:e01974.

Cowles, J., L. Templeton, J. J. Battles, P. J. Edmunds, R. C. Carpenter, S. R. Carpenter, M. Paul Nelson, N. L. Cleavitt, T. J. Fahey, P. M. Groffman, J. H. Sullivan, M. C. Neel, G. J. A. Hansen, S. Hobbie, S. J. Holbrook, C. E. Kazanski, E. W. Seabloom, R. J. Schmitt, E. H. Stanley, A. J. Tepley, N. S. Doorn, and J. M. Vander Zanden. 2021. Resilience: insights from the U.S. LongTerm Ecological Research Network. *Ecosphere* 12:ecs2.3434.

Craine, J. M., A. J. Elmore, L. Wang, J. Aranibar, M. Bauters, P. Boeckx, B. E. Crowley, M. A. Dawes, S. Delzon, A. Fajardo, Y. Fang, L. Fujiyoshi, A. Gray, R. Guerrieri, M. J. Gundale, D. J. Hawke, P. Hietz, M. Jonard, E. Kearsley, T. Kenzo, M. Makarov, S. Maranon-Jimenez, T. P. McGlynn, B. E. McNeil, S. G. Mosher, D. M. Nelson, P. L. Peri, J. C. Roggy, R. Sanders-DeMott, M. Song, P. Szpak, P. H. Templer, D. Van der Colff, C. Werner, X. Xu, Y. Yang, G. Yu, and K. Zmudczynska-Skarbek. 2018. Isotopic evidence for oligotrophication of terrestrial ecosystems. *Nature Ecology & Evolution* 2:1735-1744.

Cramer, E. R. A., E. I. Greig, and S. A. Kaiser. 2020a. Strong sexual selection despite spatial constraints on extrapair paternity. *Behavioral Ecology* 31:618-626.

Cramer, E. R. A., S. A. Kaiser, M. S. Webster, and T. B. Ryder. 2020b. Common field data limitations can substantially bias sexual selection metrics. *The American Naturalist* 196:180-196.

Cramer, E. R. A., S. A. Kaiser, M. S. Webster, T. S. Sillett, and T. B. Ryder. 2017. Characterizing selection in black-throated blue warblers using a sexual network approach. *Journal of Evolutionary Biology* 30:2177-2188.

Crowley, K. F., and G. M. Lovett. 2017. Effects of nitrogen deposition on nitrate leaching from forests of the northeastern United States will change with tree species composition. *Canadian Journal of Forest Research* 47:997-1009.

Crowley, K. F., G. M. Lovett, M. A. Arthur, and K. C. Weathers. 2016. Long-term effects of pest-induced tree species change on carbon and nitrogen cycling in northeastern U.S. forests: A modeling analysis. *Forest Ecology and Management* 372:269-290.

Danneyrolles, V., S. Dupuis, G. Fortin, M. Leroyer, A. De Römer, R. Terrail, M. Vellend, Y. Boucher, J. Laflamme, Y. Bergeron, and D. Arseneault. 2019. Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. *Nature Communications* 10:1265.

Darby, B. A., C. L. Goodale, N. A. Chin, C. B. Fuss, A. K. Lang, S. V. Ollinger, and G. M. Lovett. 2020. Depth patterns and connections between gross nitrogen cycling and soil exoenzyme activities in three northern hardwood forests. *Soil Biology and Biochemistry* 147:107836.

Davenport, J. M., and W. H. Lowe. 2018. Testing for microgeographic effects on the strength of interspecific competition. *Copeia* 106:501-506.

Doser, J., W. Leuenberger, S. Sillett, M. Hallworth, and E. Zipkin. 2021. Integrated community occupancy models: A framework to assess occurrence and biodiversity dynamics using multiple data sources. *arXiv* 2109:01894.

Driscoll, C., D. Whitall, J. Aber, E. Boyer, M. Castro, C. Cronan, C. Goodale, P. Groffman, C. Hopkinson, K. Lambert, G. Lawrence, and S. Ollinger. 2003. Nitrogen pollution: Sources and consequences in the US northeast. *Environment* 45:9-22.

Driscoll, C. T., J. J. Buonocore, J. I. Levy, K. F. Lambert, D. Burtraw, S. B. Reid, H. Fakhraei, and J. Schwartz. 2015. US power plant carbon standards and clean air and health co-benefits. *Nature Climate Change* 5:535-540.

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

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

Driscoll, C. T., G. B. Lawrence, A. J. Bulger, T. J. Butler, C. S. Cronan, C. Eagar, K. F. Lambert, G. E. Likens, J. L. Stoddard, and K. C. Weathers. 2001. Acidic deposition in the northeastern United States: Sources and inputs, ecosystem effects, and management strategies. *BioScience* 51:180-198.

Duveneck, M. J., and J. R. Thompson. 2017. Climate change imposes phenological trade-offs on forest

net primary productivity. *Journal of Geophysical Research: Biogeosciences* 122:2298-2313.

Elmore, A. J., D. M. Nelson, and J. M. Craine. 2016. Earlier springs are causing reduced nitrogen availability in North American eastern deciduous forests. *Nat Plants* 2:16133.

Fahey, R. T., J. W. Atkins, J. L. Campbell, L. E. Rustad, M. Duffy, C. T. Driscoll, T. J. Fahey, and P. G. Schaberg. 2020. Effects of an experimental ice storm on forest canopy structure. *Canadian Journal of Forest Research* 50:136-145.

Fahey, T. J., A. K. Heinz, J. J. Battles, M. C. Fisk, C. T. Driscoll, J. D. Blum, and C. E. Johnson. 2016. Fine root biomass declined in response to restoration of soil calcium in a northern hardwood forest. *Canadian Journal of Forest Research* 46:738-744.

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

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

Forester, B. R., J. R. Lasky, H. H. Wagner, and D. L. Urban. 2018. Comparing methods for detecting multilocus adaptation with multivariate genotype–environment associations. *Molecular Ecology* 27:2215-2233.

Fraser, O. L., S. W. Bailey, M. J. Ducey, and K. J. McGuire. 2020. Predictive modeling of bedrock outcrops and associated shallow soil in upland glaciated landscapes. *Geoderma* 376:114495.

Friedlingstein, P., M. O'Sullivan, M. W. Jones, R. M. Andrew, J. Hauck, A. Olsen, G. P. Peters, W. Peters, J. Pongratz, S. Sitch, C. Le Quéré, J. G. Canadell, P. Ciais, R. B. Jackson, S. Alin, L. E. O. C. Aragão, A. Arneeth, V. Arora, N. R. Bates, M. Becker, A. Benoit-Cattin, H. C. Bittig, L. Bopp, S. Bultan, N. Chandra, F. Chevallier, L. P. Chini, W. Evans, L. Florentie, P. M. Forster, T. Gasser, M. Gehlen, D. Gilfillan, T. Gkritzalis, L. Gregor, N. Gruber, I. Harris, K. Hartung, V. Haverd, R. A. Houghton, T. Ilyina, A. K. Jain, E. Joetzjer, K. Kadono, E. Kato, V. Kitidis, J. I. Korsbakken, P. Landschützer, N. Lefèvre, A. Lenton, S. Lienert, Z. Liu, D. Lombardozzi, G. Marland, N. Metz, D. R. Munro, J. E. M. S. Nabel, S.-I. Nakaoka, Y. Niwa, K. O'Brien, T. Ono, P. I. Palmer, D. Pierrot, B. Poulter, L. Resplandy, E. Robertson, C. Rödenbeck, J. Schwinger, R. Séférian, I. Skjelvan, A. J. P. Smith, A. J. Sutton, T. Tanhua, P. P. Tans, H. Tian, B. Tilbrook, G. van der Werf, N. Vuichard, A. P. Walker, R. Wanninkhof, A. J. Watson, D. Willis, A. J. Wiltshire, W. Yuan, X. Yue, and S. Zaehle. 2020. Global Carbon Budget 2020. *Earth System Science Data* 12:3269-3340.

Fuss, C. B., C. T. Driscoll, and J. L. Campbell. 2015. Recovery from chronic and snowmelt acidification: Long-term trends in stream and soil water chemistry at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Journal of Geophysical Research: Biogeosciences* 120:2360-2374.

Fuss, C. B., C. T. Driscoll, M. B. Green, and P. M. Groffman. 2016. Hydrologic flowpaths during snowmelt in forested headwater catchments under differing winter climatic and soil frost regimes. *Hydrological Processes* 30:4617-4632.

Fuss, C. B., G. M. Lovett, C. L. Goodale, S. V. Ollinger, A. K. Lang, and A. P. Ouimette. 2019. Retention of nitrate-N in mineral soil organic matter in different forest age classes. *Ecosystems* 22:1280-1294.

Gaiser, E. E., D. M. Bell, M. C. N. Castorani, D. L. Childers, P. M. Groffman, C. R. Jackson, J. S. Kominoski, D. P. C. Peters, S. T. A. Pickett, J. Ripplinger, and J. C. Zinnert. 2020. Long-term ecological research and evolving frameworks of disturbance ecology. *BioScience* 70:141-156.

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

- Gannon, J. P., S. W. Bailey, K. J. McGuire, and J. B. Shanley. 2015. Flushing of distal hillslopes as an alternative source of stream dissolved organic carbon in a headwater catchment. *Water Resources Research* 51:8114-8128.
- Gannon, J. P., K. J. McGuire, S. W. Bailey, R. R. Bourgault, and D. S. Ross. 2017. Lateral water flux in the unsaturated zone: A mechanism for the formation of spatial soil heterogeneity in a headwater catchment. *Hydrological Processes* 31:3568-3579.
- Garcia, M. O., P. H. Templer, P. O. Sorensen, R. Sanders-DeMott, P. M. Groffman, and J. M. Bhatnagar. 2020. Soil microbes trade-off biogeochemical cycling for stress tolerance traits in response to year-round climate change. *Frontiers in Microbiology* 11:616.
- Garlick, S., and K. F. Lambert. 2022. The ECO framework: Advancing evidence-based science engagement within environmental research programs and organizations. *BioScience* Submitted 23 Nov 2021.
- Germain, R. R., M. T. Hallworth, S. A. Kaiser, T. S. Sillett, and M. S. Webster. 2021. Variance in within-pair reproductive success influences the opportunity for selection annually and over the lifetimes of males in a multibrooded songbird. *Evolution* 75:915-930.
- Gilliam, F. S., D. A. Burns, C. T. Driscoll, S. D. Frey, G. M. Lovett, and S. A. Watmough. 2019. Decreased atmospheric nitrogen deposition in eastern North America: Predicted responses of forest ecosystems. *Environmental Pollution* 244:560-574.
- Gillin, C. P., S. W. Bailey, K. J. McGuire, and J. P. Gannon. 2015. Mapping of hydrogeologic spatial patterns in a steep headwater catchment. *Soil Science Society of America Journal* 79:440-453.
- Gonzales, K., and R. Yanai. 2019. Nitrogen–phosphorous interactions in young northern hardwoods indicate P limitation: foliar concentrations and resorption in a factorial N by P addition experiment. *Oecologia* 189:829-840.
- Goodale, C. L. 2017. Multiyear fate of a (15) N tracer in a mixed deciduous forest: retention, redistribution, and differences by mycorrhizal association. *Global Change Biology* 23:867-880.
- Goswami, S., M. C. Fisk, M. A. Vadeboncoeur, M. Garrison-Johnston, R. D. Yanai, and T. J. Fahey. 2018. Phosphorus limitation of aboveground production in northern hardwood forests. *Ecology* 99:438-449.
- Green, M. B., A. S. Bailey, S. W. Bailey, J. J. Battles, J. L. Campbell, C. T. Driscoll, T. J. Fahey, L. C. Lepine, G. E. Likens, S. V. Ollinger, and P. G. Schaberg. 2013. Decreased water flowing from a forest amended with calcium silicate. *Proceedings of the National Academy of Sciences* 110:5999-6003.
- Green, M. B., S. W. Bailey, J. L. Campbell, K. J. McGuire, A. S. Bailey, T. J. Fahey, N. Lany, and D. Zietlow. 2021. A catchment water balance assessment of an abrupt shift in evapotranspiration at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Hydrological Processes* 35: DOI: 10.1002/hyp.14300.
- Green, M. B., B. K. Laursen, J. L. Campbell, K. J. McGuire, and E. P. Kelsey. 2015. Stable water isotopes suggest sub-canopy water recycling in a northern forested catchment. *Hydrological Processes* 29:5193-5202.
- Groffman, P., J. Baron, T. Blett, A. Gold, I. Goodman, L. Gunderson, B. Levinson, M. Palmer, H. Paerl, G. Peterson, N. Poff, D. Rejeski, J. Reynolds, M. Turner, K. Weathers, and J. Wiens. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? *Ecosystems* 9:1-13.
- Groffman, P. M. 2019. Forest soil:atmosphere fluxes of carbon dioxide, nitrous oxide and methane at the Hubbard Brook Experimental Forest, 1997- present ver 11. Environmental Data Initiative. <https://doi.org/10.6073/pasta/0d29c499a4fafa36e32a6d1e0e6b1d6d> (Accessed 2021-12-01).
- Groffman, P. M., C. T. Driscoll, J. Duran, J. L. Campbell, L. M. Christenson, T. J. Fahey, M. C. Fisk, C. Fuss, G. E. Likens, G. M. Lovett, L. Rustad, and P. Templer. 2018. Nitrogen oligotrophication in northern

hardwood forests. *Biogeochemistry* 141:123-129.

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

Grogan, D. S., E. A. Burakowski, and A. R. Contosta. 2020. Snowmelt control on spring hydrology declines as the vernal window lengthens. *Environmental Research Letters* 15:114040.

Harms, T. K., P. M. Groffman, L. Aluwihare, C. Craft, W. R. Wieder, S. E. Hobbie, S. G. Baer, J. M. Blair, S. Frey, C. K. Remucal, J. A. Rudgers, and S. L. Collins. 2021. Patterns and trends of organic matter processing and transport: Insights from the US Long-Term Ecological Research network. *Climate Change Ecology*:100025.

Harpole, W. S., J. T. Ngai, E. E. Cleland, E. W. Seabloom, E. T. Borer, M. E. Bracken, J. J. Elser, D. S. Gruner, H. Hillebrand, and J. B. Shurin. 2011. Nutrient co-limitation of primary producer communities. *Ecology Letters* 14:852-862.

Harris, J. E., N. L. Rodenhouse, and R. T. Holmes. 2019. Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. *Biological Conservation* 240.

Harrison, J. L., R. Sanders-Demott, A. B. Reinmann, P. O. Sorensen, N. G. Phillips, and P. H. Templer. 2020. Growing-season warming and winter soil freeze/thaw cycles increase transpiration in a northern hardwood forest. *Ecology* 101:e03173.

Hayhoe, K., C. Wake, B. Anderson, X. Z. Liang, E. Maurer, J. Zhu, J. Bradbury, A. Degaetano, A. M. Stoner, and D. Wuebbles. 2008. Regional climate change projections for the Northeast USA. *Mitigation and Adaptation Strategies for Global Change* 13:425-436.

Hernandez-Santana, V., A. Hernandez-Hernandez, M. A. Vadeboncoeur, and H. Asbjornsen. 2015. Scaling from single-point sap velocity measurements to stand transpiration in a multispecies deciduous forest: uncertainty sources, stand structure effect, and future scenarios. *Canadian Journal of Forest Research* 45:1489-1497.

Hewlett, J. D., and A. R. Hibbert. 1967. Factors affecting the response of small watersheds to precipitation in humid areas. Pages 275-290 in W. E. Soper and H. W. Lull, editors. *International Symposium on Forest Hydrology* Pergamon Press, New York.

Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1-23.

Holmes, R. T., and G. E. Likens. 2016. *Hubbard Brook: The Story of a Forest Ecosystem*. Yale University Press.

Iwaniec, D. M., M. Gooseff, K. N. Suding, D. Samuel Johnson, D. C. Reed, D. P. C. Peters, B. Adams, J. E. Barrett, B. T. Bestelmeyer, M. C. N. Castorani, E. M. Cook, M. J. Davidson, P. M. Groffman, N. P. Hanan, L. F. Huenneke, P. T. J. Johnson, D. M. McKnight, R. J. Miller, G. S. Okin, D. L. Preston, A. Rassweiler, C. Ray, O. E. Sala, R. L. Schooley, T. Seastedt, M. J. Spasojevic, and E. R. Vivoni. 2021. Connectivity: insights from the U.S. Long Term Ecological Research Network. *Ecosphere* 12:ecs2.3432.

Jensen, C. K., K. J. McGuire, and P. S. Prince. 2017. Headwater stream length dynamics across four physiographic provinces of the Appalachian Highlands. *Hydrological Processes* 31:3350-3363.

Jensen, C. K., K. J. McGuire, Y. Shao, and C. Andrew Dolloff. 2018. Modeling wet headwater stream networks across multiple flow conditions in the Appalachian Highlands. *Earth Surface Processes and Landforms* 43:2762-2778.

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

Jonard, M., A. Furst, A. Verstraeten, A. Thimonier, V. Timmermann, N. Potocic, P. Waldner, S. Benham,

- K. Hansen, P. Merila, Q. Ponette, A. C. de la Cruz, P. Roskams, M. Nicolas, L. Croise, M. Ingerslev, G. Matteucci, B. Decinti, M. Bascietto, and P. Rautio. 2015. Tree mineral nutrition is deteriorating in Europe. *Global Change Biology* 21:418-430.
- Jones, J. A., P. M. Groffman, J. Blair, F. W. Davis, H. Dugan, E. E. Euskirchen, S. D. Frey, T. K. Harms, E. Hinckley, M. Kosmala, S. Loberg, S. Malone, K. Novick, S. Record, A. V. Rocha, B. L. Ruddell, E. H. Stanley, C. Sturtevant, A. Thorpe, T. White, W. R. Wieder, L. Zhai, and K. Zhu. 2021. Synergies among environmental science research and monitoring networks: A research agenda. *Earth's Future* 9:e2020EF001631.
- Juice, S. M., T. J. Fahey, T. G. Siccama, C. T. Driscoll, E. G. Denny, C. Eagar, N. L. Cleavitt, R. Minocha, and A. D. Richardson. 2006. Response of sugar maple to calcium addition to northern hardwood forest. *Ecology* 87:1267-1280.
- Kaiser, S. A., B. B. Risk, T. S. Sillett, and M. S. Webster. 2017. Ecological and social factors constrain spatial and temporal opportunities for mating in a migratory songbird. *The American Naturalist* 189:283-296.
- Kosiba, A. M., P. G. Schaberg, S. A. Rayback, and G. J. Hawley. 2017. Comparative growth trends of five northern hardwood and montane tree species reveal divergent trajectories and response to climate. *Canadian Journal of Forest Research* 47:743-754.
- Kosiba, A. M., P. G. Schaberg, S. A. Rayback, and G. J. Hawley. 2018. The surprising recovery of red spruce growth shows links to decreased acid deposition and elevated temperature. *Science of The Total Environment* 637-638:1480-1491.
- Kou, D., G. Yang, F. Li, X. Feng, D. Zhang, C. Mao, Q. Zhang, Y. Peng, C. Ji, Q. Zhu, Y. Fang, X. Liu, R. Xu, S. Li, J. Deng, X. Zheng, J. Fang, and Y. Yang. 2020. Progressive nitrogen limitation across the Tibetan alpine permafrost region. *Nature Communications* 11:3331.
- Lang, A. K., F. V. Jevon, M. P. Ayres, and J. Hatala Matthes. 2019. Higher soil respiration rate beneath arbuscular mycorrhizal trees in a northern hardwood forest is driven by associated soil properties. *Ecosystems* 23:1243-1253.
- Lany, N. K., M. P. Ayres, E. E. Stange, T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes. 2016. Breeding timed to maximize reproductive success for a migratory songbird: the importance of phenological asynchrony. *Oikos* 125:656-666.
- Leuenberger, W., J. B. Cohen, L. Rustad, K. F. Wallin, and D. Parry. 2021. Short-term increase in abundance of foliage-gleaning insectivorous birds following experimental ice storms in a northern hardwood forest. *Frontiers in Forests and Global Change* 3 DOI:10.3389/ffgc.2020.566376.
- Likens, G. E. 2019. Unusual sequence of ice cover formation on Mirror Lake, New Hampshire, USA. *Inland Waters* 9:408-410.
- Likens, G. E., F. H. Bormann, R. S. Pierce, J. S. Eaton, and N. M. Johnson. 1977. *Biogeochemistry of a Forested Ecosystem*. Springer-Verlag, Inc., New York.
- Likens, G. E., D. C. Buso, E. S. Bernhardt, and E. Rosi. 2021. A century of change: Reconstructing the biogeochemical history of Hubbard Brook. *Hydrological Processes* 35:e14256.
- Likens, G. E., C. T. Driscoll, D. C. Buso, M. J. Mitchell, G. M. Lovett, S. W. Bailey, T. G. Siccama, W. A. Reiners, and C. Alewell. 2002. The biogeochemistry of sulfur at Hubbard Brook. *Biogeochemistry* 60:235-316.
- Likens, G. E., C. T. Driscoll, D. C. Buso, T. G. Siccama, C. E. Johnson, G. M. Lovett, T. J. Fahey, W. A. Reiners, D. F. Ryan, C. W. Martin, and S. W. Bailey. 1998. The biogeochemistry of calcium at Hubbard Brook. *Biogeochemistry* 41:89-173.
- Likens, G. E., C. T. Driscoll, D. C. Buso, T. G. Siccama, C. E. Johnson, G. M. Lovett, D. F. Ryan, T. Fahey, and W. A. Reiners. 1994. The biogeochemistry of potassium at Hubbard Brook. *Biogeochemistry*

25:61-125.

LoRusso, N. A., S. W. Bailey, T. Zeng, M. Montesdeoca, and C. T. Driscoll. 2021. Dissolved organic matter dynamics in reference and calcium silicate-treated watersheds at Hubbard Brook Experimental Forest, NH, USA. *Journal of Geophysical Research: Biogeosciences* 126:e2021JG006352.

Lovett, G. M., M. A. Arthur, and K. F. Crowley. 2016a. Effects of calcium on the rate and extent of litter decomposition in a northern hardwood forest. *Ecosystems* 19:87-97.

Lovett, G. M., C. L. Goodale, S. V. Ollinger, C. B. Fuss, A. P. Ouimette, and G. E. Likens. 2018. Nutrient retention during ecosystem succession: a revised conceptual model. *Frontiers in Ecology and the Environment* 16:532-538.

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

Lovett, G. M., M. Weiss, and K. F. Lambert. 2019. Forest pests and pathogens in the United States: Community impacts and opportunities for Tree-SMART Trade. Cary Institute of Ecosystem Studies and the Science Policy Exchange. Initial publication 2016; updated 2019. [www.caryinstitute.org/tree-smart-trade](http://www.caryinstitute.org/tree-smart-trade).

Lovett, G. M., M. Weiss, A. M. Liebhold, T. P. Holmes, B. Leung, K. F. Lambert, D. A. Orwig, F. T. Campbell, J. Rosenthal, D. G. McCullough, R. Wildova, M. P. Ayres, C. D. Canham, D. R. Foster, S. L. LaDeau, and T. Weldy. 2016b. Nonnative forest insects and pathogens in the United States: Impacts and policy options. *Ecological Applications* 26:1437-1455.

Lowe, W. H., and B. R. Addis. 2019. Matching habitat choice and plasticity contribute to phenotype-environment covariation in a stream salamander. *Ecology* 100:e02661.

Lowe, W. H., B. R. Addis, M. R. Smith, and J. M. Davenport. 2018. The spatial structure of variation in salamander survival, body condition and morphology in a headwater stream network. *Freshwater Biology* 63:1287-1299.

Lowe, W. H., T. E. Martin, D. K. Skelly, and H. A. Woods. 2021. Metamorphosis in an era of increasing climate variability. *Trends in Ecology & Evolution* 36:360-375.

Lowe, W. H., L. K. Swartz, B. R. Addis, and G. E. Likens. 2019. Hydrologic variability contributes to reduced survival through metamorphosis in a stream salamander. *Proceedings of the National Academy of Sciences* 116:19563 - 19570.

Madison, C. 2018. The Photosynthesis-Foliar Nitrogen Relationship in Deciduous and Evergreen Forest of New Hampshire. University of New Hampshire, ProQuest Dissertations Publishing.

Marinos, R. E., J. L. Campbell, C. T. Driscoll, G. E. Likens, W. H. McDowell, E. J. Rosi, L. E. Rustad, and E. S. Bernhardt. 2018. Give and take: A watershed acid rain mitigation experiment increases baseflow nitrogen retention but increases stormflow nitrogen export. *Environmental Science & Technology* 52:13155 - 13165.

Mason, R. E., J. M. Craine, N. K. Lany, M. Jonard, S. V. Ollinger, P. M. Groffman, R. W. Fulweiler, J. Angerer, Q. D. Read, P. B. Reich, P. H. Templer, and A. J. Elmore. 2022. Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. *Science* In press.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, E. Mayorga, W. H. McDowell, and G. Pinay. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6:301-312.

McDermott, A. 2021. News Feature: To understand the plight of insects, entomologists look to the past. *Proceedings of the National Academy of Sciences* 118:e2018499117.

McDonnell, T. C., G. J. Reinds, T. J. Sullivan, C. M. Clark, L. T. C. Bonten, J. P. Mol-Dijkstra, G. W. W. Wamelink, and M. Dovciak. 2018. Feasibility of coupled empirical and dynamic modeling to assess

climate change and air pollution impacts on temperate forest vegetation of the eastern United States. *Environmental Pollution* 234:902-914.

McGuire, K. J., and G. E. Likens. 2011. Historical roots of forest hydrology and biogeochemistry. Pages 3-26 in D. F. Levia, D. E. Carlyle-Moses, and T. Tanaka, editors. *Forest Hydrology and Biogeochemistry: Synthesis of Past Research and Future Directions*. Ecological Studies Series, No. 216, Part 1. Springer-Verlag, Heidelberg, Germany.

McLauchlan, K. K., L. M. Gerhart, J. J. Battles, J. M. Craine, A. J. Elmore, P. E. Higuera, M. C. Mack, B. E. McNeil, D. M. Nelson, N. Pederson, and S. S. Perakis. 2017. Centennial-scale reductions in nitrogen availability in temperate forests of the United States. *Scientific Reports* 7:7856.

Melaas, E. K., D. Sulla-Menashe, J. M. Gray, T. A. Black, T. H. Morin, A. D. Richardson, and M. A. Friedl. 2016. Multisite analysis of land surface phenology in North American temperate and boreal deciduous forests from Landsat. *Remote Sensing of Environment* 186:452-464.

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

Morse, J. L., J. Durán, and P. M. Groffman. 2015b. Denitrification and greenhouse gas fluxes in a northern hardwood forest: the importance of snowmelt and implications for ecosystem N budgets. *Ecosystems* 18:520-532.

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

Mulukutla, G. K., B. T. Godbois, and S. Frey. 2015. Deployment of a large-scale soil monitoring geosensor network. *SIGSPATIAL Special* 7:3-13.

Nelson, M. P., and P. M. Groffman. 2021. Climate change is already disrupting US forests and coasts – here's what we're seeing at 5 long-term research sites. *The Conversation*  
<https://theconversation.com/climate-change-is-already-disrupting-us-forests-and-coasts-heres-what-were-seeing-at-5-long-term-research-sites-164906>.

Nevison, C., C. Goodale, P. Hess, W. R. Wieder, J. Vira, and P. M. Groffman. 2022. Nitrification and denitrification in the Community Land Model compared to observations at Hubbard Brook Forest. *Ecological Applications* DOI: 10.1002/eap.2530.

Nezat, C. A., J. D. Blum, and C. T. Driscoll. 2010. Patterns of Ca/Sr and Sr-87/Sr-86 variation before and after a whole watershed CaSiO<sub>3</sub> addition at the Hubbard Brook Experimental Forest, USA. *Geochimica Et Cosmochimica Acta* 74:3129-3142.

Ni, X., and P. M. Groffman. 2018. Declines in methane uptake in forest soils. *Proceedings of the National Academy of Sciences* 115:8587-8590.

Ouimette, A. P., S. V. Ollinger, A. D. Richardson, D. Y. Hollinger, T. F. Keenan, L. C. Lepine, and M. A. Vadeboncoeur. 2018. Carbon fluxes and interannual drivers in a temperate forest ecosystem assessed through comparison of top-down and bottom-up approaches. *Agricultural and Forest Meteorology* 256-257:420-430.

Pardo, L. H., M. B. Green, S. W. Bailey, K. J. McGuire, and W. H. McDowell. 2022. Identifying controls on nitrate sources and flowpaths in a forested catchment using a hydopedological framework. *Journal of Geophysical Research: Biogeosciences* 127:e2020JG006140.

Peterman, K., S. Garlick, J. Besley, S. Allen, K. Fallon Lambert, N. M. Nadkarni, M. S. Rosin, C. Weber, M. Weiss, and J. Wong. 2021. Boundary spanners and thinking partners: adapting and expanding the research-practice partnership literature for public engagement with science (PES). *Journal of Science Communication* 20:N01.

- Pickett, S. T., and P. S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Possinger, A. R., M. J. Zachman, A. Enders, B. D. A. Levin, D. A. Muller, L. F. Kourkoutis, and J. Lehmann. 2020. Organo-organic and organo-mineral interfaces in soil at the nanometer scale. *Nature Communications* 11:6103.
- Pourmokhtarian, A., C. T. Driscoll, J. L. Campbell, K. Hayhoe, and A. M. Stoner. 2016. The effects of climate downscaling technique and observational data set on modeled ecological responses. *Ecological Applications* 26:1321-1337.
- Prancevic, J. P., and J. W. Kirchner. 2019. Topographic controls on the extension and retraction of flowing streams. *Geophysical Research Letters* 46:2084-2092.
- Ramirez-Francel, L. A., L. V. Garcia-Herrera, S. Losada-Prado, G. Reinoso-Florez, A. Sanchez-Hernandez, S. Estrada-Villegas, B. K. Lim, and G. Guevara. 2021. Bats and their vital ecosystem services: a global review. *Integrative Zoology*.
- Rastetter, E. B., M. D. Ohman, K. J. Elliott, J. S. Rehage, V. H. Rivera-Monroy, R. E. Boucek, E. Castañeda-Moya, T. M. Danielson, L. Gough, P. M. Groffman, C. R. Jackson, C. F. Miniati, and G. R. Shaver. 2021. Time lags: insights from the U.S. Long Term Ecological Research Network. *Ecosphere* 12:e03431.
- Rastetter, E. B., R. D. Yanai, R. Q. Thomas, M. A. Vadeboncoeur, T. J. Fahey, M. C. Fisk, B. L. Kwiatkowski, and S. P. Hamburg. 2013. Recovery from disturbance requires resynchronization of ecosystem nutrient cycles. *Ecological Applications* 23:621-642.
- Reinmann, A. B., J. R. Susser, E. M. C. Demaria, and P. H. Templer. 2019. Declines in northern forest tree growth following snowpack decline and soil freezing. *Global Change Biology* 25:420-430.
- Reinmann, A. B., and P. H. Templer. 2018. Increased soil respiration in response to experimentally reduced snow cover and increased soil freezing in a temperate deciduous forest. *Biogeochemistry* 140:359-371.
- Richter, D. D., S. A. Billings, P. M. Groffman, E. F. Kelly, K. A. Lohse, W. H. McDowell, T. S. White, S. Anderson, D. D. Baldocchi, S. Banwart, S. Brantley, J. J. Braun, Z. S. Brecheisen, C. W. Cook, H. E. Hartnett, S. E. Hobbie, J. Gaillardet, E. Jobbagy, H. F. Jungkunst, C. E. Kazanski, J. Krishnaswamy, D. Markewitz, K. O'Neill, C. S. Riebe, P. Schroeder, C. Siebe, W. L. Silver, A. Thompson, A. Verhoef, and G. Zhang. 2018. Ideas and perspectives: Strengthening the biogeosciences in environmental research networks. *Biogeosciences* 15:4815-4832.
- Rodenhouse, N. L., W. H. Lowe, R. L. E. Gebauer, K. P. McFarland, and M. S. Bank. 2019. Mercury bioaccumulation in temperate forest food webs associated with headwater streams. *Science of The Total Environment* 665:1125-1134.
- Rogers, S., and S. Garlick. 2021. Impacts of COVID-19 on Nature and Economy in Northern New Hampshire" UNH Cooperative Extension, 17, <https://scholars.unh.edu/extension/17/>.
- Rosi-Marshall, E. J., E. S. Bernhardt, D. C. Buso, C. T. Driscoll, and G. E. Likens. 2016. Acid rain mitigation experiment shifts a forested watershed from a net sink to a net source of nitrogen. *Proceedings of the National Academy of Sciences* 113:7580 - 7583.
- Russo, D., V. B. Salinas-Ramos, L. Cistrone, S. Smeraldo, L. Bosso, and L. Ancillotto. 2021. Do we need to use bats as bioindicators? *Biology (Basel)* 10.
- Rustad, L. E., J. L. Campbell, C. T. Driscoll, T. J. Fahey, P. M. Groffman, P. G. Schaberg, G. J. Hawley, I. Halm, F. Bowles, W. Leuenberger, G. Schwaner, G. Winant, and B. Leonardi. 2020. Experimental approach and initial forest response to a simulated ice storm experiment in a northern hardwood forest. *PLOS ONE* 15:e0239619.
- Sabo, R. D., S. E. Scanga, G. B. Lawrence, D. M. Nelson, K. N. Eshleman, G. A. Zabala, A. A. Alinea,

- and C. D. Schirmer. 2016. Watershed-scale changes in terrestrial nitrogen cycling during a period of decreased atmospheric nitrate and sulfur deposition. *Atmospheric Environment* 146:271-279.
- Sahu, S. K., K. S. Bakar, J. Zhan, J. L. Campbell, and R. D. Yanai. 2020. Spatio-temporal Bayesian modeling of precipitation using rain gauge data from the Hubbard Brook Experimental Forest, New Hampshire, USA. Pages 77-92 in *Joint Statistical Meetings Proceedings, Statistical Computing Section*. Alexandria, VA: American Statistical Association.
- Sanders-DeMott, R., R. McNellis, M. Jabouri, and P. H. Templer. 2018a. Snow depth, soil temperature and plant–herbivore interactions mediate plant response to climate change. *Journal of Ecology* 106:1508-1519.
- Sanders-DeMott, R., P. O. Sorensen, A. B. Reinmann, and P. H. Templer. 2018b. Growing season warming and winter freeze–thaw cycles reduce root nitrogen uptake capacity and increase soil solution nitrogen in a northern forest ecosystem. *Biogeochemistry* 137:337-349.
- Savoy, P., E. Bernhardt, L. Kirk, M. J. Cohen, and J. B. Heffernan. 2021. A seasonally dynamic model of light at the stream surface. *Freshwater Science* 40:286-301.
- See, C. R., M. B. Green, R. D. Yanai, A. S. Bailey, J. L. Campbell, and J. Hayward. 2020. Quantifying uncertainty in annual runoff due to missing data. *PeerJ* 8:e9531.
- Shan, S., H. Devens, T. J. Fahey, R. D. Yanai, and M. C. Fisk. 2022. Fine root growth increases in response to nitrogen addition in phosphorus-limited northern hardwood forests *Ecosystems* DOI: 10.1007/s10021-021-00735-4.
- Shan, S., M. C. Fisk, and T. J. Fahey. 2018. Contrasting effects of N and P on rhizosphere processes in two northern hardwood species. *Soil Biology and Biochemistry* 126:219-227.
- Sharma, S., R. Andrus, Y. Bergeron, M. Bogdziewicz, D. C. Bragg, D. Brockway, N. L. Cleavitt, B. Courbaud, A. J. Das, M. Dietze, T. J. Fahey, J. F. Franklin, G. S. Gilbert, C. H. Greenberg, Q. Guo, J. Hille Ris Lambers, I. Ibanez, J. F. Johnstone, C. L. Kilner, J. M. H. Knops, W. D. Koenig, G. Kunstler, J. M. LaMontagne, D. Macias, E. Moran, J. A. Myers, R. Parmenter, I. S. Pearse, R. Poulton-Kamakura, M. D. Redmond, C. D. Reid, K. C. Rodman, C. L. Scher, W. H. Schlesinger, M. A. Steele, N. L. Stephenson, J. J. Swenson, M. Swift, T. T. Veblen, A. V. Whipple, T. G. Whitham, A. P. Wion, C. W. Woodall, R. Zlotin, and J. S. Clark. 2022. North American tree migration paced by climate in the West, lagging in the East. *Proceedings of the National Academy of Sciences* 119:e2116691118.
- Sierra, C. A., M. Müller, H. Metzler, S. Manzoni, and S. E. Trumbore. 2017. The middle of ages, turnover, transit, and residence times in the carbon cycle. *Global Change Biology* 23:1763-1773.
- Sierra, C. A., M. Müller, and S. E. Trumbore. 2014. Modeling radiocarbon dynamics in soils: SoilR version 1.1. *Geoscientific Model Development* 7:1919-1931.
- Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90:3279-3289.
- Smith, M. G., S. A. Kaiser, T. S. Sillett, and M. S. Webster. 2018. Variation in nest characteristics and brooding patterns of female Black-throated Blue Warblers is associated with thermal cues. *The Auk* 135:733-747, 715.
- Sonti, N., P. M. Groffman, D. J. Nowak, J. Henning, M. Avolio, and E. J. Rosi. 2021. Urban net primary production: concepts, field methods, and Baltimore, MD case study. *Ecological Applications* In press.
- Sorensen, P. O., A. C. Finzi, M.-A. Giasson, A. B. Reinmann, R. Sanders-DeMott, and P. H. Templer. 2018. Winter soil freeze-thaw cycles lead to reductions in soil microbial biomass and activity not compensated for by soil warming. *Soil Biology and Biochemistry* 116:39-47.
- Stelkens, R. B., G. Jaffuel, M. Escher, and C. Wedekind. 2012. Genetic and phenotypic population divergence on a microgeographic scale in brown trout. *Molecular Ecology* 21:2896-2915.

- Sullivan, T. J., C. T. Driscoll, C. M. Beier, D. Burtraw, I. J. Fernandez, J. N. Galloway, D. A. Gay, C. L. Goodale, G. E. Likens, G. M. Lovett, and S. A. Watmough. 2018. Air pollution success stories in the United States: The value of long-term observations. *Environmental Science & Policy* 84:69 - 73.
- Swanson, F. J., D. R. Foster, C. T. Driscoll, J. R. Thompson, and L. E. Rustad. 2021. How LTER Site Communities Can Address Major Environmental Challenges. Pages 223 - 241 in R. B. Waide and S. E. Kingsland, editors. *The Challenges of Long Term Ecological Research: A Historical Analysis*. Springer International Publishing, Cham, Switzerland.
- Symes, L. B., K. D. Kittelberger, S. M. Stone, R. T. Holmes, J. S. Ralston, I. P. Casteneda Ruvalcaba, M. S. Webster, and A. M.P. 2021. Calling activity of Birds in the White Mountain National Forest: Audio Recordings (2016 and 2018) ver 3. Environmental Data Initiative. <https://doi.org/10.6073/pasta/efba421dc87e077ee28010069dac7c0d> (Accessed 2022-01-12).
- Symes, L. B., K. D. Kittelberger, S. M. Stone, R. T. Holmes, J. S. Ralston, I. P. Casteneda Ruvalcaba, M. S. Webster, and A. M.P. 2022. Conceptual and analytical approaches for evaluating passive acoustic monitoring data: A case study of avian vocalizations. *Ecology and Evolution* In press.
- Templer, P., H., K. F. Lambert, M. Weiss, J. S. Baron, T. D. Charles, and D. R. Foster. 2016. Using science- policy integration to improve ecosystem science and inform decision- making: Lessons from U.S. LTERs. *Bulletin of the Ecological Society of America* 97:123-128.
- Templer, P. H., M. C. Mack, F. S. C. Iii, L. M. Christenson, J. E. Compton, H. D. Crook, W. S. Currie, C. J. Curtis, D. B. Dail, C. M. D'Antonio, B. A. Emmett, H. E. Epstein, C. L. Goodale, P. Gundersen, S. E. Hobbie, K. Holland, D. U. Hooper, B. A. Hungate, S. Lamontagne, K. J. Nadelhoffer, C. W. Osenberg, S. S. Perakis, P. Schleppei, J. Schimel, I. K. Schmidt, M. Sommerkorn, J. Spoelstra, A. Tietema, W. W. Wessel, and D. R. Zak. 2012. Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of 15N tracer field studies. *Ecology* 93:1816-1829.
- Templer, P. H., A. B. Reinmann, R. Sanders-DeMott, P. O. Sorensen, S. M. Juice, F. Bowles, L. E. Sofen, J. L. Harrison, I. Halm, L. Rustad, M. E. Martin, and N. Grant. 2017. Climate Change Across Seasons Experiment (CCASE): A new method for simulating future climate in seasonally snow-covered ecosystems. *PLOS ONE* 12:e0171928.
- Torresan, C., M. B. Garzón, M. O'Grady, T. M. Robson, G. Picchi, P. Panzacchi, E. Tomelleri, M. Smith, J. Marshall, L. Wingate, R. Tognetti, L. E. Rustad, and D. Kneeshaw. 2021. A new generation of sensors and monitoring tools to support climate-smart forestry practices. *Canadian Journal of Forest Research* 51:1751-1765.
- Townsend, A. K., E. G. Cooch, T. S. Sillett, N. L. Rodenhouse, R. T. Holmes, and M. S. Webster. 2016. The interacting effects of food, spring temperature, and global climate cycles on population dynamics of a migratory songbird. *Global Change Biology* 22:544-555.
- Trumbore, S., P. Brando, and H. Hartmann. 2015. Forest health and global change. *Science* 349:814-818.
- Vadeboncoeur, M. A., M. B. Green, H. Asbjornsen, J. L. Campbell, M. B. Adams, E. W. Boyer, D. A. Burns, I. J. Fernandez, M. J. Mitchell, and J. B. Shanley. 2018. Systematic variation in evapotranspiration trends and drivers across the Northeastern United States. *Hydrological Processes* 32:3547-3560.
- Valipour, M., C. T. Driscoll, C. E. Johnson, J. J. Battles, J. L. Campbell, and T. J. Fahey. 2018. The application of an integrated biogeochemical model to simulate dynamics of vegetation, hydrology and nutrients in soil and streamwater following a whole-tree harvest of a northern hardwood forest. *Science of The Total Environment* 645:244-256.
- Valipour, M., C. E. Johnson, J. J. Battles, J. L. Campbell, T. J. Fahey, H. Fakhraei, and C. T. Driscoll. 2021. Simulation of the effects of forest harvesting under changing climate to inform long-term sustainable forest management using a biogeochemical model. *Science of The Total Environment* 767:ARTN 144881.

- Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea - how can it occur? *Biogeochemistry* 13:87-115.
- Walker, A. P., M. G. De Kauwe, A. Bastos, S. Belmecheri, K. Georgiou, R. F. Keeling, S. M. McMahon, B. E. Medlyn, D. J. P. Moore, R. J. Norby, S. Zaehle, K. J. Anderson-Teixeira, G. Battipaglia, R. J. W. Brienen, K. G. Cabugao, M. Cailleret, E. Campbell, J. G. Canadell, P. Ciais, M. E. Craig, D. S. Ellsworth, G. D. Farquhar, S. Fatichi, J. B. Fisher, D. C. Frank, H. Graven, L. Gu, V. Haverd, K. Heilman, M. Heimann, B. A. Hungate, C. M. Iversen, F. Joos, M. Jiang, T. F. Keenan, J. Knauer, C. Körner, V. O. Leshyk, S. Leuzinger, Y. Liu, N. MacBean, Y. Malhi, T. R. McVicar, J. Penuelas, J. Pongratz, A. S. Powell, T. Riutta, M. E. B. Sabot, J. Schleucher, S. Sitch, W. K. Smith, B. Sulman, B. Taylor, C. Terrer, M. S. Torn, K. K. Treseder, A. T. Trugman, S. E. Trumbore, P. J. van Mantgem, S. L. Voelker, M. E. Whelan, and P. A. Zuidema. 2021. Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO<sub>2</sub>. *New Phytologist* 229:2413-2445.
- Weintraub, S. R., A. N. Flores, W. R. Wieder, D. Sihi, C. Cagnarini, D. R. P. Gonçalves, M. H. Young, L. Li, Y. Olshansky, R. Baatz, P. L. Sullivan, and P. M. Groffman. 2019. Leveraging environmental research and observation networks to advance soil carbon science. *Journal of Geophysical Research: Biogeosciences* 124:1047-1055.
- Weitzman, J. N., P. M. Groffman, J. L. Campbell, C. T. Driscoll, R. T. Fahey, T. J. Fahey, P. G. Schaberg, and L. E. Rustad. 2020. Ecosystem nitrogen response to a simulated ice storm in a northern hardwood forest. *Ecosystems* 23:1186-1205.
- Welti, E. A. R., A. Joern, A. M. Ellison, D. C. Lightfoot, S. Record, N. Rodenhouse, E. H. Stanley, and M. Kaspari. 2021. Studies of insect temporal trends must account for the complex sampling histories inherent to many long-term monitoring efforts. *Nature Ecology & Evolution* 5:589-591.
- Wexler, S. K., C. L. Goodale, K. J. McGuire, S. W. Bailey, and P. M. Groffman. 2014. Isotopic signals of summer denitrification in a northern hardwood forested catchment. *Proceedings of the National Academy of Sciences* 111:16413-16418.
- Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28:453-470.
- Wieder, W. R., D. Pierson, S. Earl, K. Lajtha, S. G. Baer, F. Ballantyne, A. A. Berhe, S. A. Billings, L. M. Brigham, S. S. Chacon, J. Fraterrigo, S. D. Frey, K. Georgiou, M. A. de Graaff, A. S. Grandy, M. D. Hartman, S. E. Hobbie, C. Johnson, J. Kaye, E. Kyker-Snowman, M. E. Litvak, M. C. Mack, A. Malhotra, J. A. M. Moore, K. Nadelhoffer, C. Rasmussen, W. L. Silver, B. N. Sulman, X. Walker, and S. Weintraub. 2021. SoDaH: the SOils DAta Harmonization database, an open-source synthesis of soil data from research networks, version 1.0. *Earth System Science Data* 13:1843-1854.
- Wilbur, H. M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* 11:67-93.
- Wilson, G., M. Green, J. Brown, J. Campbell, P. Groffman, J. Durán, and J. Morse. 2020. Snowpack affects soil microclimate throughout the year. *Climatic Change* 163:705 – 722.
- Yanai, R. D., C. R. See, and J. L. Campbell. 2018. Current practices in reporting uncertainty in ecosystem ecology. *Ecosystems* 21:971-981.
- Yanai, R. D., M. A. Vadeboncoeur, S. P. Hamburg, M. A. Arthur, C. B. Fuss, P. M. Groffman, T. G. Siccamo, and C. T. Driscoll. 2013. From missing source to missing sink: Long-term changes in the nitrogen budget of a northern hardwood forest. *Environmental Science & Technology* 47:11440-11448.
- Yang, Y., R. D. Yanai, C. R. See, and M. A. Arthur. 2017. Sampling effort and uncertainty in leaf litterfall mass and nutrient flux in northern hardwood forests. *Ecosphere* 8:e01999.
- Zimmer, M. A., S. W. Bailey, K. J. McGuire, and T. D. Bullen. 2013. Fine scale variations of surface water chemistry in an ephemeral to perennial drainage network. *Hydrological Processes* 27:3438-3451.
- Zimmerman, A., and P. M. Groffman. 2021. Evolving governance in the U.S. Long Term Ecological

Research network. Pages 423-444 in R. B. Waide and S. E. Kingsland, editors. *The Challenges of Long Term Ecological Research: A Historical Analysis* Springer International Publishing, Cham, Switzerland.

Zinnert, J. C., J. B. Nippert, J. A. Rudgers, S. C. Pennings, G. González, M. Alber, S. G. Baer, J. M. Blair, A. Burd, S. L. Collins, C. Craft, D. Di Iorio, W. K. Dodds, P. M. Groffman, E. Herbert, C. Hladik, F. Li, M. E. Litvak, S. Newsome, J. O'Donnell, W. T. Pockman, J. Schalles, and D. R. Young. 2021. State changes: insights from the U.S. Long Term Ecological Research Network. *Ecosphere* 12:ecs2.3433.