From Microbes to Macrosystems: Understanding the response of ecological systems to global change drivers and their interactions

Harvard Forest LTER VI   2019 – 2024

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I. Project Summary

Overview: The Harvard Forest LTER (HFR) is a thirty-year-strong integrated research and educational program dedicated to understanding how New England forest ecosystems function and respond to natural and human forces. The heart of the program is an interdisciplinary group of PI scientists, research technicians, post-doctoral fellows, and graduate and undergraduate students from dozens of universities who pursue site to regional studies that integrate four approaches: long-term measurements; large, long-term experiments; retrospective studies; and prospective modeling. HFR research tests fundamental ecological hypotheses that advance ecological theory and answer applied questions of broad relevance.

Intellectual Merit: The goal of HFR LTER VI is to apply knowledge and capacity developed during LTER-I to V to understand and predict the impacts of global change on temperate forest ecosystems from site to regional scales. The integrated research plan is designed to understand forest ecosystem responses to (*i*) the increasing magnitude and variability of climate change and climatic extremes, (*ii*) the proliferation of invasive insects that are selectively removing tree species, and (*iii*) the modern land-use regime including the variable rates, intensities, and distribution of forest harvesting, land conversion, land protection, and agriculture. Recent syntheses of HFR long-term observational and experimental studies identified key knowledge gaps that require further research and data collection to achieve the project goal. In response, the research plan establishes several new initiatives, including: *(i)* a multi-constraints approach for scaling observations of primary production, from leaf-level physiological measurements, to multiple eddy flux estimates, to site-to-satellite-based observations, which collectively will constrain simulations of regional carbon exchange; *(ii)* a belowground carbon observation network, enhanced by radiocarbon dating and analyzed with new tools and models, designed to reduce the uncertainty regarding long-term change in forest carbon stocks and fluxes; *(iii)* aquatic and soil microbial measurements within declining hemlock forests infested by the invasive hemlock woolly adelgid, which will complement long-term aboveground observations and advance a generalizable understanding of population, community and nutrient cycling responses to invasive insects; and *(iv)* the expansion of a coupled spatial modeling framework, calibrated and validated with long-term observations, and designed to simulate stakeholder-defined land-use scenarios and the interactive effects of multiple global change drivers on New England forest composition, function, and services.

Broader Impacts emphasize the translation of HFR science for management and decision-making at landowner, local, state, and national scales through collaborations with the *Science Policy Exchange*, *Highstead Foundation*, and the *Wildlands and Woodlands* regional conservation initiative. Regional engagement will utilize the network of 42 Regional Conservation Partnerships and their >500 partner organizations, agencies, and municipalities that Highstead has developed with support from HFR. In four sub-regions on a rural-urban gradient, HFR's climate and land-use change scenarios research will be utilized to engage diverse stakeholder entities, to tailor products for their specific decision context, and to develop an interactive web-based scenario exploration tool that will be rolled out regionally. HFR will continue its: *(i)* award-winning *Schoolyard Program*, which engages >3,000 students in >50 schools in hands-on ecological data collection and analysis using HFR CoI-designed curricula; *(ii)* summer undergraduate program and graduate student and post-doctoral engagement in HFR; *(iii)* 25-year-old *Keystone Project* that trains community leaders using three-day intensive workshops in natural resources and stewardship; *(iv)* programs to evaluate the impact of its engagement strategies on attitudes and outcomes for scientists and the public; and *(v)* will develop two synthesis volumes in the LTER publication series.

II. Project Description

Results from Prior Support

For 30 years the Harvard Forest LTER program (HFR) has conducted transformative research through the collection and synthesis of long-term observational and experimental data, impactful educational programs, and science-based public engagement that informs environmental decision-making from New England communities to the globe. HFR research tests fundamental ecological hypotheses that advance ecological theory and answers applied questions of broad relevance, engaging >100 researchers, >200 graduate and undergraduate students, and dozens of institutions to generate synthetic, news-making publications (Table 1), and regional, national (including cross-LTER), and international collaborations that help shape ecological, environmental, and conservation thinking and action.

Major findings from LTER I through V that will guide LTER VI, include:

- Temperate forests exhibit strong resilience to disturbance. *(i)* Despite centuries of land use, forests cover 82% of New England in patterns similar to those at European settlement, albeit with shifts in tree species abundance and structure. *(ii)* Field experiments simulating intensive hurricanes document that forests retain tight biogeochemical cycling and recover rapidly in productivity.
- Biotic and physical legacies of past disturbance interact with modern conditions to control ecological patterns, processes, and feedbacks. *(i)* The impacts of modern land use, disturbance and climate change are conditioned by the legacies of historical land use, insect/pathogen outbreaks, and hurricanes. *(ii)* Contradicting theoretical models, forest carbon (C) uptake has accelerated in HFR's maturing forests, a successional legacy of 19th century land use and the 1938 hurricane, and modern increases in atmospheric CO_2, nitrogen (N) deposition, and temperature.
- Interactions among climate change, disturbance, and chronic stresses can trigger abrupt shifts in ecosystems. *(i)* Repeated insect defoliations followed by drought have induced widespread tree mortality; *(ii)* Decades of experimental soil warming and N enrichment have induced adaptive responses in microbial communities, abruptly shifting rates of decomposition and soil C storage.
- The work of the Science Policy Exchange at HFR demonstrates new approaches that enhance science impacts on decision-making and management: *(i)* Scientists must engage early and consistently with stakeholders in the design of research; *(ii)* Effective outreach benefits from translational science products for targeted stakeholders, as demonstrated by HFR products *Changes to the Land*, *Wildlands and Woodlands* and the Keystone Community Training project; *(iii)* and public engagement can enhance research by identifying salient research questions.

Beyond advancing research across multiple levels—organisms, populations, communities, ecosystems, landscapes, and the region—HFR has played a major role in LTER Network-wide leadership, strategic planning, and research; NEON; DOE Biological and Environmental Research programs; NASA missions; Smithsonian's Forest Global Earth Observatory (ForestGEO); and state, regional, and national policy.

LTER I (1988-1994) initiated site-based measurements and long-term experiments (Fig. 1) contrasting ecosystem responses to natural disturbance (e.g., hurricanes) and human stressors (e.g., N deposition, climate change). The world's longest running forest eddy-flux site was established to quantify the C cycle. **LTER II** (1994-2000) added landscape and regional analyses of land use and disturbance, and time series of C and N dynamics. **LTER III** (2000-2006) explored mechanisms controlling inter-decadal cycles of C and N; identified interactions among organisms, climate change, and disturbance controlling forest structure and function; initiated baseline measurements of streamflow and benthos in diverse forests; produced a site synthesis volume; and advanced policy on climate change and conservation. **LTER IV** (2006–2012) added observations, experiments, and modeling of forest harvesting, exotic species, and wildlife. **LTER V** (2012-2018) integrated environmental and socio-ecological drivers into regional models of climate and land-use scenarios to quantify their consequences for ecosystem processes and services.

Table 1. Ten publcations from HFR LTER V selected to showcase impact, diversity of authors, and use of long-term data. Full citations and the datasets associated with each publication are given in the literature cited section.

[1] **Melillo, J. M., *et al.* 2017. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. Science 358: 101-105.**

[2] **Frey, S. D., *et al.* 2014. Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. Biogeochemistry 121: 305-316.**

[3] **Barker Plotkin, A. *et al.* 2013. Survivors, not invaders, control forest development following simulated hurricane. Ecology 94: 414-423.**

These three high-profile papers synthesize >20 years of response to disturbance (hurricane) and stress (N saturation; soil warming) from experiments initiated in LTER I. Each revealed surprises: a four-phase pattern of soil organic matter decay and carbon fluxes to the atmosphere with warming; enhanced soil C stocks in N-enriched soils via suppressed decomposition; despite large-scale and intense canopy damage, surviving saplings, understory vegetation, and damaged trees allowed the forest to resist changes in ecosystem processes and invasion.

[4] **Van Diepen, L. T. A., *et al.* 2017. Fungi exposed to chronic nitrogen enrichment are less able to decay leaf litter. Ecology 98: 5-11.**

This post-doc led study was the first to test if and how fungal behaviors relevant to a critical ecosystem process evolve in response to long-term environmental change.

[5] **Thompson, J. R., *et al.* 2013. Changes to the Land: Four Scenarios for the Future of the Massachusetts Landscape. Harvard Press. ISBN: 978-0-615-98526-8**

The report describing the pilot project for the scenario development and modeling approach that was central to LTER V received extensive media coverage, informs policy at the state level, and was published in multiple additional journal articles.

[6] **Duveneck, M. J., *et al.* 2017. Recovery dynamics and climate change effects to future New England forests. Landscape Ecology 32: 1385-1397.**

Scaling to New England using a ecophysiological model calibrated with long-term HFR flux and plot data, this post-doc led study predicted that climate change will influence C accrual, but continued recovery will have larger impacts on composition.

[7] **Wehr, R., *et al.* 2016. Seasonality of temperate forest photosynthesis and daytime respiration. Nature 534:680-683.**

New isotopic instrumentation at the EMS tower partitioned photosynthesis and respiration, providing the first robust evidence of the inhibition of leaf respiration by light (the Kok effect), and revising our understanding of forest-atmosphere C exchange.

[8] **Keenan, T.F., *et al.* 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. Nature Climate Change 4: 598–604.**

Combining long-term ground observations, satellite indices, and ecosystem-scale CO_2 flux measurements, this post-doc lead study showed a trend toward earlier springs and later autumns with resulting enhancement of forest C uptake.

[9] **Foster D.R. *et al.* 2014. Hemlock: A Forest Giant on the Edge. Yale University Press.**

In a narrative that spans millennia of ecological change, the authors explore hemlock forests and the invasive hemlock woolly adelgid that threatens them, and profiles the people and places behind more than a century of HFR research.

[10] **Lovett, G. M., *et al.* 2016. Nonnative forest insects and pathogens in the United States: Impacts and policy options. Ecological Applications 26: 1437-1455.**

This Science Policy Exchange synthesis showed that invasive forest insects cause >$2 billion in damage each year in the U.S., and current efforts to prevent invasions are not effective. An Associated Press feature was picked up by > 200 media outlets.

1.1. Multi-decadal Experiments

1.1.1. A 20-year synthesis of the **Simulated Hurricane** [3] showed that advance regeneration and residual vegetation minimized changes to the microenvironment, ecosystem processes, and composition. Productivity rebounded quickly and C stocks are recovering rapidly. This experiment and ongoing studies of the 1938 hurricane highlight the critical role that downed wood and pit-mound topography play in ecosystem structure and function [11, 12].

1.1.2. The 20-year synthesis of the **Chronic N Amendment Experiment** [2] (Fig. 2) showed that N-induced C accumulation in soil equaled or exceeded that in trees, but varied between hardwoods and conifers and with N levels. A decline in decomposition, due to changes in plant litter quality and microbial community composition and evolution [4, 13, 14], rather than increased C inputs from litter and roots, drove most soil C accumulation [15].

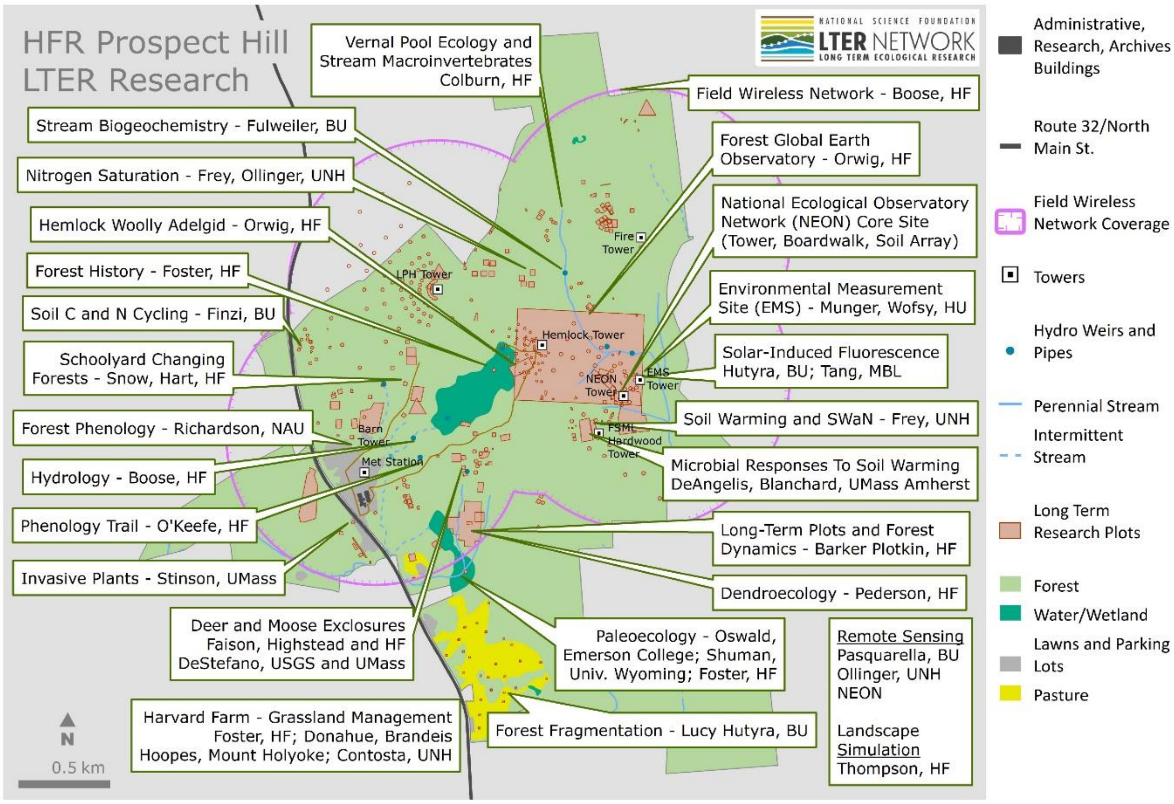

Figure 1. HFR engages dozens of researchers from multiple institutions to collect and synthesize long-term observational and experimental data. Beyond the hub of research activity and infrastructure at the Prospect Hill Tract shown here, researchers and students utilize the 1500 ha HFR land base, and regional studies using targeted sites throughout New England, remote sensing, regional datasets, and regional modeling.

1.1.3. The **Soil Warming Experiments** exhibit dynamic trajectories (Fig. 3). At the 27-year-old Prospect Hill warming study, significant soil C loss due to decomposition and CO_2 fluxes alternated with phases of no loss [1]. The 900 m^2 16-year-old Barre Woods warming plot recorded a net loss of C as soil losses outstripped tree gains [16]. Factors controlling the timing and magnitude of soil C loss include: depletion of microbially accessible C [17]; reductions in microbial biomass [17, 18] and C use efficiency [19] and shifts in microbial community composition [20]. Nonetheless, a recent synthesis of the HFR ecosystem-scale C budget proposes that in nature such soil-mediated changes will be offset by increasing plant productivity [21]. Reconciling experimental and observational studies is an important part of LTER VI (see § 2.2.1).

1.1.4. The 12-year-old **Soil Warming × Nitrogen Addition (SWaN) Experiment** demonstrates that: the microbial community is resistant to short-term changes to soil temperature and N availability [22]; microbial activity [23] and soil respiration [24] do not acclimate to warming; there are contrasting dynamics in distinct soil organic matter pools [25]; microbial respiration is enhanced; and gains in soil C storage due to N enrichment are partially offset by losses with warming [26]. The experimental introduction of exotic garlic mustard is addressing how invasion interacts with climate to alter tree seedling performance [27], microbial communities, and biogeochemical processes [28].

1.1.5. The **Detritus Input and Removal Treatments (DIRT)** 20-year synthesis [29] demonstrated that soil C pools respond slowly and non-linearly to above or belowground litter inputs, limiting the rate and magnitude of changes in soil C storage with shifts in plant productivity. A test of the long-standing hypothesis that soil bacteria are associated with fast, but leaky use of C and nutrients, whereas fungi are associated with slow but efficient nutrient use was rejected [30], demonstrating the need to revise our understanding of microbial communities and processes.

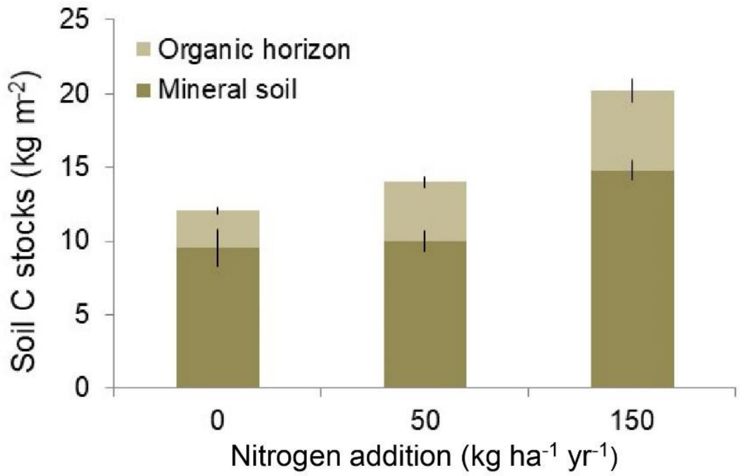

Figure 2. Decades of experimental soil N enrichment have reduced rates of organic matter decay leading to soil C accumulation[2], in part due to adaptive responses in the fungal decomposer community[4].

1.1.6. The hypothesis that eastern hemlock is a foundation species was supported by the **Hemlock Removal Experiment** [31, 32]. The girdling or logging of hemlock sharply changed forest structure [31] and microclimate [33], with cascading effects on salamanders [34–36], moose and deer [37], small mammals [38], ants [39], macroarthropods [40], and herbs [41]. Vegetation richness, cover, and density increased, associated with transient fluxes in N [31]. Regionally, hemlock decline due to the invasive insect hemlock woolly adelgid (HWA) leads to dominance by black birch. Modeling [42] and field studies [43, 44], suggest that black birch forests will exhibit increased N availability and net primary productivity. By 2014 many hemlock across HFR were infested with HWA providing a major natural experiment (See §2.3.1) [39, 45].

1.2. Long-term Measurements

1.2.1. **Three eddy-flux towers** capture long-term trends in forest-atmosphere C exchange (Fig. 4). The maturing oak-red maple forest at the **Environmental Measurement Station (EMS)** has been a C sink for 25 years (2.9 ± 1.5 Mg C ha^{-1} yr^{-1}) due to the dominance by red oak, longer growing seasons, increasing sub-canopy hemlocks that photosynthesize year-round, and rising CO_2 concentrations [46]. Partitioning observed Net Ecosystem Exchange (NEE) indicates that photosynthetic light-use efficiency is nearly constant throughout the growing season [7, 47]. Forest recovery following intense disturbance was tracked by the **Clear-cut Tower**. Annual increases in gross primary production (GPP) are attributed to expanding leaf area [48, 49] leading the new forest to return to pre-harvest annual C accumulation rates in five years. At the **Hemlock Tower** net C uptake averaged 3.9 ± 0.1 Mg C ha^{-1} yr^{-1}, before declining with HWA infestation [21]. Understory photosynthesis partially compensated the initial hemlock decline as light reached previously shaded needles and seedlings in canopy gaps. Evapotranspiration (ET) showed substantial differences between hemlock and EMS stands, with greater water availability for groundwater and streamflow in hemlock stands [50]. The eddy-flux towers and associated forest, soil, and stream studies will provide critical integrated analyses during LTER VI as hemlock declines.

1.2.2. Soil respiration: Synthesis of >100,000 soil C flux observations over 22 years casts new light on C cycling at HFR [51]. Soil respiration accounts for 40-80% of total ecosystem respiration, making belowground C pools a dynamic component of annual C exchange with the atmosphere.

1.2.3. Meteorological and hydrological stations: Data from the Fisher Met Station (since 2001), six stream and wetland gages (since 2007), and the HF Snow Pillow (since 2009) are displayed in real time on the HF website and support studies of phenology [52], stream biogeochemistry [53], and hemlock impacts on water yield [54] and benthos [55, 56].

1.2.4. Permanent plots: Syntheses of permanent plots documented a long-term shift from white pine and red maple to red oak and hemlock since 1937 and steady to modestly increasing aboveground C uptake

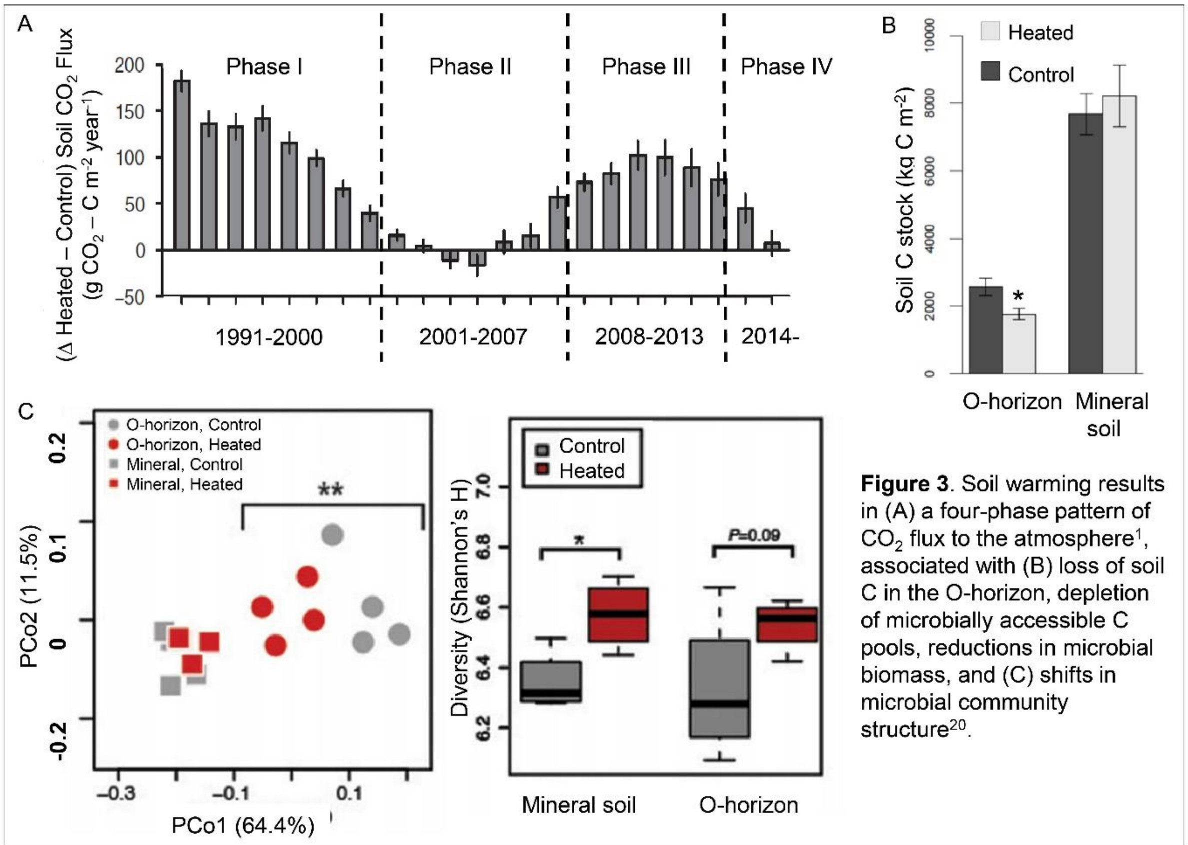

Figure 3. Soil warming results in (A) a four-phase pattern of CO_2 flux to the atmosphere[1], associated with (B) loss of soil C in the O-horizon, depletion of microbially accessible C pools, reductions in microbial biomass, and (C) shifts in microbial community structure[20].

since at least the 1960s, with a decline due to the 1981 gypsy moth outbreak [57, 58]. A century of data at the old-growth **Pisgah Tract** highlighted the role of single species, such as white pine, in controlling ecosystem patterns and processes [11]. Prior to the 1938 hurricane, C stocks in 300-year-old trees were among the highest levels recorded from New England. With white pine eliminated by the hurricane, hemlock became dominant; biomass remained much lower and is projected to never exceed 75% of former levels.

The 35 ha, stem-mapped **ForestGEO Plot** encompasses the EMS and Hemlock Towers and stream gages, and has contributed to a global analysis showing tree diversity increases with negative density dependence [59] and supporting the foundational role of hemlock [60–62]. Tracking of hemlock decline, using ground-based lidar and annual mortality surveys, documented mortality of 13% of the hemlock (Fig. 4) [63], reduced ET, increased stream discharge [54], and black birch replacement of hemlock.

1.2.5. Phenological responses to climate change: In 2008 HFR launched the PhenoCam Network, a continental-scale observatory of digital imagery tracking phenology at fine spatial and temporal resolution[64–66]. HFR continues to expand the network and pioneer research into sensitivity of vegetation phenology to climate and its role in driving ecosystem processes and feedbacks between the land surface and atmosphere. PhenoCams were deployed at nine LTER sites for cross-site syntheses complemented by ground-based thermal [67], multispectral [68], and high-resolution imagery from unmanned aerial vehicles [69, 70]. Day length has emerged as a potential constraint to springtime phenological advancement as temperatures warm [71]. Accounting for phenology, the Community Land Model (CLM) [72] indicates that future advances in spring will enhance gross and net primary production of deciduous forests worldwide while increased evapotranspiration will dry soils and reduce stream flows. Over the last 20 years, spring

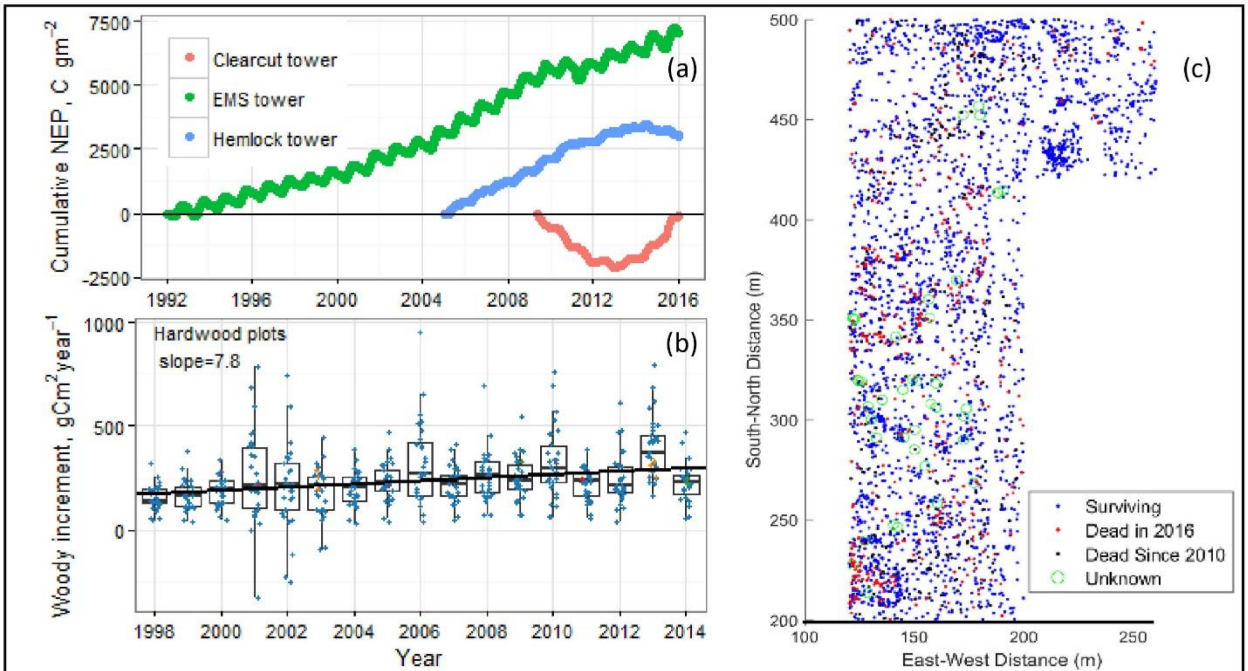

Figure 4. (a) Cumulative net ecosystem production (NEP) measured using three eddy flux towers: Green shows NEP at the EMS site in a maturing hardwood forest; Blue shows NEP at the Hemlock site where productivity began to decline in 2012 due to hemlock woolly adelgid (HWA) invasion; Red shows NEP at the Clearcut site where the site recovered to a net C sink five years after harvest. (b) Long-term plots show increasing woody increment over time. Points represent individual plots and boxplots show their distribution each year. (c) The hemlock dominated portion of 35 ha ForestGEO plot. Each dot represents a tree and the color indicates mortality due to HWA.

phenology has advanced across the east, increasing photosynthesis and net ecosystem C storage, with a small negative feedback to climate change (Fig. 5) [8].

1.2.6. Forest ecosystem impacts of ungulate populations (deer and moose) have increased regionally, with modest impacts on forest structure and function. At HFR, intensive browsing reduced saplings in regenerating forests, producing more open communities with greater herb and shrub diversity [37, 73, 74].

1.3. Recent History and Future Scenarios of Landscape Change

1.3.1. Regional Land-use Trends (1985-2015): Decisions by private landowners shape New England forests. Satellite-based land-cover analysis revealed that 350,000 ha of forest were converted to non-forest cover in the past 25 years, with strong regional variation in rates and pattern [75–77], Harvesting is the dominant forest disturbance, with great variation in rate, intensity and pattern [78–80]. Twenty-three percent of the region is legally protected from development, with half of this conserved in the last 25-years [81].

1.3.2. Future Scenarios: A two-year pilot scenario study in Massachusetts advanced regional simulation and analysis of land use and climate change [5, 82, 83], and produced a report *Changes to the Land: Four Scenarios for the Future of the Massachusetts Landscape* that targeted decision makers, received extensive media coverage and was used in state land-use and climate adaptation plans and zoning reforms. Collaborating with decision-makers, we employed participatory scenario development to explore four divergent and yet plausible land-use futures [84] and modeled the scenarios' consequences statewide in terms of ecological consequences using the LANDIS-II Forest Landscape Model (FLM).

The **New England Landscape Futures Project** expands this effort to evaluate the ecological consequences of scenarios across all six states over the next 50 years (Fig. 6). Facilitators and project scientists hosted six scenario-building workshops with approximately 120 diverse stakeholders to co-design four land-use scenarios that differ in the types, extents, intensities, and distributions of land uses and bound an

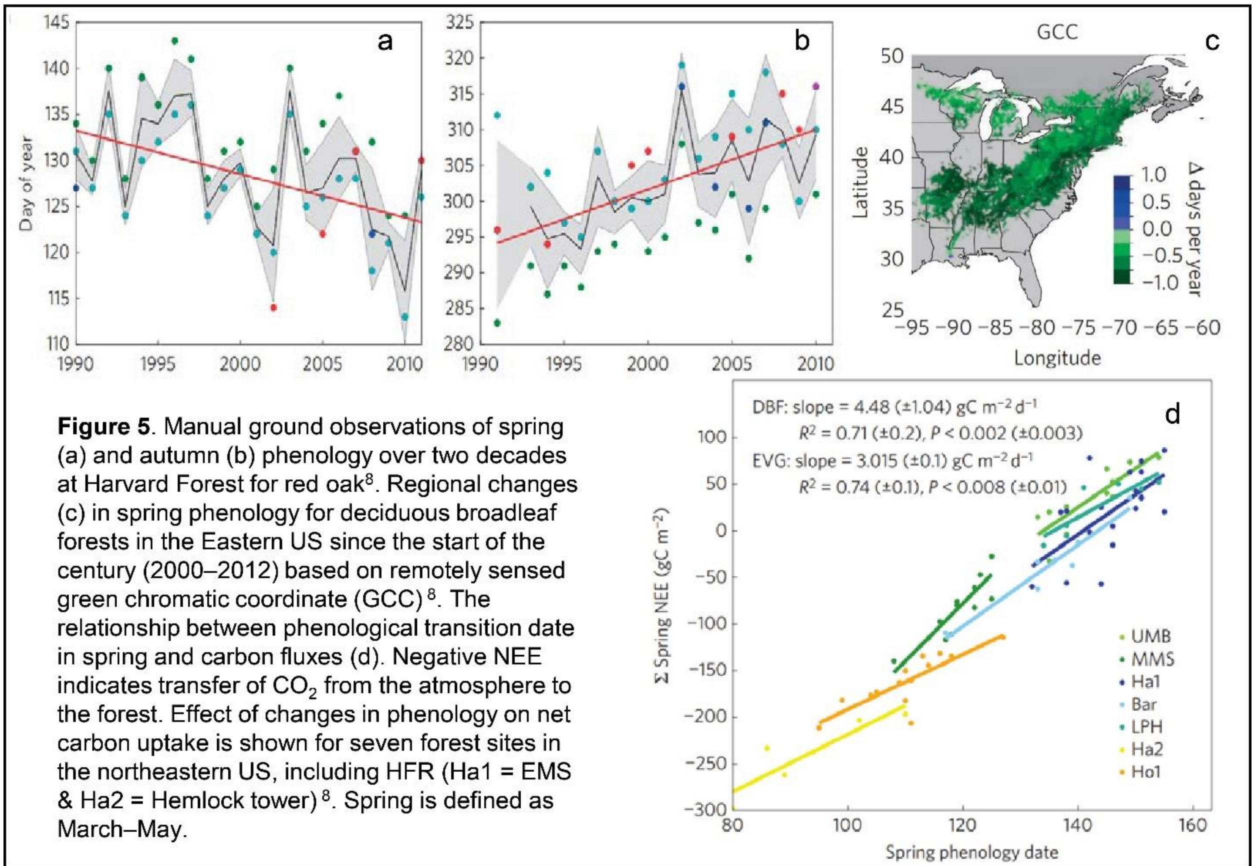

Figure 5. Manual ground observations of spring (a) and autumn (b) phenology over two decades at Harvard Forest for red oak[8]. Regional changes (c) in spring phenology for deciduous broadleaf forests in the Eastern US since the start of the century (2000–2012) based on remotely sensed green chromatic coordinate (GCC)[8]. The relationship between phenological transition date in spring and carbon fluxes (d). Negative NEE indicates transfer of CO_2 from the atmosphere to the forest. Effect of changes in phenology on net carbon uptake is shown for seven forest sites in the northeastern US, including HFR (Ha1 = EMS & Ha2 = Hemlock tower)[8]. Spring is defined as March–May.

expansive range of future conditions [85]. We improved our modeling framework for quantifying scenario impacts by coupling the LANDIS-II FLM [86] to PnET, a physiologically based ecosystem model [87–89], and to Dinamica EGO, a cellular automata land-cover change model [90]. This coupled-FLM simulates the interactive dynamics of 40 tree species across the 18 million ha region; it is initialized using U.S. Forest Service Inventory and Analysis (FIA) plots, MODIS, and environmental data [91] and calibrated for C exchange using HFR eddy-flux and long-term plot data [6]. Simulations show that: (*i*) all scenarios lead to a decline in forest area but wide variation in extent, pattern, and ecological consequences [92], (*ii*) recovery from 19th century land use will be a stronger determinant of forest structure and composition than climate change [6], (*iii*) tree migration will lag climate change [93], and (*iv*) forest net primary productivity will vary regionally and temporally due to tradeoffs between greater growth and increased summer respiration [94]. The scenarios and modeling framework will be further utilized in LTER VI (see § 2.2.3., 2.3.1., 2.4.1. and 2.5.1), including an analysis of the land-use scenarios' impacts on climate, which builds off a study of the effects of 19th century forest clearing on New England climate [95] that indicated that regional increases in surface albedo across agricultural landscapes had a 1-2°C cooling effect, particularly in winter.

1.4. Retrospective Studies

1.4.1. We assembled > 300,000 **land-survey records** to examine changes in Northeastern forest composition since European settlement [96]. Late-successional beech and hemlock declined while successional red maple increased. Nonetheless, great similarities persist despite centuries of land use, climate change, and species introductions. Confirming HFR paleoecological studies [97–99], modern forests are more homogeneous and less coupled to climate.

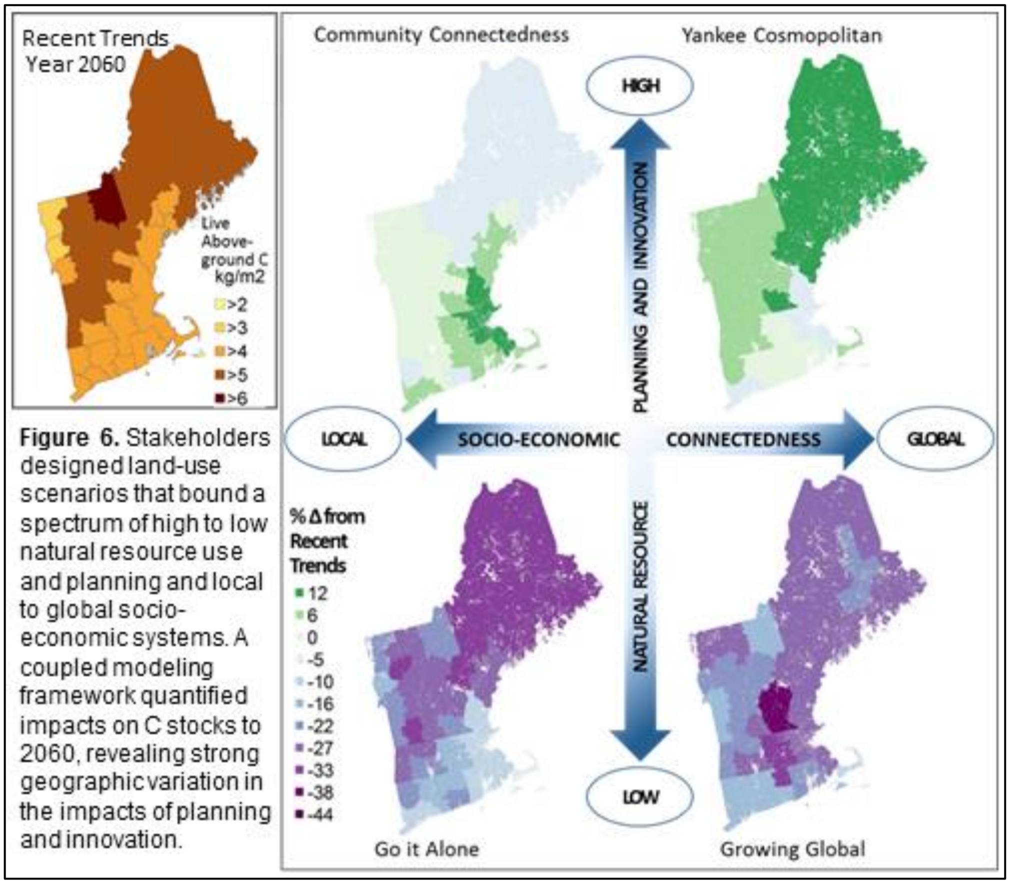

Figure 6. Stakeholders designed land-use scenarios that bound a spectrum of high to low natural resource use and planning and local to global socio-economic systems. A coupled modeling framework quantified impacts on C stocks to 2060, revealing strong geographic variation in the impacts of planning and innovation.

1.4.2. Lake-sediment, charcoal, and pollen from 25 sites documented the relationships among climate, fire, and human activity in driving vegetation dynamics [100, 101]. Charcoal records exhibited no relationship to pre-European cultural changes, but varied with climate, fuel loading, [100] and European land clearance.

Major episodes of drought and associated vegetation dynamics were identified within the long-term trend of increasing moisture [102].

1.4.3. We built a **dendrochronology network** spanning 800,000 km^2 and five centuries to assess the consequences of climate events [103] and identified regionally synchronous episodes of tree recruitment linked to tree mortality from repeated droughts and late spring frosts. LTER VI will incorporate climate variability and extreme climate events into regional modeling (see § 2.2.3.).

1.5. Research Infrastructure Improvements during LTER V

With LTER funds we developed and deployed twelve automated soil respiration chambers to quantify changes in belowground C cycling associated with HWA infestation. With NSF FSML and Harvard University support we deployed a new Hemlock eddy-flux tower, an observational tower for education on the suite of flux towers, and acquired the 40 ha Harvard Farm (see § 2.4.2.).

Table 2. Summary of HFR datasets in EDI repository, February 2018. Some datasets address multiple core areas.

Total number of data sets in EDI repository	**304**
Datasets by LTER core area	
Primary production	59
Populations	109
Organic Matter	36
Inorganic Nutrients	49
Disturbance	174
Long-term measurements (at least 10 years)	63

1.6. Information Management (IM) and Technology

We greatly improved HFR IM, submitted all datasets to the EDI repository (Table 2), and created a new online database for the Schoolyard program (see § 3.2.). We expanded our long-term research on data provenance with support from an NSF Software Infrastructure for Sustained Innovation grant and the HF REU program [104, 105].

1.7. Synthesis: Six New Books

We added three volumes to the LTER Publication series: (*i*) *Hemlock: A Forest Giant on the Edge* [9] synthesizes HFR studies on eastern hemlock and the consequences of its future loss; (*ii*) *A Meeting of Land and Sea. The Nature and Future of Martha's Vineyard* [101] distills LTER research on the history, ecology, and conservation of the diverse coastal landscape. (These two and the 2004 HFR synthesis volume *Forests in Time: The Environmental Consequences of 1000 Years of Change in New England* lead the LTER Network in sales); and (*iii*) *Stepping in the Same River Twice. Replication in Biological Research* drew from LTER and ILTER studies to highlight the importance of reproducibility in science [106]. Three additional books boost the LTER Arts collaboration: *(i) And Again: Photographs from the Harvard Forest* [107] explores the HFR science landscape through photographs and essays; *(ii)* in *Witness Tree* environmental journalist Lynda Mapes [108] examines HFR climate change research for general audiences; and *(iii) Thirty Eight: The Hurricane that Transformed New England* by Steve Long [109], editor of Northern Woodlands Magazine, uses eye witness accounts and HFR studies to examine the ecologically transformative nature of hurricanes.

1.8. Broader Impacts

1.8.1. HFR's **REU-based Summer Program** draws 20-30 undergraduates annually for mentored team-based projects integrating long-term data, quantitative analysis, and science communication. The program earned the Human Diversity Award from the Organization for Biological Field Stations (2014) for sustained support for traditionally under-represented students and collaborations with ESA SEEDS and the Community College Undergraduate Research Initiative. The program reaches students from traditionally under-represented groups and lacking previous research experience [110].

1.8.2. The Schoolyard LTER Program (sLTER) engages > 50 teachers through a Summer Institute training, spring workshop sharing best practices and lesson plans, data workshop, and Schoolyard blog. sLTER field protocols were developed by LTER Co-Is to focus on key HFR studies (phenology, invasive insects, hydrology, C dynamics, land use) and engage > 3000 students. Teachers present at state and national conferences; several benefit from NSF RET grants and have received statewide education awards. All sLTER data can be accessed and graphed in an interactive database on the HFR website.

1.8.3. Graduate and post-doctoral students are integrated into HFR LTER through Lab Group meetings, the annual HFR Symposia, site- and LTER-wide graduate student events, and by contributing to undergraduate and K-12 education. The HFR *Annual Ecology Symposium* draws >100 participants, including researchers, students, conservationists, policy makers and educators, and is streamed online.

1.8.4. The **Science Policy Exchange** (SPE) based at HFR includes seven research institutions, four LTER sites, and ecologists, economists, and communication experts to develop policy-relevant syntheses and communicate results to decision-makers and the media. SPE initiatives on clean energy, land use, and invasive insects generate high-impact journal articles with wide media coverage and are shared through Congressional and agency briefings and webinars [111]. The SPE "Tree Smart Trade" synthesis on invasive tree pests [10] engaged many HFR Co-Is and was covered by the *New York Times* and *Wall Street Journal,* distilled into a summary shared with Congress, public agencies, and conservation organizations, and provides the basis for a draft bill in the U.S. House of Representatives.

1.8.5. Community Engagement: Over 25 years, the *Keystone Project* trained 450 community leaders and landowners in ecology and conservation themes. They have volunteered nearly 40,000 hours to conservation-related activities. The new *Wildlands and Woodlands* conservation report for New England [81] incorporated HFR findings and was released at Harvard University to a policy and stakeholder audience. Visual artist David Buckley Borden's forest art exhibition, *Hemlock Hospice* conveyed HFR insights along a trail and through many presentations. Training in science communication and policy engagement is provided to HFR scientists and students leading to consistent media presence in the *Boston Globe, NY Times, Science, Nature, NPR, USA Today, Washington Post, National Geographic, BBC,* and *The Atlantic*.

1.9. Response to Mid-term Reviews

The mid-term review provides HFR a vital opportunity to define the program's objectives, review accomplishments, and receive constructive feedback to improve future activities. For LTER V, HFR researchers synthesized early accomplishments within the context of our 27-year history and shared these activities with all students and researchers at the annual LTER Symposium six months in advance of the review. During the review we shared our progress, successes, challenges, plans for future leadership and senior scientist transitions openly with the review team and Program Officer Saran Twombly through productive presentations, informal exchanges, and lengthy field discussions. The reviews gave validation to the strength and directions of the research program and provided substantive input that is reflected in our LTER VI proposal. The team lauded our approach for linking historical perspectives, long-term data, and experiments with regional models to simulate alternative climate and land-use change scenarios. They cited the use of this framework to advance basic and applied research, outreach to diverse stakeholders, and education across levels as effective and exciting, calling it "a transparent translation of scientific research into societal consequences that should be a model across LTER projects."

The review team made two primary recommendations with regard to the scenarios project: (1) to describe the landscape scenario and simulation process and its integration of scientific data through publications and outreach materials and (2) to communicate uncertainty as a key component of the modeling. In strong agreement, we have developed publications [76, 85, 94, 112, e.g., , 113] that describe the scenario-to-simulation process and are building a web-based platform for users to access and explore the scenarios, and simulation outputs (§ 3.1.1.). In LTER VI we will strengthen linkages between long-term data and our modeling framework by constraining models with remote sensing (§ 2.1.1., 2.3.3., 2.4.1.), paleo (§ 2.2.3.), and eddy flux data (§ 2.1.1.). We expanded our quantification and communication of uncertainty by improving the characterization of multiple future land-use trajectories via stakeholder-defined scenarios [85, 112], reduced and measured uncertainty in our initial conditions [91, 114], and quantified global and local parameter uncertainty within the FLM [115]. We are also integrating our modeling framework into the Predictive Ecosystem Analyzer (PEcAn), an informatics toolbox for ecosystem modeling [116, 117] that facilitates uncertainty analysis and model-data synthesis.

The review team appreciated the open discussion of leadership and PI transition and emphasized the importance of thoughtful succession. They endorsed the transition to Thompson, a senior researcher based at the Harvard Forest who has shared six years of close collaboration with the Forest's director and current LTER PI Foster. The team recognized the importance of maintaining close alliance between the leadership of HFR LTER and the Harvard Forest, as well as strong academic, administrative, and facilities support from Harvard University. This close coupling of the LTER program, lead institution, and university will be bolstered by the reformulated HFR leadership team comprised of diverse Co-Is drawn from multiple institutions to assist with management and decision-making (see Project Management Plan).

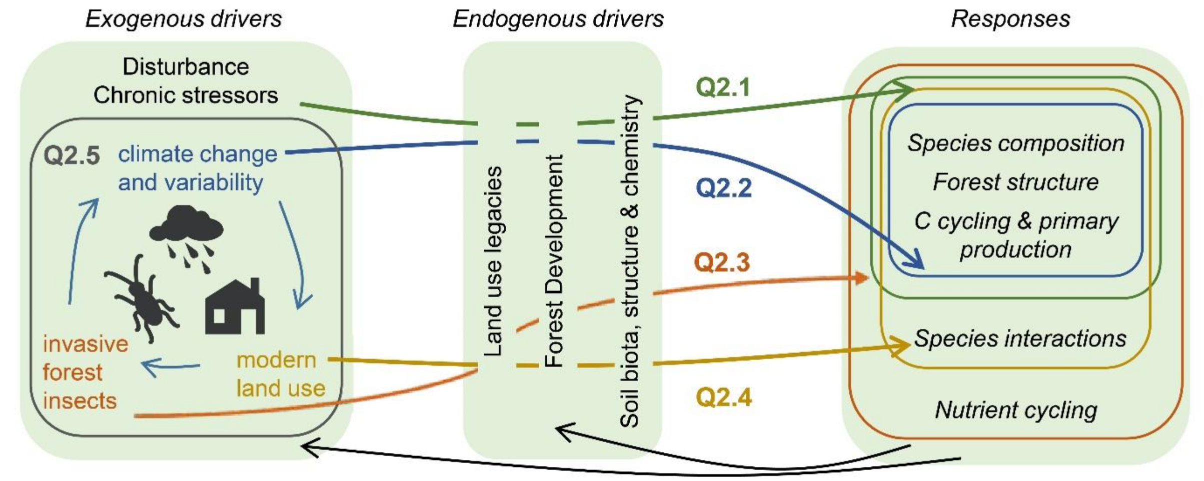

Figure 7. Conceptual Diagram: Thirty years of HFR LTER shows that temperate forest ecosystems are dynamic, with change driven by a complex mix of endogenous and exogenous factors. How these drivers change forests at the ecosystem, landscape, and regional scales is the focus of HFR LTER. Overarching questions (Q2.1 – Q2.5) are developed in Sections 2.1 – 2.5.

2. Integrated Research Plan

Intellectual Merit

The goal of HFR LTER VI is to apply knowledge and capacity developed during LTER I to V to understand and predict the impacts of global change on temperate forest ecosystems from site to regional scales (Fig. 7)**.** Through more than a century of sustained research (30 years as an LTER site), HFR scientists have developed a robust understanding of temperate forests and the drivers that govern their dynamics. Over that entire history, climate change, invasive insects, and land use have informed our conception of forest ecosystems. However, the intensity with which these global change drivers (GCDs) are affecting forests is unprecedented and is expected to increase in coming decades [118, 119]. The question looms as to how the rate, quality, magnitude, and interactions among GCDs will alter New England's (i.e. the region's) ecological trajectory and the resilience of its forests.

HFR's Integrated Research Plan is designed to understand ecosystem responses, locally and regionally, to (*i*) the increasing magnitude and variability of climate change and climatic extremes, (*ii*) the proliferation of invasive forest insects that are selectively removing tree species, and (*iii*) the modern land-use regime including the variable rates, intensities, and distribution of forest harvesting, forest conversion, land protection, and agriculture. We will also investigate interactions among GCDs, with an emphasis on identifying the ecosystem components that are particularly vulnerable (or resilient) to these factors. The Research Plan is organized around the following overarching questions:

1) *What are the primary drivers, mechanisms, and characteristics of forest development, in terms of long-term and broad-scale changes to primary production, composition, and structure?*
2) *How will climate change, climatic variability, and extreme events interact with these underlying and ongoing ecological processes to alter the composition, structure, and function of forest ecosystems?*
3) *How is the proliferation of invasive insects in New England altering forest dynamics from microbial to ecosystem to regional scales?*
4) *How does New England's human land-use regime—i.e. the types, frequencies, intensities, and spatial patterns of land use—affect forest structure and function at local to regional scales?*
5) *What are the relative and interactive effects of climate change, invasive insects, and human land use on New England forests?*

Table 3. HFR LTER VI proposed research, indicating activities, global change driver (GCD) foci, and proposal section in which the activity × GCD is addressed.

Method	Color-coding: New; Continuing; Phasing down; Completed	Pattern & Process	Climate Change	Forest Insects	Land Use	Inter-acting GCDs
Long-term observations	Eddy-flux (EMS[1,2], Hemlock[1,2,5], CC, model integration)	2.1.1	2.2.2	2.3.1		
	Soil respiration plots; automated soil C flux array[3,5]			2.3.1		
	Permanent plots (ForestGEO[1,2], Lyford[1,2], Pisgah[2,3,5], etc.)	2.1.2	2.2.4	2.3.1		
	Phenology[1,2] (tree observations, PhenoCams, modeling, barn tower instrumentation)		2.2.2			
	Meteorology & hydrology[3,4]	2.1.2	2.2.2	2.3.1.2		
	Grassland management studies[2,3]				2.4.2	
	Soil C network ('BeCON')[3,4]	2.1.2		2.3.1.1	2.4.2	
	Invasive forest insects and tree species loss (HWA /hemlock: aquatic ecology & hydrological modeling; microbial drivers of response; EAB/ash; GM/oak)[1,2,5]			2.3.1; 2.3.2		
	Invasive plants[2,5]		*		*	
	Indicators of primary production[1] (Solar-induced fluorescence, sap-flux, canopy nitrogen/NIR)	2.1.1			2.4.1	
	Forest fragmentation & edge effects on C cycling[1,3,5]				2.4.1	
Experiments	Simulated hurricane[1,2,3,5]		2.2.4			
	Chronic N[3,4,5]: Hardwood Low N; Pine plots phased out in LTER IV; Hardwood High N; microbial drivers[2,3]	*				
	Soil warming[3,4,5] (Prospect Hill; Barre Woods); focus on microbial drivers of response[2,3]		2.2.1			
	SWaN[3,4,5]; focus on microbial drivers of response[2,3]		2.2.1			
	DIRT[3]	*				
	Hemlock Removal[1,2,3,4,5]			2.3.1		
	Deer & Moose Exclosure experiments[1,2,5]				2.4.3	
Landscape Analysis & Modeling	Recent trends & future scenarios (land conversion & conservation, timber harvesting, agricultural use, forest insects, wildlife habitat; forest insect outbreaks)[1,2,3,4,5]			2.3.3; 2.5.2	2.4.1; 2.4.3	2.5.1
	30 year disturbance mapping using LANDSAT[5]			2.3.3	2.4.3	2.4.1
	Landscape simulations of climate variability/extreme events (builds on LTER V landscape modeling)[1,5]		2.2.4			
	Climatic response to changing land-use[5]					2.5.2
Retro-spective	Past land cover, disturbance, and vegetation based on pollen, historical records, and tree-rings[1,2,5]		2.2.3			
	Pollen and lake levels – change & variability)[5]		2.2.3			
Education & Outreach	Subregional case studies to support decision-making					2.5.3
	Science Policy Exchange					3.1.1
	Wildlands and Woodlands				3.1.1	
	Writing & arts collaborations	3.1.3				3.1.3
	Educational programs (sLTER, undergrad, grad/post-doc, Keystone, symposium/seminars, PES@LTER)	3.2	3.2	3.2	3.1.1; 3.2	3.1.2; 3.2

Superscripts indicate activity's relationship to LTER core areas: 1 = Primary production; 2 = Populations; 3 = Organic matter; 4 = Inorganic matter; 5 = Disturbance. * indicates activities that will continue in LTER VI but that are not specifically addressed in the Proposed Research due to limited space.

Our overarching questions emerge from 30 years of LTER observational, experimental, and synthetic study. In several instances, recent syntheses of HFR long-term data and experiments [e.g., , 1, 21, 51, 93, 102] have revealed divergent conclusions and/or identified knowledge gaps that require additional data collection and analyses to achieve our project's goals and answer the questions outlined above. In response, our Integrated Research Plan builds on previous efforts and establishes several new initiatives. First, we will complement our network of long-term plot-based measurements with regional forest inventories, remote sensing, and landscape simulations to test theories of forest development and better describe the underlying drivers of ecological change. Relatedly, in recognition of the importance of primary production and ecosystem C exchange for mitigating climate change, we will integrate new measurements, tools and models with our 30-year stream of eddy-flux and plot-based measures to better partition and constrain above and belowground C fluxes during secondary forest succession (§ 2.1). We will also leverage decades of experimental soil warming and chronic nitrogen additions, phenological observations, and paleoecological perspectives to improve predictions of forest responses to climatic change, variability, and extreme events (§ 2.2). We will initiate new measurements within declining hemlock forests infested by the invasive HWA to include repeated aquatic and soil microbial measurements, which will complement the comprehensive suite of aboveground observations and be used to advance a generalizable understanding of population, community and ecosystem response to invasive insects (§ 2.3). Finally, we will assimilate remote sensing with public databases, surveys, and field studies and use these data to constrain and validate our coupled spatial modeling framework, designed to simulate stakeholder-defined land-use scenarios and the interactive effects of GCDs on New England forest composition, function and services (§ 2.4 & § 2.5).

2.1. Pattern and process during forest development

Overarching Question:

> *What are the primary drivers, mechanisms, and characteristics of forest development, in terms of long-term and broad-scale changes to primary production, composition, and structure?*

For over a century, Harvard Forest researchers have reconstructed and studied the recovery of forest ecosystems from Colonial-era land use. Modern forests continue to develop in structure, composition and function as a result of this history, subsequent disturbances, and recent environmental changes. They would continue to change even in the absence of novel GCDs; however, they are now changing in conjunction with overlying and interacting GCDs. This leads to several major questions regarding the patterns and processes that characterize forest recovery in a global change context. Our long-term studies of these ecosystems (*i*) enable us to understand their current condition and dynamics, (*ii*) use models forced with and without GCDs to explore their interactive effects of forest structure and function, and *(iii*) allow us to predict the outcome in response to future environmental change. With this information, we are poised to improve the understanding of long-term ecosystem change and the impacts from intensifying GCDs with unprecedented historical and ecological knowledge.

Specific Research Questions:

Q1. After a century of forest recovery, do observed patterns of temperate forest composition and structure support theories of forest development?

Q2. How, why, and where does C move into and out of temperate forest ecosystems?

Proposed Activities

2.1.1. Secondary forest succession (*Q1*)

Lead Investigators: Barker Plotkin, D'Amato, Foster, Orwig, Pederson, Stinson, Thompson

Permanent plots are unrivalled for assessing long-term changes in forest characteristics and offer validation sites for the eddy-flux, remote sensing, and modeling studies discussed below. The HFR network of permanent plots varies in plot size (400 m^2 to 35 ha) and temporal depth (< 10 to > 80 years) and provides an array of measurements describing forest composition and structure; growth increment, mortality, recruitment and stocks of live biomass and dead wood; C and N dynamics; and plant and microbial community structure and function.

As the forest matures, theories of forest ecosystem development [120, 121] predict a transition from strong biomass aggradation, low canopy mortality, and early-to-mid-successional species' dominance to slowing biomass growth and stochastic mortality forming canopy gaps that replenish dead wood pools that are missing in the secondary forest and allow late-successional species in the understory to recruit into the canopy. More than a century after agricultural abandonment and 80 years after a region-wide hurricane, observations from permanent plots indicate that the aggradation phase continues well beyond 80 – 120 years. Red oak, a mid-successional species, shows low canopy mortality, increasing dominance, and continuing or increasing rates of C storage, whereas mid-late-successional red maple is declining at the tree and stand level [57]. Barring exogenous disturbance, dead wood pools remain diminished compared to those in old-growth stands [11]. Although late-successional species are present in the sapling layer [57, 122] it is unclear whether they will eventually ascend to the canopy or remain suppressed.

We will continue permanent plot measurements to test for how long the aggradation phase lasts in forests dominated by endogenous drivers, and how exogenous disturbances hasten or alter succession. Plots in oak-maple and hemlock sites allows us to observe differences in development as a function of forest type, and large plots such as the Lyford Grid (3 ha) and ForestGEO (35 ha) allow scaling up from the plot to the landscape via remote sensing and modeling. Comparison of permanent plots to experiments simulating GCDs (e.g. soil warming, hurricane, hemlock removal) facilitate parsing forest response to endogenous vs. exogenous forces, and informs how we propose to study intensifying exogenous forces (see §2.2 – §2.5).

2.1.2. The how, why, and where of ecosystem C dynamics (*Q2*)

Lead Investigators: Finzi, Hutyra, Moorcroft, Munger, Ollinger, Tang, Thompson, Williams, Wofsy

Through LTER I –V, we have brought together hundreds of thousands of observations on the C cycle at HFR, which has experienced a land-use history of harvesting, agricultural land clearance and reforestation that is shared by much of eastern North America [21]. The data are derived from a wide range of temporal and spatial scales and collectively describe the mixture of conifer- and hardwood-dominated forests as active C sinks with soils and tree biomass having nearly equal contributions to C storage. Thirty years of eddy-covariance measurements show that the HFR C sink is increasing owing to continued forest development and changes to climate and atmospheric chemistry [21, 122–124]. On average, net primary production (NPP) is 730-970 g C m^{-2} y^{-1}, with belowground NPP contributing 30-60% of the total. Including C losses from decomposer microbes, net ecosystem production averages 300-400 g C m^{-2} y^{-1}.

While we have established a strong baseline for understanding the C cycle of HFR, our present understanding raises new questions for analysis and guidance for future research. Key questions include: How long and how much more C can be stored in woody biomass? Is the soil C sink changing over time? How best to measure and scale HFR observations across New England? The overarching approach is to couple our long-term measurements of primary production and ecosystem C exchange with new aboveground measurements (e.g., solar induced fluorescence, sap flux and stomatal conductance), a new belowground C observation network, and relevant NEON data streams.

Ground-based Measurements of C Pools and Fluxes. Long-term biometric inventory plot data highlight the importance of woody biomass as a sink for atmospheric CO_2 [21, 57, 122]. Although interannual variations are large, long-term inventories now show that forest productivity is increasing in response to succession, longer growing seasons and possibly rising atmospheric CO_2 and is altered by winter climate [8, 21, 46]. The pace and pattern of forest development strongly influences the rate of woody biomass accumulation, so continued observation of permanent plots (see §2.1.1) is critical to understanding whether and when forest development will slow C accumulation in live and dead woody biomass.

A recent effort to construct a full C budget for HFR identified soil C dynamics as least well constrained component of forest C stocks and fluxes [21]. Soil contains about half of the forest C sink, but it is uncertain whether C is accumulating in the soil over time, as it is in woody biomass. Consequently, we will establish a new belowground C observation network ("BeCON") to measure changes in C pools over time in soils, including roots and soil organic matter. Heavily replicated "Conant" plots [sensu, 125] will be established in existing permanent plots and elsewhere to measure belowground C across the diversity of forest types and land-use histories found at HFR. Measurements of radiocarbon in both roots and soils [126] combined with estimates of root production and turnover from minirhizotrons and a new generation of root and microbial models [127] will give critical insights and predictive capacity to describe spatial and temporal variability and uncertainty in belowground C pools and fluxes.

Eddy-Covariance, Remote Sensing and Scaling of HFR C Pools and Fluxes. HFR's EMS eddy-flux tower is the world's longest continuous record of forest ecosystem C, water, and energy exchanges with the atmosphere. Biometric inventory plots within the tower's footprint provide an estimate of above-ground NPP as an independent constraint on the annual carbon balance from the eddy covariance measurements. We will continue eddy-covariance measurements of C fluxes and their associated meteorological (temperature, light, precipitation), and atmospheric chemistry variables (e.g., O_3 and gaseous N deposition). We also propose to continue measurements of growth, mortality, recruitment and C in live and dead biomass in biometric and other permanent plots within the tower footprint (see §2.1.1).

We will build on a recent, spatially explicit study of C fluxes in the EMS tower footprint showing that daytime NEE during the growing season is higher in sectors with greater proportions of deciduous canopy trees using newly collected data from the NEON flux tower [54]. The EMS and NEON towers are separated by ~125 m. Using a comparative approach based on the differences in the vegetation composition of their footprints will enable us to look more deeply into the role of soils, species composition, and stand structure in regulating C fluxes [128]. As a part of this work, we also propose a major synthesis of the long-term flux data to identify forest functional responses to key environmental drivers such as temperature, soil moisture and PAR, and how they may have been altered by climate change, climate extremes and rising atmospheric CO_2.

To enhance understanding of GPP, the most uncertain flux estimate in eddy-covariance studies, we propose new measurements of solar induced fluorescence (SIF), an emerging technology in remote sensing [129]. In brief, fluorescence is a leakage of photons from photosystem II. The amount of fluorescence is directly related to the quantity of absorbed PAR (aPAR) and the yield of fluorescence. This is essentially the same way in which GPP is modeled from remotely-sensed data (i.e., aPAR * light-use efficiency). SIF has a distinct advantage, however, in that it correlates with spatial and temporal variations in NEE better than most other remotely-sensed vegetation indices [129, 130]. Most importantly, it offers an opportunity to model GPP independently of eddy-covariance estimates and thus acts as a constraint on the partitioning of NEE into its component fluxes, ecosystem respiration and GPP. Tower-based measurements of SIF will be accomplished using a new leveraged, sub-nanometer imaging spectrometer at the EMS tower (for information on this leveraged grant, see the supplemental Facilities Document (hereafter "Fac.") § L5). These measurements will be complemented by new studies of whole-canopy transpiration via the measurement of sap fluxes and stomatal conductance based on carbonyl sulfide fluxes [131].

We will use a multiple-constraints approach based on remote sensing and simulation modeling to scale our results across HFR and New England. Satellite-based remote sensing data products on near-infrared reflectance via AVIRIS and NEON [132] and SIF from GOME-2, GOSAT and OCO-2 will be used to drive models of light-use efficiency and primary productivity. NIR is broadly correlated with canopy N concentration, maximum photosynthesis, and canopy level light-use efficiency (LUE) [132]. The strength of this trend suggests the potential to use broad-band sensors (e.g., Landsat 8) to estimate canopy N, LUE and primary productivity at regional scales [21, 133]. Because these associations stem from biologically driven, but incompletely understood, relationships [134], we will advance understanding in this area by synthesizing new and existing field and remote sensing data, including leaf-level photosynthesis, structural properties estimated using lidar and species-level vertical leaf profiles [135], hyperspectral data from NEON, and leveraged high-resolution hyperspectral data obtained from a drone-based sensor (see Fac. § L8). Making explicit ties between leaf physiology, canopy structure, C assimilation, SIF, and canopy reflectance at a variety of scales will provide a more direct and seamless approach to scaling from leaves and towers to entire regions than has thus far been possible. We will use the improved estimates of regional variation in primary production to better constrain our coupled forest landscape model (FLM), which was developed as a focal activity during LTER V (see § 1.3.2) and will be used extensively in LTER VI. The FLM simulates spatial and temporal variation in ecophysiological processes (using the PnET model [88]) and species-specific forest dynamics (using LANDIS-II [86, 93]) as they are influenced by scenarios of future GCDs.

A key element of LTER VI modeling will be validating regional simulations and upscaling ground-based data using atmospheric CO_2 mixing ratios as top down constraints. We will use an atmospheric transport model, the Stochastic Time-Inverted Lagrangian Transport model (STILT)[136], with the simple Vegetation, Photosynthesis, and Respiration Model (VPRM) [137, 138] forced by weather, land-cover classification, and spatiotemporal variations in vegetation activity. VPRM provides an *a priori* gridded C flux estimate that can be convolved with an atmospheric transport model to predict CO_2 mixing at a downwind receptor. Discrepancy between predicted and observed CO_2 can be inverted to provide an optimal model of C exchange at regional scales. Evaluating regional models provides scale-appropriate validation that is not possible by comparing the modeled fluxes to observations at a single point. Including regional validation of the present-day simulations enhances confidence in simulations of future scenarios.

2.2 Climate Change, including Ecosystem Responses to Climatic Extremes and Variability

Overarching Question:

> *How will climate change, climatic variability, and extreme events interact with underlying ecological processes to alter the composition, structure, and function of forest ecosystems?*

Climate change and variability, including changes in long-term averages and extremes of temperature and precipitation at scales from days to seasons to decades, are having significant impacts on New England forests. The region is the fastest warming in the contiguous U.S. [139], has experienced the country's largest increase in extreme precipitation events [119] , and is predicted to have an increase in the frequency and severity of extreme weather—hurricanes, droughts, and flooding [140].

Recent climate change has been modest compared to predictions for the next 100 years; nonetheless, it has left a discernible imprint on forest dynamics. Phenological observations and modeling support interpretations of the flux measurements by probing the environmental drivers and consequences of seasonal events. Longer growing seasons and increased atmospheric CO_2 concentrations [8] and trends in precipitation [141] are altering ecosystem processes such as C uptake. However, photoperiod (day length) has emerged as a potential constraint to springtime advancement as temperatures warm.

Our paleoecological studies, augmented by new dendroecological studies, reveal persistent (multi-centennial) interactions between GCDs and shifts in forest structure and composition associated with episodic (decadal to centennial) deviations in precipitation and temperature [102]. Understanding how past climate change and its variation structured ecological dynamics will greatly improve our ability to forecast future dynamics in an era of rapid climate change. While insights have emerged from LTERs I-V, they have also raised conflicting interpretations that we seek to resolve through new retrospective studies integrated with simulations.

Specific Research Questions:

Q1. Will New England forests continue active C uptake as climate warming increases? Soil warming experiments at HFR have resulted in significant soil C loss, an apparent positive feedback to warming. In contrast, our whole-ecosystem analyses of C pools over the last three decades suggest that soil C sinks are stable and slow to change. How do we reconcile these apparently divergent conclusions?

Q2. How is vegetation phenology changing, what are the key drivers of this change, and how do these changes influence ecosystem patterns and processes?

Q3. How do we resolve conflicting findings regarding tree species migration with climate change? At increasingly finer temporal and spatial resolution, paleoecological studies indicate tight coupling of climate and vegetation with little difference in species' projected and realized niches. In contrast, mechanistic models project strong compositional inertia and century-scale lags in species turnover and migration.

Q4. *What role do large, infrequent disturbances (hurricanes, droughts) play in controlling landscape to regional-scale patterns of biomass, tree diversity, and distribution?*

Proposed Activities:

2.2.1 Experimental soil warming (Q1)

Lead Investigators: Blanchard, DeAngelis, Finzi, Frey, Melillo, Stinson

Twenty-seven years of soil warming has revealed a complex and multi-phased response of soil C storage and loss. Several factors affect the timing and magnitude of soil C fluxes (i.e., soil respiration), including depletion of labile C pools and shifts in microbial biomass, C use efficiency, and community composition [1]. Over the same 27-year period, however, biometric inventories and eddy-covariance data demonstrate a consistent forest C sink (biomass + soil) two to seven times larger than the apparent soil C loss from continuous chronic warming at +5˚C [21]. Reconciling these records and interpretations is a research priority for LTER VI.

To better understand and constrain the response of soil C to long-term warming, we will continue measurements (soil temperature, moisture, respiration, N mineralization, C stocks, and microbial biomass) at the three experiments that represent a temporal chronosequence of warming since 1991 (Prospect Hill), 2001 (Barre Woods), and 2006 (SWaN). At the Barre Woods site [16], where the 30 x 30 m plots encompass whole trees, we will quantify above- and belowground C pools and fluxes to separate the effects of long-term soil warming on tree versus soil C storage, thereby addressing the potentially divergent conclusions between the soil warming studies and whole-ecosystem C measures. At all three sites, and by leveraging recently-funded grants (see Fac. § L3), we will describe microbial assemblages and soil C chemistry using phylogenetic, metagenomic, and meta-transcriptomic approaches coupled with culture-based studies, stable isotope analysis, pyrolysis GCMS, nuclear magnetic resonance spectrometry, fluorescence-activated cell sorting, and Raman-spectroscopy. The possibility that soil warming is affecting C availability to microbial decomposers through changes in soil structure (e.g., aggregation and mineral association of organic matter) will be tested, along with the hypothesis that changes in microbial community structure and/or activity are associated with warming-induced changes in soil organic matter chemistry and its protection within soil aggregates. In parallel to these studies of physical and chemical characteristics, we will expand studies of microbial evolution and functional capacity using genomes of fungal and bacterial isolates and metagenomic sequences to discover genetic or genomic markers of key microbial physiological parameters (e.g., C use efficiency). These data will be integrated into ecosystem-scale soil organic matter models, including the Microbial-Mineral Carbon Stabilization [142] and Stoichiometrically Coupled, Acclimating Microbe-Plant-Soil [143] models.

2.2.2. ***Changing phenology (Q2)***

Lead Investigators: Munger, Ollinger, Richardson

To quantify trends in phenological timing and variability in spring and fall, we will couple ongoing ground observations of woody plant phenology (since 1992) [144] with phenocam observations at canopy scale (since 2008) [65, 145] and phenological metrics from tower-measured CO_2 fluxes and diel pattern of ambient CO_2 mixing ratios. We will place these trends in a regional context using long-term phenocam data from Hubbard Brook LTER and Bartlett Experimental Forest [146] and satellite remote sensing [8, 69, 147].

Long-term data are also essential for understanding drivers of phenological change, as unusual and extreme weather events leave a unique mark on observed transitions [148]. Variation in snowmelt dates, first and last frosts, and extremes of temperature and precipitation make each year a natural experiment from which we can infer, using a model-based framework, the drivers of vegetation phenology, on a species-by-species or canopy-scale basis [71, 147]. Based on predictions of vegetation phenology, we will then address the impacts of changing phenology on ecosystem patterns and processes by altering the phenological subroutines in PnET and the CLM. Building on previous work focused on the start of the growing season [71, 72], we will quantify the impact of changes in the end of the growing season on ecosystem productivity, ET, soil water content, runoff, and surface energy balance, using methods developed by Burakowski et al. [149] and proposed to be extended in LTER VI (see § 2.5.2). These model-based predictions will be evaluated using CO_2, water, and energy fluxes measured at the EMS and Hemlock tower.

2.2.3 ***Paleoecological perspectives on climate change (Q3)***

Lead Investigators: Foster, Oswald, Pederson, Shuman, Thompson

Prehistory yields empirical perspectives on the drivers, patterns, and processes surrounding abrupt and long-term forest ecosystem dynamics. At least five major forest transitions from the past represent the consequences of GCDs (climate and its variability, insects, hurricanes, land use) that provide insights for predicting future changes and placing HFR research in space and time [97, 150, 151]. Two early state changes were rapid and large: regional temperatures rose 7-17^{o} C in <300 years at the Pleistocene-Holocene transition, driving a shift from boreal to mixed forests [151, 152], and a large increase in effective precipitation (>300 mm) 9-8000 years ago punctuated by extreme cold (the '8.2 ka event') drove a ca. 150-year transition to deciduous forests [151, 153]. A third transition spans the mid-late Holocene, the regional expansions of hickory, chestnut, and spruce, and the range-wide decline of hemlock [97]. The hemlock decline was attributed to insects or pathogens, but new evidence implicates the interaction of changing temperatures and drought through a period of increasing moisture [154, 155]. Around the time of European settlement, droughts, severe frosts, and hurricanes are correlated with episodes of synchronous tree mortality and regeneration and changes in dominant taxa that increased with novel European land uses [99, 156, 157]. Finally, five centuries of forest clearance, logging, fire, farming, and reforestation altered regional forest composition and structure [96, 158].

By examining forest transitions in different climate and GCD settings using reconstructive approaches and modeling, we will explore the mechanisms underlying these episodes and future transitions. A key focus will be the rate and pattern of species dynamics. Paleo data indicate that tree taxa abundance changed in near equilibrium with climate [102], whereas taxon ranges varied asynchronously (Fig. 8) [97]. Many discussions of future climate change assume rapid shifts in both [cf. , 159], while HFR scenario simulations project long lags in species dynamics [6, 93]. Other studies have argued that interactions among climate and other GCDs can shorten these lags [160, 161 but c.f. , 93].

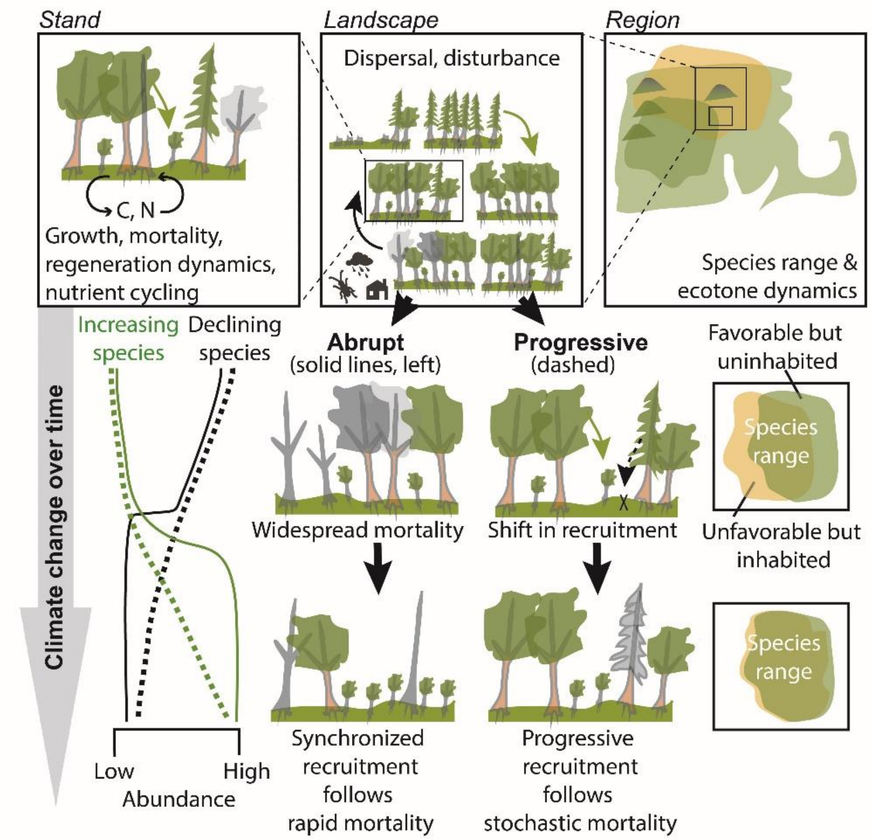

Figure 8. Climate change affects processes at the stand, landscape, and regional scales (top row). Responses can be abrupt, if extreme weather events, forest insects, or land-use prompts widespread mortality, or progressive (middle). Abrupt changes at local scales may blend into progressive changes at regional scales if not synchronized, thus affecting the pace at which regional species ranges shift (lower right). Direct observation can show ongoing processes, but retrospective and modeling approaches can evaluate the balance of processes and outcomes that played out in the past, and may occur in the future.

We aim to address these divergent perspectives using highly resolved pollen records analyzed in detail akin to the modeling of landscapes at decadal intervals. Each transition will be analyzed for vegetation, climate, fire, and other disturbances across a regional network of sites bracketing major ecotones. A new tree-ring network will add detail on stand, landscape, and regional forest dynamics and underlying demographic and structural changes occurring during the last five centuries [103, 157], supported by historical data including witness tree surveys [96]. These high-resolution data will be compared to simulation experiments and sensitivity tests using the FLM to test hypotheses regarding the ecological responses and to reconcile divergent interpretations of the driving factors, dynamics involved, and relative significance of equilibrium-disequilibrium processes [e.g., 151, 162] and to isolate the physiological, ecological, and spatially interactive mechanisms that would be required to produce the observed changes.

2.2.4 ***Role of infrequent disturbances on forest dynamics (Q4).***

Lead Investigators: Barker Plotkin, Boose, D'Amato, Foster, Pederson, Thompson

In LTERs I-V, we reconstructed the meteorological characteristics and impacts of all hurricanes affecting New England (since 1635) at a coarse resolution and demonstrated their enduring landscape impacts through field studies and experiments [163–165]. In LTER V, we used an eco-physiologically based FLM to show that expected increases in temperature and precipitation will enhance the rate of C uptake but have little impact on forest composition and structure as these develop from past land use and the 1938 hurricane [6]. Though our results parallel other modeling studies [e.g., 166, 167], all neglected to examine the effects of increased climate variability, extreme weather events, or the increased intensity of hurricanes. To address these more complicated scenarios we will draw on our growing empirical understanding to improve our modeling framework. We will simulate alternative scenarios of climate variability that incorporate variance patterns of drought, frost, and heat waves observed in historical weather records, but apply them along with the global circulation model projections of climate change. We will also rewrite the Hurrecon model[168] to enable modeling regional-scale meteorological scenarios and ecological dynamics, to generate finer resolution forest damage patterns, and to integrate with the FLM. Results from the Simulated Hurricane Experiment and long-term hurricane recovery plots, regarding differential susceptibility and regeneration, will help calibrate and validate the model. We will use this modeling framework to test hypotheses related to disturbance effects on regional forest dynamics and interactions between hurricanes and changing land uses, such as salvage logging (see § 2.5.1, 2.5.2).

2.3 Invasive Insects as a Global Change Driver

Overarching Question:

> *How is the proliferation of invasive insects in New England altering forest dynamics from microbial to ecosystem to regional scales?*

The northeastern U.S. leads the country in the number of invasive forest insects [169], resulting in major ecological and economic impacts [10]. Insects selectively alter forest structure and composition [170–172] and carbon, water, and nutrient cycles [54, 173, 174], and undermine the provisioning of ecosystem services [175, 176]. They have direct ecosystem impacts and interact with other GCDs. We plan to focus on the three insects of most concern in New England: hemlock woolly adelgid (HWA), emerald ash borer (EAB),and gypsy moth (GM). For each insect we will explore the gradient of impacts, with a focus on virulence, host specificity, host role in forest ecosystems, range of human responses, and successional dynamics.

Within 5-10 years of infestation, HWA selectively kills eastern hemlock, a foundation species that is often dominant, strongly shapes its environment, and is functionally unique. Hemlock is likely to be abruptly replaced by hardwoods, generating an immediate shift in ecosystem characteristics that is often exacerbated by preemptive and salvage logging. EAB kills all species of ash within 2-4 years; ash trees generally occupy less than 40 percent of a forest and overlap functionally with other hardwoods. Ash is a high value timber species and is selectively logged with fewer impacts than hemlock. EAB is present in isolated populations across Massachusetts and we are monitoring for it at HFR. GM has resurged after 25 years of suppression by a fungus-virus complex and is variably defoliating oaks, a dominant and functionally important group, along with other species. Tree mortality generally requires repeated infestations in patterns that vary regionally, but GM defoliation statewide increased 10-fold from 2015 to 2016. Across much of the region, including HFR, outbreaks are sporadic and light. Affected areas exceeding 10,000 km^2, experience chronic outbreaks that are essentially unstudied due to their slow decline, low mortality, and minimal human response. These three insect-host-systems span a wide gradient within the conceptual space of insect virulence and magnitude of ecosystem change; by contrasting their impacts we will advance a generalizable understanding of population, community and ecosystem response to invasive insects.

Given the very different nature of these insect-host complexes, anticipated type and magnitude of the subsequent ecosystem and human responses, and timing of their spread and impact to HFR, we plan to take distinct approaches and devote different levels of resources to studying each. For EAB and GM we plan an approach similar to our earlier efforts on HWA: establish studies remote to HFR to develop an understanding of the impacts across a range of sites and to guide intensive studies at HFR when it arrives. We have studied the slow spread of HWA across southern New England since LTER II and have conducted a parallel long-term hemlock removal experiment (see § 1.1.6.). We have developed a comprehensive study at HFR—including eddy-flux, large stem-mapped plots, above- and belowground measurements, intensive lidar profiles, and aquatic and hydrological studies—of this natural experiment as it unfolds during LTER VI. We expect a substantial transformation as evergreen forests switch to deciduous hardwoods, especially black birch, but question the timing, magnitude and duration of changes in primary production, organic matter, N cycling, and hydrology.

The following activities will: (*i*) build on our integrated research program to interpret the consequence of hemlock loss and (*ii*) examine differences among the three forest insect-host systems to understand the long-term and broad-scale effects of invasive forest insects on ecosystem dynamics.

Specific Research Questions:

Q1. How does the loss of a foundation species – hemlock—due to an invasive insect alter ecosystem function, especially the cycling of C, N, and water? What are the impacts of replacing this unique conifer with hardwoods on belowground processes and aquatic ecosystems?

Q2. How do population, community, and ecosystem responses to invasive insects differ depending on the host tree's ecological role, infestation pathway, and mortality rate?

Q3. What are the extent, rate, and variability of invasive insect damage at a regional scale, how do these differ by insect, and what are the potential impacts on future forest communities and ecosystems?

Proposed Activities

2.3.1. *Hemlock Decline and Replacement* (*Q1*)

Lead Investigators: Barker Plotkin, Blanchard, Colburn, DeAngelis, Finzi, Foster, Frey, Fulweiler, Melillo, Munger, Orwig, Williams

We will expand our integrated studies on the consequences of hemlock loss including: (*i*) ecosystem measurements in permanent plots (established in 1995) in a 7500 km^2 transect from Connecticut to Vermont; (*ii*) comparison of ecological responses between logged, girdled, and HWA-infested trees in the hemlock removal experiment; and (*iii*) comprehensive measurements of ecosystem dynamics in the hemlock-dominated section of the 35 ha stem-mapped ForestGEO Plot, including integrated changes in ecosystem C cycling. We will initiate two new long-term studies to address major gaps in the understanding of foundation species loss: (*i*) comparative study of soil microbial responses in association with established belowground measurements and (*ii*) analyses of biogeochemical, hydrological, and biotic responses in hemlock-dominated streams.

Soil Ecology of Hemlock Loss. The limited work addressing how hemlock loss alters belowground properties and processes suggests that the transition from hemlock to black birch will result in a loss of soil C from the organic horizon, a stimulation of the N cycle (i.e., enhanced net nitrification and N mineralization)[177] and an increase in soil pH. In LTER VI we propose a comprehensive assessment of belowground C pools and fluxes, along with characterization of microbial communities and soil organic matter chemistry. We will establish soil C monitoring plots as part of the belowground observatory, BeCON, described above (see § 2.1.2). We will couple biogeochemical (root and microbial biomass, soil C and N pools, soil respiration, N cycling), microbial physiological (growth, activity, and C use efficiency), molecular (fungal and bacterial diversity and community composition) and soil chemical (pH, soil organic matter chemistry) approaches to assess ecosystem responses.

Aquatic Ecology of Hemlock Loss. Hemlock loss and replacement by hardwoods is expected to lead to changes in litterfall inputs, forest evapotranspiration, surface water hydrology (e.g., seasonal streamflow/stormflow dynamics), stream temperature, decomposition, and nutrient release [178–181]. These dynamics will have far reaching effects as they alter downstream receiving water primary productivity and food web structure [182, 183] by changing watershed N:P:Si export ratios and nutrient availability [e.g., 184–186]. New measurements in LTER VI will include weekly stream nutrient sampling, as well as targeted seasonal storm sampling, to quantify nutrient export, including N, P, and Si at our three gaged stream locations; resampling (since LTER IV) of stream invertebrate communities; and use of the RHESSys hydrologic model in conjunction with long-term forest, soil, hydrological and ET measurements to quantify water yield responses to hemlock loss.

2.3.2. *Contrasting effects of individual insect pests (Q2)*

Lead Investigators: Barker Plotkin, D'Amato, Orwig, Pan, Pederson, Thompson

To assess EAB and GM effects in comparison to HWA we will establish a network of long-term plots regionally and bolster existing permanent plots at HFR. We hypothesize that EAB will induce a rapid, but modest, decline in forest productivity but little change in above and belowground environments, soil processes [cf., 187], and composition as existing species (e.g., sugar and red maple, birches) replace ash. In stands with chronic GM defoliation we expect reduced oak growth and forest productivity and a diminishing role for oak – in contrast to its increasing role in stands not affected by insect pests [e.g., 57]. Plot selection will be guided by Landsat analyses (see § 2.3.3) that identify oak forests repeatedly defoliated by GM over the past decade. We will measure the pace of decline and mortality of the host species, the pace of regeneration by replacement tree species, short- and long-term changes in forest productivity and N cycling, and changes in vegetation composition and structure of different age classes, from tree seedling to canopy trees. Repeated measurements of individual trees will be complemented by tree-ring reconstructions of growth declines and releases over the history of each stand.

2.3.3. *Regional impacts of invasive insects (Q3)*

Lead Investigators: Ollinger, Orwig, Pasquarella, Thompson

We will examine the spread and host-mortality associated with HWA, EAB, and GM using Landsat observations of New England's forests. With imagery every 8 to 16 days, the complete 30+ year Landsat record (1985-present) enables characterization of abrupt changes, long-term trends, and short-term changes in forest condition associated with insect damage. We will extend the approach of Pasquarella et al. [188] that fit harmonic regression models to time series of Landsat observations at each 30 m pixel to map historic and ongoing GM defoliation (Fig. 9). This approach is well suited to analyzing long-term trends and for generating near-real-time infestation maps that are useful for management. We will modify these analytical approaches for spatiotemporal mapping of HWA and EAB impacts in ways that best capture their distinct spectral signatures. Ongoing work with Landsat to improve maps of forest composition [114] will aid in understanding spatial patterns in damage and landscape-scale host-pest relationships. Landsat results will be validated using FIA plots, monitoring plots, and ground-based lidar measurements (see § 1.2.4.).

Regional spread and mortality maps will help parameterize the FLM for scenario modeling. Regional simulations of infestations will be further anchored by site-specific observations where spectral properties from tower-based and drone-deployed imagers are coupled with eddy-flux, sap-flow, and vegetation biomass/growth to define the functional relationship between ecosystem function and remotely-sensed properties. We will use the FLM to simulate scenarios of infestation and quantify impacts on forest composition and function (i.e., C cycling) and services (see § 2.5.1).

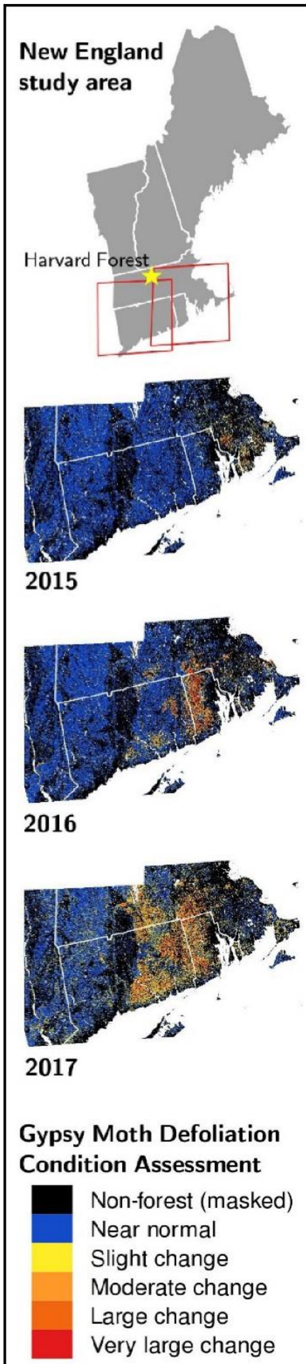

Figure 9. Spatial and temporal patterns of gypsy moth defoliation, reconstructed from Landsat time series for two pilot scenes. Additional time series approaches will be developed for HWA and EAB to examine regional trends in invasive insect damage.

2.4 The Modern Human Land-use Regime

Overarching Question:

How does New England's land-use regime—i.e. the types, frequencies, intensities, and spatial patterns of land-use—affect forest structure and function at local to regional scales?

For the past 400 years, human land use has been an inexorable driver of ecosystem change in New England. From the microbial to macrosystem scale, the region's history reveals the power of land use to reshape ecosystems and leave an enduring legacy. In the past, however, forest ecosystems recovered to re-exert functional control over ecosystem processes at local to regional scales. Modern land use is distinct in quality and intensity, leading to landscape alterations that are more pronounced and persistent than the impacts of Colonial agriculture. The land-use regime [sensu, 189] includes variable rates, patterns, and intensities of forest conversion, harvesting, land protection, and agriculture. Research during LTER I-V support the hypothesis that the near-term (<100 years) ecological consequences of modern land-use—in terms of its effects on the distribution, structure, composition, and function of ecosystems—will far exceed those of natural disturbance regimes and/or other GCDs. Nonetheless, large knowledge gaps limit our ability to understand and characterize New England's land-use regime and predict its consequences to the region's ecosystems and society.

The properties of New England's land-use regime vary along complex natural and human gradients, creating challenges for characterization or prediction. Forests cover >80% of the region, with 70% occurring in more than 800,000 parcels managed by individual private landowners [190], whereas agriculture covers only 7% of the region and is relatively stable or slightly expanding due to growing demand for local food. Since 1985 more than 350,000 ha of forest have been converted to commercial, residential, and energy (e.g., transmission and pipe lines, solar arrays) development, marking a reversal of a 150-year trend of forest expansion [75, 76]. Today, more than 20% of forest area is within 30 m of a non-forest edge, with strong regional gradients in edge type and density [191]. While harvesting is a less intense and ephemeral land use, it is widespread and exerts significant impacts on regional C stores and forest composition and structure. Indeed, harvesting is a larger cause of canopy tree mortality than all other causes combined [192]. Annually, ~3% of privately-owned forests are harvested—twice the rate of public land. More than 50% of private harvests remove < 25% of the woody biomass [78]. Robust conservation initiatives permanently protect 23% of the region from development, half of this since 1990. However, protected lands are disproportionally rural with little threat of intensive development [81].

We propose to expand our understanding of regional land-use regimes and their consequences on ecosystem functions and services through: (*i*) remote sensing and data assimilation of public databases, surveys, and studies; (ii) field studies, and (*iii*) expansion of our regional land-use scenarios and simulation framework developed during LTER V. Specifically, we propose to answer the following questions:

Specific Research Questions:

Q1. How do major changes in regional land use and land cover—the fragmentation of forests by development, regionally variable timber harvesting regimes, and increasing pace of land protection—impact forest C cycling, structure, and composition and alter the long-term trajectory of regional forest development?

Q2. How is the focus on local food production altering grassland (pasture, hay) management, the balance between forest and farmland, regional C storage, and conservation management for biodiversity?

Q3. What are the consequences of these shifts in land use on regional wildlife habitat and how are these altering the distribution and consequences of species with major landscape impacts—moose, deer, and beaver?

Proposed Activities

2.4.1. ***Land use impacts on forest composition and C storage (Q1)***

Lead investigators: Hutyra, Pasquarella, Meyer, Thompson, Williams, Wofsy

Through their protracted recovery from past land use, New England forests continue to accrue biomass and serve as a globally important C sink [6, 21]. However, forest conversion and harvesting decrease the rate of sequestration and restrict the region from reaching its C storage potential. In LTER VI we will use the Landsat record, long-term U.S. Forest Service FIA data, and our FLM to quantify spatial and temporal patterns and uncertainties of the land-use regime's impact on forest C. We will compare the region's realized forest C sink to its potential sink in the hypothetical absence of land use [sensu, 193]. By partitioning the impacts of forest harvesting versus conversion we will quantify variation in land-use effects across the region (e.g., rural, suburban, urban) and by land owner groups (e.g., private woodland owners, public agencies, forest industry). We will then examine the effect of public and private land protection on the land-use regime and on forest C stores. Using the FLM, we will test hypotheses and explore scenarios for achieving sustainable provision of goods and services while minimizing impacts on forest C.

Understanding how the spatial configuration of land use affects forest dynamics will be a major topic of study. Conversion is fragmenting and perforating forests and creating forest edges that may strongly alter ecosystem processes. A recent study [194] reported a 64% increase in forest biomass growth within 20 m of forest edges in suburban Massachusetts, which has potentially significant implications for regional C accounting. However, questions abound. We will expand a set of forest edge plots at HFR (est. 2015) to quantify rates of C cycling at different edge positions as a function of their light and microclimatic environments. New plots will be established in forest fragments of various sizes along an existing 100 km transect from the urban Harvard campus to HFR in rural Petersham. Measurements will focus on characterizing biotic and abiotic conditions as a function of distance from different types and aspects of forest edges, including light, soil temperature/moisture, air temperature, leaf area, tree growth, and soil respiration.

To scale plot-level analyses of edge effects to the region, we will build on a recent USDA grant (see Fac. § L5) by coupling tower-based SIF measurements in the EMS tower footprint (see § 2.1.2) with satellite-based regional assessments of SIF and land use. Specifically, we will quantify variations in SIF as a function of land use, land-cover adjacency, and proximity to edge through a spectral unmixing of GOME-2 SIF measurements. We will also analyze spatial patterns in biomass and growth estimates from FIA plots in relation to edge distances (using precise FIA locations). The FIA analysis will help regionalize our results and explore how soils, climate, and species interact with landscape fragmentation to affect C dynamics. Finally, we will use these results to modify the FLM to account for species-level differences in productivity and mortality in relation to edges and to improve estimate of forest C and composition in alternative land-use scenarios.

Forest harvesting is less apparent than conversion, but its impacts on C and composition are greater and more widespread. To assess the consequences of harvest regimes on forest structure and function, we will expand our recent analyses of social and biophysical variation in regional harvest frequency and intensity. Using FIA data and unique state harvest databases we will quantify patterns of trees harvested and retained. We will use the FLM to simulate the long-term consequence of alternative harvest regimes, including the removal of select species and sizes (e.g. high-grading) on composition and test hypotheses related to the role of harvesting in the long-term regional decline of oak and concurrent expansion of red maple. We will also use the 30+ year Landsat record to quantify changes in harvest regimes and forest structure in northern New England, where there have been a widespread ownership transitions from traditional forest industry to investment organizations. Landsat time series approaches, including the Continuous Change Detection and Classification algorithm [195, 196], will be used to characterize the spatial distribution of harvesting, with particular emphasis on developing new algorithms for improved detection of low intensity changes in forest structure, i.e. partial harvesting.

2.4.2. ***Regional agricultural dynamics (Q2)***

Lead Investigators: Contosta, Donahue, Foster, Frey, Hoopes

Farmlands play important ecological roles in New England, driving climate change through C dynamics and land surface properties; providing habitat for declining plant and animal species; impacting hydrology and non-point-source pollution; and shaping forest patterns. Determining the spatial and temporal patterns of agricultural land use is essential to understanding regional processes, biodiversity and forest dynamics. New land-use regimes have arisen with the growing demand for local meat, vegetables, and fruits [197]. These agricultural practices include forest conversion to agriculture; pasturing to improve forage quality and soil C storage; shifts in the timing of haying to improve habitat quality; organic approaches and reduced nutrient inputs; intensification of practices to increase yield per unit area. We will analyze the Landsat record and other spatial environmental and ownership datasets to assess land-use change and integrate the results with existing forest cover and land-use information.

We will inform our regional understanding and modeling of land use through new studies and coordination of a growing network of agricultural and conservation collaborators, with a focus on grassland (pasture and hay) management. For centuries pasture has been the major agricultural land cover in New England. Grassland management is changing rapidly, yet despite considerable study in the Midwest and northwestern Europe, there is poor understanding of the extent and ecological and conservation consequences of these approaches in New England. The interaction of these approaches and GCDs is even less well-understood. To begin to fill this gap we will leverage ongoing funding from NSF, the Wildlands and Woodlands project, and regional foundations (Fac. § L2) to focus particularly on consequences of the timing and intensity of grazing and hay production on above- and belowground ecosystem structure, composition, and function (especially soil C and N) and on vascular plant, bird, and lepidoptera species of conservation concern. This work will focus on the new 40-ha Harvard Farm.

2.4.3. ***Land-use impacts on wildlife*** **(Q3)**

Lead Investigators: DeStefano, Faison, Foster, Pasquarella

Historical transformations of New England's landscape have generated major changes in habitat quality and distribution that have driven a wholesale change in animal communities [198]. Most notably, in the past 150 years, the southern New England region has shifted from supporting abundant species of grasslands and early successional habitats and a few large native vertebrates [199] to supporting large and generalist forest species such as coyote, fisher, bobcat, black bear, deer and moose. Additionally, since their expansion and reintroduction in the 1960s, beaver have shaped many waterways and regional hydrology, with great impacts on adjoining forests [200]. HFR research has focused strategically on three aspects: (*i*) regional syntheses to utilize our strengths in history and land use [101, 201], (*ii*) species of conservation concern tied to cultural landscapes (e.g., grassland species; see § 2.4.2), (*iii*) and the dynamics and consequences of species with strong feedbacks on forest landscapes (e.g., beaver, deer, and moose) [73, 202].

In LTER VI we will strengthen this research by capitalizing on our regional analyses of land-cover change interactions with GCDs. Our regional syntheses will expand by integrating wildlife habitat and distribution data along with vertebrate species richness data from the USGS Gap Analysis Program with historical and simulated land-use scenarios [203]. The focused studies on key grassland taxa at HFR will be strengthened by a comprehensive synthesis of the dynamics of grassland habitats and species across all six New England states. Finally, our studies of wildlife influence on ecosystem dynamics will incorporate expanded ungulate studies and new analyses of landscape changes driven by the expansion of beaver. Our effort to engage conservation groups and municipalities in the study of long-term changes in New England forests and ungulates [74], has greatly expanded the number of exclosure studies on moose and deer. We will also undertake new efforts to characterize beaver impacts and, as part of our regional change detection analysis, we will use the Landsat record to document and analyze the timing and patterns of this significant ecological force.

2.5 Interacting Global Change Drivers

Overarching Question:

What are the relative and interactive effects of climate change, invasive insects, and land use on the underlying forest template? How do these effects vary across ecosystems with different land-use regimes (e.g., rural, suburban, and urban landscapes)?

The future of New England, like all regional socio-ecological systems, will be the product of integrated human and natural processes that are affected by multiple GCDs at local to global scales [204–206]. Research to understand and disentangle the relative, aggregate, and interactive effects of GCDs on forest ecosystems is crucial to informed environmental policy and decision-making [207].

Beyond their direct impacts, GCDs have indirect and interactive effects on ecosystems that are qualitatively distinct and potentially as impactful. In some cases, GCD interactions can affect the extent of impacts, such as when climate change increases or constrains the spread of invasive insects. In other cases, GCD interactions are mediated by human land use, as is the case when invasive insects or climatic extremes (e.g., ice storms, hurricanes) motivate landowners to harvest their threatened or dead trees. Frequently, such harvests include undamaged trees to increase income or to gain economies of scale. Similarly, climate change has led to emerging markets for biomass fuels and C credits, which ostensibly mitigate C pollution, while changing land-use regimes by incentivizing either harvesting or land protection, respectively. Predicting these types of interactions among GCDs and quantifying their effects on socio-ecological systems is often intractable; nonetheless, integrated assessments and system dynamics models can be valuable for testing assumptions, generating new insights, and taking meaningful action.

In LTER V we developed a regional simulation framework that has proven useful for projecting the effects of individual and interactive GCDs. We also developed and simulated five land-use scenarios co-designed with diverse stakeholders from across the region (Fig. 6); one projects a linear continuation of the recent land-use trends while the others portray plausible alternative land-use regimes [85]. We showed that a continuation of recent land-use trends will have a much greater near-term impact on forest composition and C storage than climate change. Further, we showed that alternative scenarios of land use that envision different societal responses to climate change could increase or diminish land-use effects, depending on the scenario. In LTER VI we propose a suite of activities designed to examine the interactive and indirect effects of GCDs in ways that can contribute key ecological insights and inform policy and management. We will build upon the multi-factor simulation experiments conducted through the New England Landscape Futures Project (see § 1.5) and will significantly expand our development and application of a whole-system modeling framework to explore scenarios of global change.

We will broaden the development of the scenario-to-simulation-to-society research platform through: (*i*) tighter linkages between empirical data and the model, including improved maps of disturbance and forest species composition based on the full Landsat record and other environmental datasets (See § 2.3.3.); (*ii*) the addition of new model capabilities, such as representation of invasive insects and climate variation and extremes (See § 2.2.4.); (*iii*) improved and expanded analysis of model outputs with an emphasis on ecosystem services, and (*iv*) engagement with stakeholders to explore scenario implications in specific locations that represent differing land cover-land-use regimes (e.g., rural, suburban, urban) and decision contexts (e.g., conservation priority-setting, land-use planning, climate action planning).

Specific Research Questions:

Q1. Will the ecological impacts associated with the land-use response to climate change (e.g. biomass energy, carbon credits) and invasive insects (e.g. salvage and pre-emptive harvests) exceed the direct impacts of those GCDs?

Q2. What feedbacks to the climate system are associated with alternative land-use regimes?

Q3. How do interacting GCDs affect land use and natural resource decision making at sub-regional scales?

Proposed Activities:

2.5.1. ***Land-use response to changing environments (Q1)***

Lead Investigators: Foster, Lambert, Meyer, Ollinger, Orwig, Thompson

Leveraging a recent CNH systems award (Fac. § L11), we will expand the FLM modeling framework to simulate the land-use response to the presence of HWA, EAB, and GM (see § 2.3.3) as they interact with climate change. In the case of HWA, we will quantify and project the interactions among climate change, HWA spread, and host-mortality. HWA is killed by cold winter temperatures, and the northward spread of hemlock loss has been qualitatively linked to winter temperature thresholds [208, 209]. We will first map the spatiotemporal pattern of hemlock loss in New England since 1985 (using Landsat) in association with high-resolution (800m) weather data (PRISM), then predict northward spread in the FLM to 2100 using multiple climate scenarios. Once the insects are fully incorporated into the FLM, we will then couple it to an interactive landowner behavior model to simulate alternative patterns of harvest in response to insects. Through the CNH award, we recently conducted a survey of ~1000 landowners to understand how changing social and environmental conditions may affect harvest behavior. Using these data, we will create a land owner typology to capture regional variation in the harvest response to the threat or presence of invasive forest insects. We will then map the typologies at the parcel level and use it to parameterize harvest behavior in the FLM. Using this simulation framework, we will test the hypothesis that forest land-use change *in response to* invasive insects will have greater ecological consequences than the insects by themselves (Fig. 10).

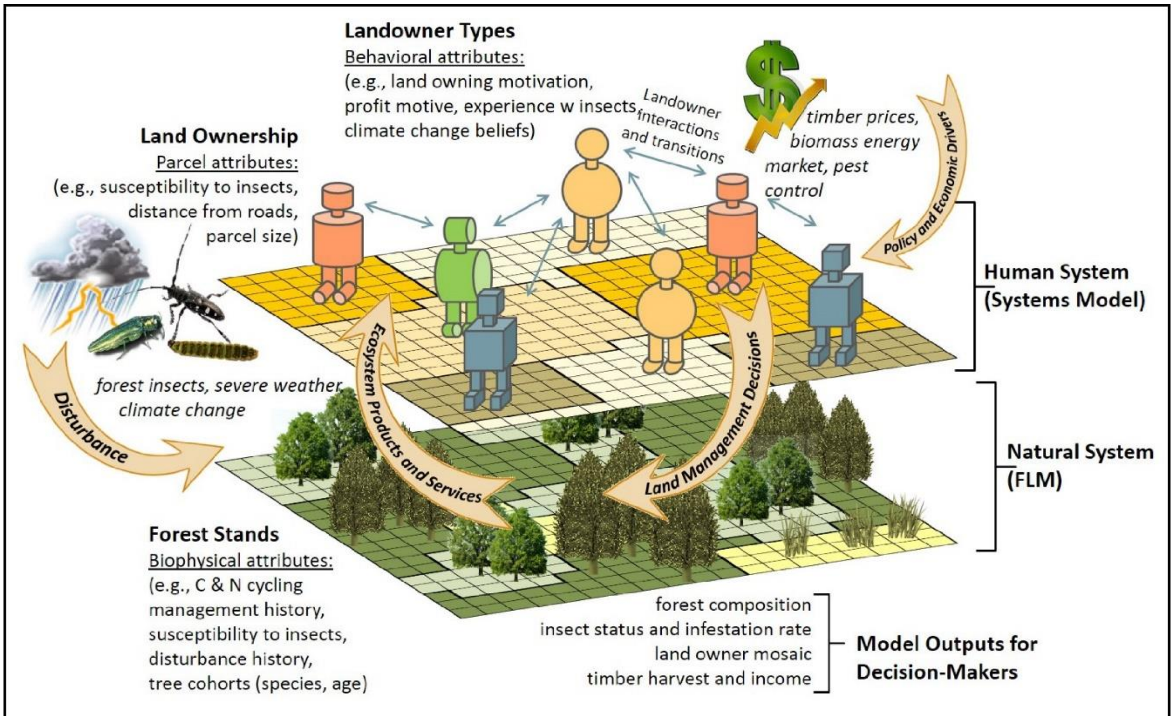

Figure 10. By coupling a systems model that represents diverse landowner behaviors to the FLM we will test the hypothesis that forest land-use in response to GCDs will have greater ecological consequences than the GCDs by themselves.

This coupled landowner and FLM modeling framework offers great potential to examine the land-use response to a range of plausible changes to the environment and society. We will simulate a series of land-use scenarios that represent different conditions imposed by GCDs to better understand the regional ecological consequences (e.g., changes to aboveground C, tree composition, wildlife habitat) of the aggregate landowner response to: (*i*) changes in biomass energy markets; (*ii*) changes in land protection incentives (e.g., C credits, payments for ecosystem services); and (*iii*) frequency of climate change related disturbances (e.g., wind and ice storms) and associated salvage response.

2.5.2. *Climatic response to changing land use (Q2)*

Lead Investigators: Munger Ollinger, Thompson

Although land-use effects on CO_2 exchange capture much of the climate forcing effects when averaged globally, effects on biophysical processes such as evapotranspiration, albedo and surface roughness (i.e. vegetation structure) typically dominate at local to regional scales[210]. Collectively, these variables can cause substantial variation in local surface temperature, soil moisture, and other factors that have important ecosystem consequences and potential climate feedbacks. We began to address these processes in LTER V using a retrospective modeling approach that asked whether the widespread historical conversion of forest to pasture in 18th and 19th century New England could have altered the region's climate [95]. Model validation was based on data collected from a cluster of eddy-covariance towers in NH that were established for side-by-side comparison of land-atmosphere exchange in forest and agricultural landscape units [149]. In LTER VI, we will advance this line of inquiry using a three-stage process of data assimilation and modeling: (*i*) we will combine soil, productivity, and land management data from existing forest, residential, pasture, and agroforestry systems with productivity and land-atmosphere exchange data from HFR. These data will be used to conduct and validate point-based simulations with Community Land Model v5 for prediction of land-use-climate feedbacks representative of New England land-cover types; (*ii*) we will link the CLM model to the simulated land-use scenarios (see § 1.3.) to connect future changes in land use with changes in local and regional climate. Model biases and areas of uncertainty identified during stage one will be used to identify areas of sensitivity and parameter uncertainty in future climate and land-use feedbacks simulations; (*iii*) climate forcing datasets from CLM simulations of regional land-use-climate feedbacks will be used to inform other LTER VI ecosystem model simulations of productivity, water dynamics, and biogeochemical cycling.

2.5.3. *Interacting GCDs at the sub-regional scale (Q3)*

Lead Investigators: Foster, Lambert, Meyer, Thompson

Sub-regional case studies enable more detailed examination and comparison of the relative influence of interacting GCDs within rural, suburban, and urban landscapes. Sub-regional analyses are also useful when regional simulations are at too coarse to be useful for stakeholders working in land-use planning and conservation. Accordingly, we will leverage existing RCN and AISL awards and foundation grants (see Fac. § L6) to conduct case studies in four sub-regions in collaboration with established partners and stakeholders to assess the relative influence of the direct, indirect and interactive effects of GCDs. For each analysis, we will undertake analyses relevant to conservation, planning, and management that are likely to include consequences of the landscape scenarios on ecosystem services, such as storm-water runoff and flooding, air and water pollution removal, habitat quality and connectivity, recreation, and human health benefits. We will further evaluate the potential impacts of alternative conservation incentive and policies schemes (e.g., creation of parks, avoided development incentives) on landowner behavior with regard to management and conservation. The sub-regions are diverse landscapes with varying amounts of rural, suburban, and urban land, and different land-use regimes and decision contexts, where the stakeholders have strong interest and the capacity to utilize scenarios research. These subregions include: (*i*) Charles River Watershed Association in metropolitan and suburban Boston, (*ii*) the

Hudson to Housatonic Regional Conservation Partnership in southwestern Connecticut with its mixture of post-industrial and wealthy suburban landscapes; (*iii*) Kestrel Land Trust in the rural to urbanizing Connecticut River Valley with a mixture of productive farmland and expansive forests, (*iv*) Hubbard Brook watershed in rural forested northern New Hampshire; and (*v*) the Sebago Clean Waters partnership in southwestern Maine. The case studies will advance the science with greater spatial and mechanistic specificity, while enhancing avenues for application and engagement.

3. Broader Impacts

3.1 Strategic Outreach & Communication

3.1.1. Engaging Decision-makers

***New England landscape futures (scenarios):* from local- to regional-scales.** Our broader impacts are centered on stakeholder engagement through the landscape scenarios research (see § 2.5.3). At the local scale, we focus on landowners, land managers, land trust staff and town officials working at local scales. Our macro-scale focus includes conservation, land use, and policy entities working at regional to national levels. Our primary vehicles for engagement include: *(i)* an interactive scenario exploration process in the four specific sub-regions with their diverse social and biophysical characteristics along a rural-urbanizing gradient (see § 2.5.3); and *(ii)* the creation and sharing of an online scenario explorer tool for New England. These activities will be coordinated by the SPE and will build from the science products of LTER V, the Scenarios, Services and Society Research Coordination Network, and the work of the Highstead Foundation, leveraging substantial funding from a NSF AISL grant (see Fac. § L6).

For each case study (see § 2.5.3), we will engage with the lead stakeholder organization to tailor science products for their sub-region by convening listening sessions to define stakeholder information needs, determining the demography of their audiences, and co-designing effective science communication products (e.g., digital and paper maps, research summaries, newsletter articles or blogs, social media posts, presentations). We will collaborate with the stakeholders to integrate the online scenario explorer tool and digital maps for their region into their organizations' websites to create seamless information sharing that expands the reach of our science.

In addition to local products, we will partner with stakeholders to develop and deploy an interactive scenario exploration process and online tool that will engage stakeholders and scientists across the region to broaden understanding of the scenarios and their implications for ecosystem services, and to build the capacity of organizations across the region to use the scenarios in their conservation and policy decisions. The interactive process will entail professionally facilitated workshops across New England that bring together scientists, local managers, and state organizations to promote mutual learning and use of the scenarios for environmental decision-making. Workshop participants will engage with the new online scenario explorer tool and participate in small-group exercises. The workshops will be designed so that attendees will gain the knowledge and skills needed to bring the scenario explorer tool and interactive process back to their organizations and communities, thereby increasing their capacity and magnifying the impact of our work using a train-the-trainer model. This interactive process will use the scenario science products to promote social learning and the capacity of stakeholder groups to make land-use decisions in the face of high uncertainty [211].

The online scenario explorer tool will exist in two forms: *(i)* a DataBasin repository of all of the simulation products for scientists and GIS users, and *(ii)* a story-based tool, like ESRI Story Maps, with an interface accessible to broad audiences. Through the AISL grant, we have engaged FernLeaf Interactive as a consultant for the tool's graphic design and computer programming. In addition, we anticipate that local to national decision-makers will benefit from supplemental synthetic materials that distill the broader policy implications of our research. To serve those groups we will generate four-page policy briefs and conduct in-person meetings to share the key points and discuss their application to pending land-use policy decisions (e.g., adaptation and resilience plans, land-use incentives, zoning, conservation finance).

Wildlands and Woodlands (W&W). W&W has become one of HFR's most influential science outreach activities by synthesizing LTER research into publications, presentations, and online resources for managers, policymakers, and leaders seeking to conserve and manage the New England landscape of forests, farmlands, and communities for the benefit of nature and society. W&W publications (2005, 2010, 2017) were developed with extensive input from stakeholders and scientists regionally to nationally and accompanied by press releases, webinars, stakeholder briefings, high-profile public events, and ongoing engagement. The vision has been embraced by the media (editorials in every New England state), state and federal decision-makers, and regional conservation and forestry organizations. In LTER VI, we will continue to use W&W to bring HFR science to bear on important policy and management issues.

Much of the success of W&W is due to the partnership forged with the non-profit Highstead Foundation whose staff and support have helped advance our science, accelerate landscape-scale conservation, host W&W events, and develop and disseminate information on science and regional conservation activity. We will collaborate with Highstead to advance future scenarios research and engage decision-makers in activities that link HFR scenarios with regional conservation priorities, land-use planning, and forest- and carbon-policy developments. Two other Highstead-funded W&W initiatives will be central to LTER VI outreach: (1) Academics for Land Protection in New England (ALPINE), which connects faculty, students, administrators, and alumni at New England colleges and universities to advance research, education, and practice in land conservation; and (2) research on conservation finance innovation.

Massachusetts Keystone Project. Recognizing the importance of private landowners, we will continue to advance science to action through the successful *Keystone Project*, a 25-year collaboration between HFR, University of Massachusetts, and state extension offices that educates community leaders in natural resources and conservation, and integrates science, decision-making, and stewardship. The program annually trains 25 community leaders in a three-day workshop at HFR, led in part by HFR Co-Is. Participants pledge to educate others in conservation topics afterward; to date, over 325 graduates of the program form the state-wide Keystone network and serve as conservation leaders in their communities.

3.1.2. Engaging Media Professionals

Expanding media coverage. The Harvard Forest Outreach Manager collaborates with Co-Is, staff from the Science Policy Exchange, Wildlands and Woodlands, Highstead and the LTER, NSF, and Harvard news offices, to boost media coverage of HFR research and promote the value of long-term ecological research. The number of high-impact media clips published about HFR research has doubled since LTER V began. In LTER VI, we will expand these efforts, including strategic placement of op-eds and editorials that broaden our science findings to policy- and community-relevant practice.

Journalist training. In LTER VI, we will continue site visits from mid-career science journalists from the Knight Fellowship Program at MIT, science journalism students from Boston University, and an array of practitioners from the New England Science Writers, to expand ecological knowledge in all phases of journalistic training and to create new opportunities to feature long-term research in the media.

Scientist training. We will offer communication trainings to students and Co-Is, focusing on techniques that build strategic storytelling skills and develop a nuanced understanding of audience and targeted communications approaches. LTER VI workshops will focus on LTER themes, such as global change drivers, scenarios, uncertainty, and long-term data and ecological processes.

Assessing impact. Through the leveraged PES@LTERs grant (see Fac. § L6), in LTER VI we will provide engagement pathways for audiences to access HFR research (e-news, podcasts), and will systematically assess the impacts of this engagement on attitudes/outcomes for both scientists and the public.

3.1.3. Engaging the Wider Public
The Harvard Forest Outreach Manager (Co-I Hart) and Co-Is coordinate several projects that engage the public in HFR research and increase understanding of the value of long-term ecological research through: *(i)* museum programs; *(ii*) LTER Arts; *(iii*) online resources; and *(iv)* books written for broad audiences.

***Museum programs*.** The newly renovated Fisher Museum (re-opened in 2017) provides a nearly limitless platform for new educational tools and exhibits. The focal exhibit remains the 1930s-era dioramas depicting 230 years of land use in New England; during LTER VI, a variety of new displays will augment these, including: (*i*) a timeline that connects 110 years of Harvard Forest research to 30 years of LTER research, (*ii*) a lidar-based 3D "diorama" of the modern-day Harvard Forest, projecting LTER research sites continuously onto an auditorium wall, developed in collaboration with a 2018 Bullard Fellow, (*iii*) new interpretive signage and maps depicting the range of ecosystems and research explored in the forest and new Harvard Farm, and (*iv*) displays of real-time data and footage from meteorological and hydrological sensors, eddy-flux towers, phenology web-cams, and wildlife cameras. New content will include interpretive trail materials; evening events for the public; and exhibits and presentations at the Harvard Museum of Natural History in Cambridge and the Arnold Arboretum in Boston.

LTER Arts. Through the Bullard Fellowship program, artists and writers will continue to engage with Co-Is to produce interpretive works that are publicized widely with public audiences, school groups, and the media. Works will be exhibited in the Fisher Museum, on HFR interpretive trails, at the Harvard Museum of Natural History in Cambridge (which hosts tens of thousands of visitors each year), and in exhibits at national science meetings (e.g., ESA, LTER ASM). In LTER VI, we will support artists whose work collaboratively investigates key GCDs, and is displayed regionally and nationally.

***Online resources*.** Enhanced tools for public engagement will include a fully updated, mobile-friendly HFR website that includes: *(i)* real-time streaming of, and distance participation in, weekly HFR research seminars and annual LTER Symposium; *(ii)* (near-) real-time sensor data and visualizations from meteorological and hydrological sensors, eddy-flux towers, phenology web-cams, and wildlife cameras; *(iii)* the interactive scenarios mapping tool; *(iv)* virtual tours of Harvard Forest interpretive trails, and *(v)* a new online Field Guide to the Harvard Forest Laboratory and Classroom to encourage student and public explorations of ecologically and cultural unique sites at the Forest. All online resources are amplified through a comprehensive social media strategy that includes Facebook, Twitter, and Instagram – followed by over 5,000 people and receiving over 50,000 impressions a month.

***Publications for broad audiences*.** HFR has a strong record of producing books with strong uptake from non-scientists and the media. LTER VI products will include two booklets: *Voices from the Land* will describe the scenarios process and stories, and *Changes in New England* will present the modeling results from scenarios and their ecological consequences. A new synthesis volume will engage original LTER I investigators and LTER VI Co-Is in revisiting the major findings from the Foster and Aber's synthesis volume and chart future directions. Finally, a new diorama booklet will integrate the history, details, and lessons of the Fisher Museum dioramas for the modern landscape.

3.2 Training and Scholarship: K to Post-Graduate Education

The *K-12 Schoolyard LTER Program* *(sLTER)* engages >3,000 students in >50 schools in hands-on data collection and analysis through four Co-I generated research protocols linked to GCDs (climate and phenology, invasive insects, land use). We will strengthen these connections by leveraging foundation and NSF Macrosystems funding to: *(i)* broaden the forest dynamics project to include C sequestration and land change around each school, and *(ii)* integrate a new phenology curriculum.

Three annual teacher professional development workshops will be led by Co-Is to: (*i*) provide protocol training; (*ii*) guide data analysis; and *(iii)* enhance peer-to-peer mentorship and curriculum-sharing. The annual data workshop will accommodate differing levels of teacher familiarity with the sLTER database and graphing system to (i) enter and organize classroom data online and (ii) work toward self-determined graphing objectives. The sLTER database is publicly available and growing. We will expand the capacity for comparison/graphing of cross-site data with HFR graduate students and Co-Is to improve this platform for comparing and analyzing regional trends.

Additional sLTER goals include: (*i*) advance network-wide K-12 data literacy initiatives of the LTER Education Committee; (*ii*) create pathways for schools with high proportions of underserved students to visit HFR and begin an sLTER project; and (*iii*) continue engagement of teachers in RET experiences, to increase teacher retention and generate new lesson plans connected to field protocols.

The HFR Summer Undergraduate Research Program in Ecology (>30 years) supports diverse students from colleges across the U.S. in interdisciplinary, team-based field and laboratory research, long-term data analysis, and science communication. With support from NSF REU, NASA, NEON, LTER, Harvard, and other sources, we will host 20-30 students annually in our 11-week program by recruiting in partnership with ESA's SEEDS program and the Community College Undergraduate Research Initiative. Seminars and workshops supplement students' capacity for successful research, including a 3-phase workshop in data analysis using R, a two-part science communication training, orientation to diversity and inclusion issues, and a seminar in spatial analysis. We track students' long-term educational and career goals/outcomes through pre-, post-, and annual surveys, and facilitate their continued connection to HFR and LTER through social networking and reunions at national meetings.

For Harvard students, we will offer intensive courses centered on HFR research and sites, including a Freshman Seminar on global change studies, conservation ecology and practice, and a short course focused on land-use change and stakeholder engagement. In LTER VI we will host Graduate School of Design courses that employ future scenarios and ecosystem research in urban design.

Students from dozens of colleges and universities are guided on HFR field trips by Co-Is and education staff each year. In LTER VI, we will work with faculty to document the use of HFR resources in university courses and internships and develop a shared faculty resource on the HFR website. Using leveraged NSF funding through PES@LTERs (see Fac. § L6), we will assess how the online tool for the landscape futures project is used by public groups, including university classrooms.

For our *graduate students and post-docs*, spread across more than a dozen institutions in the Northeast, we will increase opportunities for networking by *(i)* hosting students and post-docs as presenters in our annual LTER Symposium and weekly Lab Group meetings, *(ii)* hosting follow-on meals and mixers for HFR students and Co-Is and advertised, with travel support, to students from other LTER sites in the region, and *(iii)* providing mini-grants for on-site synthesis summits. By hosting annual workshops on LTER-related tools, HFR graduate students are integral to our education of K-12 and undergraduate audiences. To address demand from graduate students for outreach opportunities, LTER VI will support their time and training in leading HFR site tours and contributing to sLTER projects.

The *Bullard Fellowship Program* annually supports eight scientists, conservationists, historians, artists, etc. for 6-12 months at HFR investigating regional GCDs. Fellows bring new perspectives to LTER research and its relevance to policy and practice. In LTER VI, we will use this program to advance cross-site activities by encouraging individuals or teams to collaborate on synthetic studies.

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(Top Ten Publications referenced in Table 1 are listed in blue followed by their associated datasets.)

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IV. Project Management Plan

S3.1. Administration and Oversight. HFR is unusual in the LTER Network as it is administered at the research site, which is home to: the PI, many Co-Is, postdocs, and students; major field sites and research facilities; data management; and administrative and financial offices. Harvard Forest is a department in the Faculty of Arts and Sciences of Harvard University; administers the Masters in Forest Science, Charles Bullard Fellowship, the Summer Undergraduate Research Program in Ecology; offers undergraduate and graduate-level courses on-site and in Cambridge; and mentors Ph.D. students through on-campus departments and LTER Co-Is. Funding for core operations and senior staff at the Forest comes from university endowments with research, education, and policy activities strongly supported by grants and foundations.

As PI and Director of the Harvard Forest, David Foster is responsible for project administration, coordination of science meetings and the HFR research group, and site representation in the LTER Science Council. Other Harvard Forest-based senior scientists and co-Is include Jonathan Thompson, Kathy Lambert, Aaron Ellison, Emery Boose, Clarisse Hart, David Orwig, Audrey Barker Plotkin, and Neil Pederson. The local LTER team meets approximately monthly with Director of Administration Edythe Ellin, and regularly with the LTER Science Team (co-Is Jonathan Thompson, Serita Frey, Lucy Hutyra, Audrey Barker Plotkin, Adrien Finzi, Bill Munger, Dave Orwig, Emery Boose), which is responsible for data management, research and educational policies and directions, inter-site collaborations, and representing HFR in the scientific community. LTER Co-Is focus much their research on Harvard Forest-based and regionally distributed studies. All proposals for new research are submitted through an on-line system, reviewed and approved by the Science Team based on compatibility with existing research and the long-term HF Land Use Master Plan (Barker Plotkin et al. 2015. More than 500 applications have been received since 2005, including ~100 new scientists.

Information management and technology activities are overseen by Emery Boose (Information Manager) and Julie Pallant (System and Web Administrator) with assistance from Julie Hall (Data Analyst), Mark Van Scoy (Field Technician), Manisha Patel (Laboratory Manager), Brian Hall (GIS Assistant), and Elaine Doughty (Archivist). Clarisse Hart (Outreach Manager) oversees public relations, informal education via the Fisher Museum and, with Schoolyard LTER Coordinator Pamela Snow, K-12 education. Edythe Ellin (Department Administrator), oversees facilities, finances, personnel and assists the summer undergraduate research program leadership of Aaron Ellison (REU PI) and Manisha Patel. The skilled Facilities staff is equipped for experimental manipulations, forestry operations, and construction and maintenance of research projects.

S3.2. Enhancing Collaborations. The growth of integrated research, education, and policy programs at HFR has been accompanied by an exploding user-group of national and international scholars, educators, students, agencies, and organizations: >100 outside scientists representing >40 institutions; more than three dozen state and federal agencies and NGOS; and >3,000 K-12 students from >50 schools. The Summer Undergraduate Research Program annually draws a diverse student body from >400 applicants. More than 30% of the 265 students hired since 2005 come primary undergraduate institutions including community colleges; one-third of the students are from groups traditionally underrepresented in science. The Summer Program also serves to recruit new researchers as we prioritize new investigators and projects to receive intern funding. Undergraduates are engaged in team projects that link multiple students and multiple mentors in broad projects; these teams expand collaborations between new and long-term projects. We actively seek to enhance collaboration by non-LTER scientists, educators, artists, and practitioners by widely advertising all opportunities—Bullard Fellowships, Summer Research Program, Annual Ecology Symposium, weekly seminars, special events, facilities, and long-term field sites, measurements and experiments—through our web page, social media, e-mailings, and print venues.

S3.3. The Annual HFR Ecology Symposium (third week in March) is paired with workshops and focused discussions as forums for synthesis, exchange, mentoring, and development of new research directions and collaborations. The symposium engages 125+ attendees, including all researchers working at the Harvard Forest, is widely advertised, open to all scientists, students, and professionals in the northeastern US, and is a major venue for forging new collaborations. The symposium is well attended by agency staff, conservation and forestry leadership, and educators, with abstracts published on-line (http://harvardforest.fas.harvard.edu/symposia). The schedule emphasizes synthesis, critical review of program development, and opportunities for interdisciplinary interactions (*e.g.,* microbial, historical, population, community, and ecosystem ecologists, atmospheric scientists, and social scientists).

S3.4. Strategic Assessment, Planning, and Investment. HFR has exhibited strong stability over 25 years: a single lead institution whose director has served as PI; a small group of lead collaborating institutions (University of New Hampshire, Boston University, Ecosystems Center at MBL, University of Massachusetts and three departments at Harvard University); one Information Manager (co-I Boose), and a core set of experiments and measurements. The management framework has effectively accomplished major personnel transitions—LTER PI from John Torrey to David Foster (1994); collaborator leaderships from John Aber to Serita Frey and Scott Ollinger (2006); Steve Wofsy to Bill Munger (2006); Fakhri Bazzaz to numerous Harvard PIs (2006); Jerry Melillo in transition to Serita Frey (2018)—and has integrated new institutions, research directions, senior personnel and students, with a strong focus on diversifying participant age, gender, and backgrounds.

In LTER VI, we will use this platform to broaden and strengthen HFR based on a process of strategic assessment, planning, decision-making, and investment that we initiated in LTER V and that engaged the HFR community, the mid-term Site Review, NSF Program Officer and Harvard University administration. This strategic planning exercise was grounded in the need to prepare for changes in senior science, information management, and educational personnel; new or expanded collaborations with national partners (Smithsonian Institution ForestGEO plot, NEON's Northeast Domain construction, USFS, DOE/Ameriflux); the formation of the Science and Policy Exchange; and planned expansion of collaborating institutions and PIs.

S3.4.1. Transitions in HFR Leadership in Science, Administration, and Education. LTER VI will embrace two major transitions. David Foster will continue as PI through the grant submission, strongly assisted as he has been since 2016 by Jonathan Thompson, senior ecologist at the Forest and lead in the scenarios, modeling and landscape ecology team. During the first year of the new grant Thompson will transition to PI, while Foster will remain Director of the Harvard Forest and actively engaged with the LTER program as a Co-I. Administration of the LTER will lie with Thompson, with strong financial, site, and administrative support continuing from the Harvard Forest. To further ensure a smooth succession, a leadership team representing diverse science themes and management activities will aid Thompson with decision making and project management (Frey representing below-ground studies; Orwig representing studies of pests and pathogens; Barker Plotkin representing long-term plots and REU integration; Hart representing outreach and education; Boose representing Information Management; and

Foster representing the host institution). Aaron Ellison, Senior Research Associate and long-time leader of the REU and Summer Undergraduate Research Program will retire in 2020. Senior Researcher and Site Coordinator Audrey Barker Plotkin, who has shared an increasing role in this important program will assume its leadership at that time. Other Co-Is who will be departing from active participation in LTER VI include Elizabeth Chilton, Elizabeth Crone, Eric Davidson, Dianna Doucette, David Kittredge, and William Sobczak.

S3.4.2. New Investment in Individuals and Infrastructure. Beginning in LTER VI we have initiated new programs and utilized new funds to diversify PI and institutional participation. In LTER VI this will include

- Valerie Pasquarella (BU), regional forest change using the 30-yr LANDSAT archive
- Robinson (Wally) Fulweiler (BU), stream biogeochemistry in declining hemlock stands
- Lucy Hutyra (BU), carbon cycling in fragmented forests
- Martha Hoopes, biodiversity in agricultural landscapes
- Yude Pan (USFS), GCD impacts on regional C cycling
- Bryan Shuman (U Wyoming), paleo reconstructions of climate change impacts on forests
- Spencer Meyer (Highstead), land use science
- Alix Contosta (UNH), agricultural land use.

S3.4.3. Leveraging investments from partnering institutions through LTER. The Smithsonian invested in the installation and first survey of the 35-ha, stem-mapped ForestGEO plot, which encompasses major LTER hydrological, ecosystem, and eddy flux infrastructure. Beginning in LTER VI, HFR and the Harvard Forest will cover one-half of the costs of plot censuses.

V. Data Management Plan

The Harvard Forest Data Archive contains scientific data collected over the last 30 years by scientists working at Harvard Forest plus selected data from earlier studies recorded in the Harvard Forest Archives. As a rule, datasets are included if they support a publication or are deemed to have long-term scientific or historical value, regardless of the source of funding. The Harvard Forest endorses the LTER Network data access policy and (with rare, documented exceptions, primarily for student thesis projects) data are made freely available online within two years of collection. New datasets and updates are posted simultaneously to the Harvard Forest (HF) Data Archive and to the Ecological Data Initiative (EDI) repository (with a few exceptions explained below); the former contains the most recent version of a dataset, while the latter maintains permanent copies of all submitted versions.

Personnel

The following personnel at Harvard Forest have duties related to information management or information technology:

- Dr. Emery Boose (Information Manager). Duties include scientific information management, networking and telecommunications, database programming, meteorological and hydrological measurements, and informatics research.
- Julie Pallant (System & Web Administrator). Duties include system administration, website management, HF Archives and Library management, and user support.
- Brian Hall (GIS Specialist). Duties include GIS support for research and conservation projects.
- Julie Hall (Assistant Data Manager). Duties include preparation of data and metadata files for long-term archiving.
- Elaine Doughty (Archivist). Duties include management of archives and library collections.

Boose serves on the LTER Information Managers Committee and participates regularly in LTER technical working groups and workshops.

Cyberinfrastructure

The location of HFR administration and core researchers on the field site (120 km west of the Harvard main campus in Cambridge MA) provides many advantages, but also presents challenges for developing the cyberinfrastructure (CI) required for an LTER site. After many years of effort and resources from NSF and Harvard University, the Forest now has CI capabilities comparable to those on campus (Table 1).

Table 1. Cyberinfrastructure Development at Harvard Forest

Year	LTER Cycle	Internet Access (bps)	Campus Network (buildings)	Servers	Computers	Field Network (sites)	Real Time Data	Pheno-Cams	HF Datasets Online	K12 Datasets Online
1988	I	none	0	0	6	0	0	0	0	0
1994	II	14.4K	0	0	30	0	0	0	0	0
2000	III	1.5M	3	0	60	0	0	0	47	0
2006	IV	1.5M	6	4	100	0	1	0	95	46
2012	V	100M	7	Virtual	100	7	1	5	193	189
2018	VI	100M	8	Virtual	100	20	8	11	305	301

During LTER V, there were substantial increases in the number of sites on the field wireless network, the number of sites with real-time data posted on the HF website, the number of phenology cameras (Phenocams) in the forest, and the number of online datasets in the HF Data Archive and the LTER Schoolyard database.

HF Data Archive

Metadata in the HF Data Archive are encoded in EML version 2.1.0 and stored in eXist (a native XML database) on the HF web server. Data files are stored in a structured file system on the same server. The Data Archive includes direct links to data files and numerous options for searching (by ID number, investigator, keyword, taxon, dates, and general search) and browsing (by ID number, title, investigator, keyword, taxon, location name, research topic, study type, LTER core area, and project status) through XQuery forms. Web pages for individual datasets are generated directly from the EML using an XSL style sheet stored in eXist. All submitted materials (data and metadata) and an exact copy of the materials posted on the web server are stored on a separate server. Servers are backed up daily at the university.

As a rule, the data in the HF Data Archive exactly match the most recent data in the EDI repository, with a few exceptions: (1) Meteorological and hydrological data are archived monthly to the HF Data Archive and annually to the EDI repository, with a note in the dataset abstract to consult the HF website for the most recent data. (2) In a few cases where datasets are large enough to raise storage issues on the HF web server (~1 gigabyte), the data reside in the EDI repository only and the data links in the HF Data Archive point there. (3) In rare cases where datasets are exceptionally large (many gigabytes), data may be stored in other suitable repositories with appropriate references. These include genomics data (GenBank), Lidar data (ORNL DAAC), and high-resolution scenario model output (Data Basin).

The HF Bibliography is also stored in eXist, with direct links to PDF files on the HF web server for most publications and various options for searching (by author, title, and research topic) and browsing (by author and year). Datasets and publications are cross-indexed (many to many), so users can identify publications associated with a particular dataset or datasets associated with a particular publication.

During LTER V, submission of Harvard Forest datasets to the EDI repository was initiated and completed. Following up on a recommendation from the LTER IV mid-term review, dataset previews for each data object were added to the HF Data Archive to make it easier for users to assess data objects for possible use; the PDF preview files include variable definitions, summary statistics, and time-series plots or scatterplot matrices generated by an R script (hf-dataset-preview.R) available on the HF website. To facilitate use of this script and data analysis in general, all datasets were standardized to use common date-time formats and R-compatible variable names and missing value codes. Other improvements to the HF Data Archive included using the browse feature to identify and correct misspellings, adding MD5 checksums for all data objects, updating the intellectual rights statement to use the Creative Commons CC BY license, and checking and updating cross-references between datasets and publications.

Data Life Cycle

The role of data management in the data life cycle at Harvard Forest is described below.

Experimental Design. All scientists conducting research at the Forest are required to submit or update an online research project application (RPA) annually for each of their projects. The RPA includes a data section where the applicant must indicate acceptance of the HF data access policy (i.e. data will be submitted for publishing online within two years of collection unless the project is a student thesis project; other exceptions must be approved by the Director). The RPA system makes it easier to track the progress of research projects and the submission of data. New RPAs are not approved if the applicant has not met his or her past data obligations.

The Information Manager is regularly consulted for large projects and proposals and is available for consultation on any project. Scientists submitting proposals for research at the Forest are strongly encouraged to include a line item for information management in the proposal budget.

Data Collection & Processing. Project scientists are responsible for collecting, entering, and processing their own data. The Information Manager and other HF staff are available to help with questions in many areas, including data logger and instrument setup, network communications, data processing, database programming, quality control, and statistical analysis.

Validation. Project scientists are ultimately responsible for the quality of their own data. However many problems are discovered by IM staff in the process of preparing datasets for archiving, by (1) visual inspection of the data, (2) running the dataset preview R script (mentioned above), which detects many data type errors and creates exploratory plots that can be used to spot outliers or unexpected patterns, and (3) evaluating the dataset in the EDI repository, which provides numerous checks for consistency, completeness, and congruence between data and metadata. Simple problems with the data are corrected by the IM staff; more complicate problems are referred back to the scientist.

Documentation. Project scientists are required to complete and submit a metadata form (available for download on the HF website) for all new and updated datasets. IM staff use this information to create an EML file for the dataset (currently this is done using Oxygen, an industry-standard XML editor, and Morpho, a software tool developed at NCEAS for creating EML files), often supplementing the information provided by the scientist with additional knowledge about how keywords, titles, location names, etc. have been used in the HF Data Archive. The resulting EML file is then checked for completeness and correctness. If essential information is missing, incomplete, or unclear, the IM staff engage in a dialogue with the scientist to resolve the problem.

Curation. All submitted materials (data and metadata) are archived in a shared file system on a university sever, organized by dataset ID and date of submission. When a new or updated dataset is ready to publish online, it is uploaded simultaneously to the HF Data Archive and to the EDI repository (with a few exceptions as noted above). For the former, this means adding the EML file to the eXist database and copying the data files to the HF web server. For the latter, it means using the EDI tools for uploading a dataset to the repository.

Access. All Harvard Forest datasets can be discovered and accessed via the HF Data Archive and the EDI repository and discovered via DataONE. As noted above, the HF Data Archive supports many options for searching and browsing made possible through eXist and XQuery forms. Keywords are drawn from the LTER controlled vocabulary and a much shorter HF controlled vocabulary. Other useful information not currently supported in EML is stored under the EML element *additional Metadata* and can be browsed in the HF Data Archive. This includes project status (ongoing or completed), research category (one or more of the 12 major research categories used throughout the HF website), and study type (long-term measurement, short-term measurement, historical, paleological, and modeling). All HF datasets can be freely downloaded under a Creative Commons CC BY license.

Analysis. As noted above, all HF datasets were standardized during LTER V to use common date-time formats and R-compatible variable names and missing value codes. These changes facilitate integration and analysis of HF datasets for R users (who can download and use the data directly) and for users of other analytical tools (who can more easily modify the data to meet the requirements of other tools).

The Information Manager and other HF staff are available to help scientists working at Harvard Forest with questions related to data integration and analysis.

Publication. HF datasets in the EDI repository receive a digital object identifier (DOI) that may be used to reference a particular version of a dataset in a publication.

Related Projects

HF Archives. The HF Archives contains extensive records of institutional research and forestry operations from the establishment of Harvard Forest in 1907 to the present, including original research data and notes, publications and theses, a map library, comprehensive forestry and vegetation records of all HF properties, photographs and slides, regional records such as historical soil and forest surveys and census data, and physical research samples. An online catalog of the Archives is stored in eXist and available on the HF website.

HF Website. The HF website provides current information on all aspects of Harvard Forest, including research, education, and conservation. Features include news and highlights, current events, real-time data, and photo galleries, as well as information on conducting research, educational opportunities, initiatives in policy and conservation, and making reservations for visits and conferences. Content is tagged (e.g. to major research category) to support comprehensive browsing. The website is implemented in Drupal on a Linux server on the main campus.

Schoolyard Database. An online database for the LTER Schoolyard program was created in LTER V using the same server and software stack as the Administrative Database (described below). The new system allows teachers and students participating in the LTER Schoolyard program to submit their data online, where it is reviewed by HF staff and uploaded to the main database. Once uploaded, the data can be freely downloaded or graphed in various ways (using built-in R scripts) to create downloadable JPEG files. Over the course of LTER V the database was extended to include the new Changing Forests protocol (permanent forest plots) and to support cross-site analyses. A similar online database for the **Wildlands & Woodlands** project was also implemented during LTER V.

Administrative Database. The Harvard Forest has an extensive online database system for applications (research projects, REU students, Bullard Fellows, etc.) and reservations (housing, lab space, field sites, vehicles, research equipment, etc.). The system utilizes an Apache-MySQL-Perl/PHP software stack on a Windows server on the main campus. Originally designed by outside consultants, the system is managed by Boose with database programming by Pallant (Perl) and Boose (PHP).

Field Wireless Network. The Harvard Forest field wireless network (HFFW) was commissioned in 2010 and provides high-speed Internet access to field sites with line power across the Prospect Hill Tract. The HFFW is an extension of the Harvard University network and uses a combination of 5.8 GHz radios (for tower-to-tower transmissions above the canopy) and 900 MHz radios (for tower to ground transmissions through the canopy). At each major research site, radios are connected via Ethernet to a network switch and Wi-Fi access point. The HFFW allows collaborating scientists to access their field equipment and download data remotely using a Harvard VPN. The HFFW is jointly managed by Harvard Forest (Boose) and Harvard Network Operations.

During LTER V, 11 new sites were added to the HFFW, including 4 stream gages, 2 wetland gages, the HF snow pillow, and 2 new Phenocams at the Harvard Farm. The real-time system that collected and posted meteorological data to the HF website every 15 minutes was converted to R and extended to include data from the stream gages, wetland gages, and snow pillow and to create 30-day plots (updated every 15 minutes) for each site.

Informatics Research. In 2015 Co-Is Boose and Ellison and computer scientists Margo Seltzer (Harvard University) and Barbara Lerner (Mt. Holyoke College) received an award from the NSF SSI program to continue research in data provenance, with a focus on the R statistical language. The goal of the project is to develop software tools that collect and use provenance to make data analyses easier, more transparent, and more reliable for scientists. More detailed information and all software tools are available on GitHub at: http://github.com/End-to-end-provenance.

VI. Postdoctoral Mentoring Plan

Postdoctoral Research Fellows supported by HFR are mentored directly by senior research personnel and have access to outstanding training opportunities at Harvard and collaborating universities, and throughout the network of HFR collaborators. For example, post-doc strategic professional development resources are offered by Harvard's Office for Postdoctoral Affairs, including: monthly talks; panels; discussions on *curriculum vitae* and resume writing, interviewing, mentoring, writing grant proposals, formal speaking, and presentation development; an informational series on starting and managing a lab; individual, one-on-one career counseling; grants to attend training courses (*e.g*., R Programming, GIS methods, etc.); and a course on professional and ethical practices in research to meet NSF and NIH requirements. HFR postdocs will be provided with office space, lab space, computer, and internet access at the Harvard Forest, Boston University, and University of New Hampshire where they can regularly interact and meet with their direct supervisors to discuss research progress, data analysis, manuscript development, and long-term career opportunities. Post-docs typically attend at least one national conference per year, attend weekly seminars by outside speakers, and are able to participate either in person or electronically, in weekly Harvard Forest lab meetings, where research staff regularly share ideas, datasets, and manuscripts for feedback, and have opportunities to practice presentation skills in a collegial, supportive academic environment. They are also invited to participate in the annual graduate student and post-doc gathering described in section III.A. Finally, post-docs from all institutions can mentor undergraduates in the Harvard Forest Summer Research (REU) program and often lecture or teach courses in nearby colleges and universities.

VII. Facilities, Equipment, and Other Resources at the Harvard Forest

Section 1. HF Facilities and Equipment.

A stand-alone department in Harvard University's Faculty of Arts and Sciences with a full-time staff of approximately forty, the Harvard Forest in the central Massachusetts town of Petersham has operated as Harvard University's 1500 ha field laboratory and classroom for ecological research and education since 1907. With intensively documented and diverse forests, wetlands, streams, water bodies, and pastures complemented by expansive research, educational, and residential facilities, the Harvard Forest provides a complete base for research, education, and outreach/demonstration in forest, ecosystem, and historical ecology, conservation, land-use policy, and biosphere-atmosphere interactions.

Since the launch of LTER I in 1988, the Harvard Forest has witnessed phenomenal growth in scientists, educators, students, collaborators, research, education, and outreach programs, and associated laboratory, computing, archival, teaching, housing and field-based research facilities. The Harvard Forest is the core site for the Northeast domain of the National Ecological Observatory Network (NEON), which provides remote sensing, biosphere-atmosphere, ecological, and organismal data streams that strongly complement the LTER program. It is also a sentinel site in the DOE Ameriflux program, and hosts a 35 ha forest plot that is part of the Smithsonian Institution's Global Earth Observatory (ForestGEO).

Shaler Hall, the 2,800 m^2 central building for research, administration, and education, contains 30 offices, a 10,000-volume library, dining facilities for 50, laboratories for paleoecological, morphological, computational, and GIS studies, and a complete herbarium of the local flora. There is teleconferencing available in the seminar room (cap. 35) and video-teleconferencing in conference room (cap. 12) as well as meeting space for up to 125 in the Fisher Museum and 100 in the Common Room. The recently renovated **Fisher Museum** houses the Harvard Forest Models, twenty-three dioramas portraying the history, ecology, and management of central New England forests, video displays for visitors, extensive displays featuring LTER and related research and outreach, and the auditorium used for the annual LTER Ecology Symposium.

Laboratories. The 370 m^2 John G. Torrey Laboratory is a multi-investigator, multi-institutional facility adapted for diverse research interests and educational activities. It includes two fully automated research greenhouses, offices, and wet-labs for ecophysiology, biogeochemistry, microbial/molecular ecology, and microscopy. Facilities include chemical storage and fume hoods, two biosafety (laminar-flow) hoods, LI-3100 Area Meter, Lachat 8500 autoanalyzer, Elementar CHN analyzer, distilled and RO water system, ultra-clean dishwashers, autoclave, -80^{o} C freezer, refrigerators, microplate reader, spectrophotometer, precision balances, dissecting microscopes, muffle furnace, and drying ovens. The Paleoecology Laboratory includes several compound and dissecting microscopes, a pollen and spore reference collection, drying and combustion ovens, and a fume-hood and centrifuge for preparation of pollen, charcoal, macrofossil, and ^{14}C samples. The Dendrochronology Lab contains two Velmex tree-ring measuring systems and International tree ring data base (ITDRDB) software.

The Landscape Ecology Lab at Harvard Forest provides support for a range of high-performance research computing applications and specializes in large-scale spatial simulation modeling. Computing resources include a Dell Server Cluster with 64 Intel cores running at 2.4 GHZ with 20M cache and a total of 256 GB RAM, a 1.4 TB Solid State Drive, and 36 TB of storage space. The lab has a contract with Harvard Research Computing center for offsite backup to ensure data security and access to the 100K+ core Harvard Odyssey Cluster, which has been configured for running CLM, LANDIS-II and other forest models.

The **Harvard Forest Archives,** the physical part of the Information Management system, includes a soil/plant tissue archive facility that can provide storage for over 32,000 samples, a cold storage facility, and an extensive document archive of the Harvard Forest, comprising maps, photos, data sheets and related materials representing >110 years of research activity and electronic cataloging for all types of materials. The archives also include the Harvard Forest Herbarium, which contains >3,400 specimens of >700 species collected locally over the last 110 years.

Field Facilities. The four major tracts of the Harvard Forest are managed under a long-term plan that includes three land-use zones: wildland reserves (no active management or destructive research); experimental forests (active manipulation allowed for scientific, educational and demonstration purposes); and woodlands (harvesting and scientific manipulation allowed). The Environmental Measurement Station (EMS), the oldest continuously operated eddy-flux and micrometeorological tower in North America (*est*. 1989 as a central measurement system in LTER I), is located approximately 1.7 km from Shaler Hall, in the middle of the 400 ha Prospect Hill Tract. The Hemlock flux tower provides parallel measurements in an old hemlock forest in the early stages of infestation by the hemlock woolly adelgid. A flux tower located in a rapidly re-growing clearcut has been decommissioned as part of LTER V planning. NEON has established a 39 m Fundamental Instrument Unit (FIU) tower that is running in parallel with the EMS at a distance of ~125 m. Two walk-up towers (funded by a NSF Facilities grant in 2012) provide access for canopy measurements, additional instrumentation and education. A mobile canopy access vehicle with a 22 m reach (funded by a NSF MEU grant in 2001) and three-person platform adds great flexibility for diverse studies. Collaboration with NEON has extended primary electrical service throughout the core area of Prospect Hill to the towers, existing stream gages, biogeochemical measurements, and numerous long-term experiments. An automated weather station (*est*. 2001) complying with LTER Climate Committee guidelines replaces the earlier manual station (*est*. 1964) while a snow pillow (*est*. 2009) measures the water content of snow pack.

Large experiments. Core LTER experiments accommodate many outside collaborators and include: Soil Warming (*est.* 1991, 2001, 2006), Nitrogen Saturation (*est*. 1988), Hurricane Manipulation (*est.* 1990), Detritus Inputs and Removal Treatments (DIRT, *est.* 1990), four large clear-cuts with deer/moose exclosures (*est*. 2008-12), and Hemlock Removal Experiment (*est.* 2003). Forest harvesting for timber and cordwood to fuel the central biomass heating facility is conducted under a long-term management plan to support studies of ecosystem dynamics and a comprehensive analysis of carbon dynamics with small-scale biomass heat production.

Permanent plots address the diverse needs of HFR and collaborating scientists, and include: >100 400 m^2 plots across all forest types on Prospect Hill (*est*. 1937); control plots associated with each experiment (*est*. 1988-2012); Lyford Grid (*est.* 1969), a 3 ha oak forest measuring all stems, downed wood and disturbances; and a 0.7 ha Hemlock Grid (*est.* 1989) for measuring tree structure and function. The 35 ha ForestGEO forest dynamics plot (*est.* 2011-2012) encompasses hemlock, oak and wetland communities, two eddy-flux towers, and aquatic infrastructure. All stems (>1 cm) are measured and mapped and extensive non-destructive complementary measurements are taken on ecosystem process, plants, and animals. With support from the Smithsonian, Harvard Forest, DOE, and the LTER program, the Forest will conduct its first recensus in the summer of 2018.

Information Technology. An optical fiber circuit (100 Mbps) connects Harvard Forest to Harvard University's main campus and to the Internet. Wired and wireless network access is available in all offices and labs and in some residences. The field wireless network (funded by NSF and jointly managed by the Harvard Forest and Harvard Network Operations) provides high-speed Internet access to major experimental sites across the Prospect Hill Tract. Scientific data from all projects (regardless of funding) are documented and posted in the HFR data archive within two years of collection. Virtual servers for the HFR website and associated databases (as well as shared disk space for HF staff) are provided by the university on the main campus in Cambridge MA.

The **five-person facilities staff** is skilled in experimental manipulations, forestry operations, construction, and maintenance. Large equipment includes a back-hoe, tractor, skidder, dump truck, flat- bed truck, three pick-up trucks, and a 12-passenger van. The staff operates a wood-working shop and small technology shop that serves as the center for equipment design and building maintenance. A new sawmill (2018) is operated as needed.

University-owned **housing** includes Raup and Fisher Houses located adjacent to Shaler Hall that accommodate visiting groups and the summer undergraduate research program (capacity of 40), and an additional 15 residences occupied by visiting faculty, graduate students, and post-doctoral fellows and their families.

Section 2. Leveraging of LTER Funds, Institutional Support, and Personnel

Leveraging of Funding

The metaphor commonly used to describe the LTER program is the "glue" for holding long-term studies together and inspiring collaborative research (J.T. Callahan, S. Collins, H. Gholz; pers. comm.). This statement is certainly true for the HFR LTER where an extremely active group of scientists undertake a wide range of site-based, cross-site, and regional studies with support from many major public funding agencies in the US (see Current and Pending). Thus, while the LTER funding provides absolutely essential support for long-term sampling, measurements, and data management, additional activities (e.g. paleoecology, hydrology, HWA studies, future scenarios modeling, regional sampling of N effects, and expansive outreach programs, etc.) are leveraged through funding from other competitive grants to individual CoIs. HFR PI and Harvard Forest Director Foster coordinates integration of HF and HFR budgetary activities to advance key LTER objectives (e.g., IM, Computer Infrastructure and Web Site, Archives, Laboratories, Education and Outreach, LTER Research Coordination, LTER Research Assistants, GIS, facilities, Vehicles, Administrative support).

Leveraged awards explicitly referenced in the proposal are listed by name below, other more general support listed by program.

L1. Finzi – DOE; NSF-DEB
L2. *Foster* - Highstead Foundation; NSF Ecosystems
L3. *Frey* - NSF LTREB: "Soil warming and forest ecosystem feedbacks to the climate system"; DOE: "Resolving Conflicting Physical and Biochemical Feedbacks to Climate In Response To Long-Term Warming"; DOE: "The "Who" and "How" of Microbial Control over Soil Carbon Dynamics: a Multi – omics, Stable Isotope Probing, and Modeling Approach"; Additional support leveraged from NSF-DEB,
L4. *Hart* - Foundation funding from: Highstead, New England Forestry, Blue Hills, Conservation & Research Foundation, Orchard, and Fields Pond; New England Natural Resource Council; NSF LTEaRts; Harvard Museum of Natural History.
L5. Hutyra – NASA: "Validation and Application of OCO-2 Data in the Northeast Corridor"; USDA: "Fragmentation effects on forest productivity across managed ecosystem gradients"; Additional support leveraged from NIST, USDA, and NASA
L6. *Lambert* – NSF ASIL: "Embedding Public Engagement with Science at Long-Term Ecological Research Sites"; NSF-SEES RCN: "Scenarios, Services, and Society"; Additional support leveraged from the Highstead Foundation
L7. *Munger* – DOE "AmeriFlux Core site: Operation of the Harvard Forest Core Site in the AmeriFlux

Network Management Project (ANMP)"
L8. *Ollinger* – NSF-Macrosystems; USDA Northern Research Station
L9. *Orwig* – Smithsonian: "Forest Global Earth Observatory – Partial Support for Harvard Forest re-census"
L10. *Richardson* - NSF Macrosystems: "PhenoCam project"; NOAA: "Modeling analysis of long-term trends and variability in tower fluxes";
L11. *Thompson* – NSF Coupled Natural and Human Systems: "Assessing the potential for climate change and forest insects to drive land-use regime shifts"; USDA: "Fragmentation effects on forest productivity across managed ecosystem gradients"; NSF-SEES RCN: "Scenarios, Services, and Society"; Additional support leveraged from the Highstead Foundation

Institutional Support

The HFR LTER program receives strong support from each of the institutions and departments that collaborate on this program (i.e., , University of New Hampshire – Complex Systems Research Center, Northern Arizona University, Boston University and Harvard University - Department of Organismic and Evolutionary Biology, Earth and Planetary Sciences, and Harvard Forest). In particular, the Harvard Forest provides the 1400 ha land base for the program, facilities for research, housing, and public as well as formal education, and personnel involved in many of the research, educational, and administrative activities described in this proposal, including: D. Foster (Director), D. Orwig (Senior Ecologist), N. Pederson (Senior Ecologist), J. Thompson (Senior Ecologist), C. Hart (Outreach and Development Manager), J. Pallant (Network and Web Administrator), E. Ellin (Director of Administration), J. Bowlen (Accountant), J. Meskauskas (Administrative Assistant), and E. Doughty (Librarian/Archivist Assistant). In addition, graduate student involvement in HFR LTER activities is supported by the Master's and Ph.D. programs at Harvard University.

Senior Project Personnel contributing directly to the project. (* Partial support from LTER VI funds)

David Foster (PI) is Director of the Harvard Forest and has three decades of experience with the design and implementation of regional-scale vegetation and conservation studies. He will be regularly engaged in project development, design, and execution as well as the administration of personnel and financial aspects. He will represent HFR at LTER Science Council Meetings.

***Jonathan Thompson (CO-PI)** is a Senior Ecologist at Harvard Forest. He leads the regional forest modeling and other landscape ecology research. He will transition to LTER PI during the term of LTER-VI. He will be engaged in project development, design, and execution as well as the administration of personnel and financial aspects. He will also represent HFR at LTER Science Council Meetings.

***Serita Frey (CO-PI)** is a Professor in the Department of Natural Resources, University of New Hampshire. She runs the Soil Warming × N Addition Experiment, will take on leadership of the soil warming experiments from Melillo, and will advance microbial ecology work.

***Adrien Finzi (CO-PI)** is Professor of Biology at Boston University. He will be involved in synthesis and modeling of coupled biogeochemical cycles and controls on forest carbon and nutrient dynamics and establish the "BECON" soil carbon plot network.

Andrew Richardson (CO-PI) is Professor in the School of Informatics Computing and Cyber Systems at Northern Arizona University. He will be involved in phenology and remote sensing research to link the carbon cycle from leaves to regional scales.

Senior Personnel:

*__Audrey Barker Plotkin__ is HFR's Long-Term Ecological Research site coordinator and a Senior Scientist leading permanent plot studies, the Hurricane Pulldown Experiment, and will be involved in forest insect studies and many aspects of site management.

Jeff Blanchard is an Associate Professor in the Biology Department at the University of Massachusetts. He will be involved with microbial research in the soil warming experiments.

***Emery Boose** is Information Manager at HFR, will ensure that all data and metadata relevant to the project are archived and available electronically through the HFR web site, and will represent HFR in LTER information manager activities.

Elizabeth Colburn is an aquatic ecologist at Harvard Forest. She will lead benthos sampling in hemlock dominated streams.

Alix Contosta is a Research Scientist in the Earth Systems Research Center at the University of New Hampshire. She will be involved with the study of effects of pasture management systems on above and belowground ecosystems.

Anthony D'Amato is Associate Professor at the University of Vermont. He will be involved with long-term forest plot measurements and analysis.

Kristen DeAngelis is Assistant Professor in the Department of Microbiology at the University of Massachusetts. She will be involved in all soil microbial research.

Stephen DeStefano is Research Professor and USGS Massachusetts Cooperative Fish and Wildlife Unit Leader. He will be involved with wildlife research at HFR.

Brian Donahue is Associate Professor of American History at Brandeis University**.** He will be involved with studies of land-use change and their effects on New England ecosystems.

Edward Faison is Senior Ecologist at the Highstead foundation**.** He will be involved with wildlife research at HFR.

***Robinson 'Wally' Fulweiler is** Associate Professor in the Earth and Environment Department at Boston University. She will lead the biogeochemical analyses of streams within hemlock dominated stands.

Clarisse Hart is Outreach & Development Manager for Education & Research Programs. She will lead education and outreach to K-12, undergraduate and graduate students, media professionals, and the general public and will be involved in stakeholder engagement.

Martha Hoopes is Professor of Biological Sciences at Mount Holyoke College. She will be involved with the study of effects of pasture management systems on above and belowground ecosystems.

***Lucy Hutyra** is Associate Professor in the Earth and Environment Department at Boston University. She will be involved with C cycle research at all scales and will lead the forest edge research at Harvard Forest.

Jerry Melillo is Senior Scientist at the Marine Biological Laboratory Ecosystems Center. He will be involved with the long-term soil warming experiments, regional modeling, and synthesis activities.

Spencer Meyer is Senior Conservationist at the Highstead Foundation. He will be involved with analyses of land-use and land protection in their impacts on forest ecosystems.

Paul Moorcroft is Professor of Organismic and Evolutionary Biology at Harvard University. He will be involved with regional analysis of carbon exchange and forest dynamics.

***William Munger** is Senior Research Fellow in the Harvard School of Engineering and Applied Sciences. He will lead the operation of the EMS measurements and the synthesis of the carbon flux and reactive trace gas data.

***Scott Ollinger** is Professor in the Department of Natural Resources and the Environment and Institute for the Study of Earth Oceans and Space at the University of New Hampshire. He will be involved in regional remote sensing and modeling studies.

David Orwig is Forest Ecologist at the Harvard Forest. He will lead both the large study evaluating forest response to the hemlock woolly adelgid and the 35 ha ForestGEO plot. He also will work on old-growth forests, forest reconstructions, and the hemlock removal experiment.

Wyatt Oswald is Associate Professor of Science at Emerson College and a Research Associate at HFR. He will be investigating the pre-European and more recent dynamics of the vegetation associated with climate change, natural disturbances, human activity and pests and pathogens.

Yude Pan is Research Scientist at the U.S. Forest Service Northern Research Station. She will be involved with analyses of the impacts of invasive forest insects on tree communities.

***Valerie Pasquarella** is Research Assistant Professor at the Center for Remote Sensing at Boston University. She will lead the Landsat-based analyses of long-term and broad-scale patterns of forest change.

Neil Pederson is Senior Ecologist at Harvard Forest. He will lead the dendroecological research and be involved with studies of long-term forest dynamics.

Bryan Shuman is Professor in the Department of Geology and Geophysics at the University of Wyoming. He will be involved with paleoecological research to understand long term climate impacts on ecosystems.

***Pamela Snow is the** Schoolyard Ecology Coordinator.

Kristina Stinson is Assistant Professor in the Department of Environmental Conservation at University of Massachusetts. She is a population and evolutionary ecologist who will be involved in studies of exotic plants, and linkages among population, community, landscape and ecosystem studies.

Jianwu 'Jim' Tang is Associate Scientist at the Marine Biological Laboratory. He will be involved with carbon cycle and phenological studies, often based on solar induced florescence.

Christopher Williams is Associate Professor of Geography at Clark University. He will be involved in ecosystem-climate interactions studies, including dynamics of carbon, water and energy fluxes between land and atmosphere following timber harvest.

Steve Wofsy is Professor of Atmospheric and Environmental Science in the School of Engineering and Applied Sciences at Harvard University. He will be involved with measures of gas exchange between forests and the atmosphere.