Harvard Forest LTER IV – Project Summary

The Harvard Forest (HFR) LTER is an integrated program investigating forest response to natural and human disturbance and environmental change over broad spatial and temporal scales. Involving >25 researchers, 150 undergraduate and graduate students, and a dozen institutions, HFR LTER embraces the biological, physical, and social sciences to address fundamental and applied questions for dynamic ecosystems. Our work on the ecological effects of the primary drivers of forest change in New England (Human Impacts, Natural Disturbances, and Climate Change) has resulted in synthetic publications, cross-site collaborations, and effective outreach in conservation and environmental policy. HFR LTERs I-III generated: >600 publications, including 37 theses and 21 books; major syntheses: *Forests in Time*, which integrates our long-term studies of ecosystem structure and function and a Special Issue of *Forest Ecology and Management* summarizing 15 years of results from the Chronic Nitrogen Addition Experiment; a Summer Research Program (NSF-REU site) engaging ~30 undergraduates annually; inter-site investigations with regional, national and international colleagues; and comprehensive web-based databases plus 100 years of archives and samples.

At the dawn of the 21st century, we are confronted with rapidly increasing rates of land conversion, steady to increasing rates of atmospheric deposition of pollutants, continued increase in temperature and atmospheric CO_2, and the potential for more frequent *and* more intense hurricanes. Although these are global trends, the forests of eastern North America are being (sub)urbanized and fragmented more rapidly than elsewhere in the U.S., and regional impacts of pollution and climate change may be especially dramatic due to New England's location at the end of the nation's "tail-pipe". Our proposed work for LTER IV focuses on the impacts of the changes in rates and magnitudes of these key drivers of landscape change in New England and explores their consequences for regional populations, communities and ecosystems.

The transition to LTER IV represents a shift in focus from the impacts of the primary, physical drivers of forest change examined largely at a single site or landscape to a comprehensive analysis of both primary and secondary forces and responses operating across the entire New England region. This mandates a greater emphasis on the biological components of landscape change such as invasive species and pests, and the contributions of individual taxa to ecosystem processes. In addition to considering drivers we have explored in LTER I-III, we will incorporate new mensurative and experimental studies of land-cover change (resulting from forest harvesting, conversion, and land protection) and the spread of invasive species (plants, pests, and pathogens) and native ungulates that are (re)colonizing our region. Our broadened research agenda is a consequence of an increasing regional perspective, greater interdisciplinary participation, a strong commitment to inform conservation, management, and policy efforts through collaboration with mission-oriented agencies and non-profit organizations (e.g., The Nature Conservancy), and a commitment to position the HFR LTER program for inter-site and emerging research opportunities outlined by the LTER Strategic Task Force (STF) and NEON planning processes.

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HFR LTER-IV Integrated Studies of the Drivers, Dynamics and Consequences of Landscape Change in New England

I. Results from Prior LTER Support (see Section II for supporting figures)

The Harvard Forest (HFR) LTER is an integrated program investigating forest response to natural and human disturbance and environmental change over broad spatial and temporal scales. Involving >25 researchers, 150 undergraduate and graduate students, and a dozen institutions, HFR LTER embraces the biological, physical, and social sciences to address fundamental and applied questions in dynamic ecosystems (Foster and Aber 2004). The major focus of HFR LTERs I-III was on the primary drivers of forest change in New England: Human Impacts, Natural Disturbances, and Climate Change. Our work on the ecological effects of these forces has resulted in synthetic publications, cross-site collaborations, and effective outreach in conservation and environmental policy.

LTER I emphasized site-based studies of forest patterns and processes in relation to current conditions, and initiated large experiments contrasting responses to natural physical disturbance (hurricanes) vs. anthropogenic stress (N deposition and climate change). Major findings showed:

- historical land-use conditions modern ecosystem structure, processes, and dynamics;
- ecosystem functions and trajectories exhibit large inter-annual variation;
- interpretations of pattern and process require broad spatial and temporal investigations.

Consequently, **LTER II** added retrospective (historical/paleoecological) and landscape-scale analyses and incorporated land-use history and inter-annual variation in experimental design. Broadened temporal and spatial studies improved interpretations of controls of land-use history, natural disturbance, and climate on vegetation, C and N dynamics.

LTER III expanded this work, synthesizing results in journal volumes and books; investigating inter-decadal dynamics of key processes controlling C and N cycling; pursuing mechanistic studies of ecosystem and atmospheric processes to interpret long-term trajectories; contributing to local, national, and global policies in climate change and conservation; initiating hydrological, biodiversity, and wildlife studies; and expanding regional collaborations. Results from LTER III elucidated the compounding nature of multiple stressors on forest structure and function, and led to investigations of the effects of secondary drivers of forest change, including exotic species, current logging practices, interacting climatic changes and atmospheric pollution, and altered hydrology. One emergent theme from LTER III is the increasingly important role of biotic agents of forest change, such as the introductions of exotic pests, pathogens, and plants and the contribution of altered soil microbial communities, to ecosystem fluxes.

HFR LTERs I-III generated major publications, educational programs, collaborations, and data, ranging from paleoecological research to evolutionary theory and conservation policy:

- > 650 publications including 37 theses, 21 books, and two videos.
- major syntheses: *Forests in Time* (Foster and Aber 2004), which integrates our long-term studies of ecosystem structure and function; a Special Issue of *Forest Ecology and Management* (Aber and Magill 2004) summarizing 15 years of results from the Chronic Nitrogen Addition Experiment.
- a Summer Research Program (NSF-REU site) engaging ~30 undergraduates annually;
- inter-site investigations with regional, national and international colleagues; and
- comprehensive web-based databases plus 100 years of archives and samples.

Human Impacts on the Physical Landscape

In LTERs I-III, ***paleoecological and historical-geographical studies*** at millennial time scales were used to interpret major processes shaping ecosystem dynamics, assess changing relationships between humans and the environment, and provide conservation insights (Motzkin et al. 2004; Foster et al. 2005, 2006; Oswald et al. 2006). ***Vegetation, climate and disturbance histories*** based on lake-sediments and witness tree records indicate that New England was heavily forested before European settlement with regional vegetation and climate gradients controlled by topography and latitude (Cogbill et al. 2002). Late Holocene warm/dry periods at ~500-year intervals paralleled changes in oxygen isotopes recorded in Greenland (Stuiver et al. 1995) and generated substantial vegetation dynamics (Fuller et al. 1998; Oswald et al. 2006). An abrupt decline in hemlock c. 5500 BP was apparently driven by insect pests and climate change (Foster et al. 2006), whereas hurricanes were the major natural disturbance, with regional gradients in frequency and intensity (Boose et al. 2001). Native American populations were small, concentrated in river valleys and on the coast, and subsisted on hunting and gathering (Chilton et al. 2001). Fire was uncommon except in coastal regions (Parshall and Foster 2002). ***Historical ecological studies*** provide a spatially explicit record of the sequence of deforestation, agriculture, farm decline, reforestation, and forest homogenization that followed European settlement (Foster et al. 1998; Hall et al. 2002). Ecological legacies of this history include strong relationships between land-use history and forest composition and structure (Motzkin et al. 1996; 1999, 2002, 2004; Bellemare et al. 2002; Eberhardt et al. 2003), ecosystem properties (Compton and Boone 2004; Ollinger et al. 2002a, b), and invasive plant distributions (McDonald et al. 2006a; Stinson et al. 2006b; Von Holle et al. 2006). This work highlights the regional importance of ***human-mediated impacts on physical environmental processes*** and resulting secondary effects: enhanced N deposition and ozone pollution (Ollinger et al. 1993, 1997); invasive pests (Orwig et al. 2002); forest harvesting, conversion to other land cover, and ownership parcelization (Kizlinski et al. 2002; Kittredge et al. 2003); and forest protection from conversion (Kittredge et al. 2003; Foster et al. 2005; Malizia et al. 2006). ***A synthetic special issue*** of the *Journal of Biogeography* (Foster 2002) included 20 articles with lessons from historical geography for ecology and conservation. A new policy document, *Wildlands and Woodlands*, applies these lessons to regional forest conservation (Foster et al. 2005).

Cross-site studies examined broad-reaching impacts of human activities on landscape change. HFR and five contrasting LTER sites comprise a ***Biocomplexity Study*** investigating ecosystem and social dynamics when humans impose spatial and temporal signatures on ecological regimes and then respond to these coupled systems. An LTER synthesis volume from this study emphasizes the land-use legacies, cross-scale interactions, feedback loops, and changing stability regimes that govern system change and human response (Redman and Foster 2006). Interactions among land-use and natural disturbance in controlling landscape dynamics were also summarized for New England, Puerto Rico (LUQ), and the Yucatan, supported by LTER, NSF-International, and NASA (Boose et al. 2001; Foster and Aber 2004; Turner et al. 2003). In each area, past and present land-use are stronger drivers of forest structure and function than natural disturbance or environmental change. These studies identified commonalities among landscapes, re-oriented research programs, and encouraged **scientist and student exchange**. A HFR-led **Cross-site Workshop** examined population, community, and ecosystem response to the loss of foundation species (Ellison et al. 2005a). Hypotheses generated by participants from HFR, HBR, LUQ, AND, CWT, and BES LTER sites are being tested in replicated experiments at HFR and CWT. The **DIRT Network (**HFR, AND, and three

additional sites) used responses of treated plots to test predictions of biogeochemical-microbial process models for newly established sites.

HFR researchers played major roles in **LTER and national science efforts**, including NEON (HFR led Northeast regional effort; Foster, Frey, Ollinger, Munger served on committees), Ameriflux (Munger, Science Steering Committee), the LTER Strategic Task Force (Frey), the LTER Strategic Task Force Advisory Committee (Melillo, Chair), the LTER Information Management Executive Committee and NISAC (Boose led efforts to formulate review criteria for LTER information management systems), and LTER Schoolyard Collaborative (Snow). HFR scientists (Foster, Motzkin, Stinson, Orwig) collaborate with regional and national organizations to develop science-based management for invasive species.

Experiments on Natural and Human Disturbances and Climate Change

Long-Term Experiments evaluate regionally important processes and compare ecosystem responses to natural disturbance versus anthropogenic stress. The ***Experimental Hurricane*** (est. 1990) mimics the most intense New England storm (1938) to study forest reorganization (Carlton and Bazzaz 1998a, b), changes in nutrient cycling, micro-environments and biomass distribution (Bowden et al. 1993a), and long-term recovery (Cooper-Ellis 1999; Foster and Aber 2004). Findings of modest changes in many ecosystem parameters forced re-evaluation of the impacts of the 1938 hurricane (Foster et al. 1997; Foster and Aber 2004) and generated policy recommendations regarding salvage logging (Foster and Orwig 2006; Lindenmeyer et al. 2003). The ***Soil Warming Experiments*** explore climate warming impacts on forest ecosystems by raising soil temperatures 5ºC above ambient at two sites (six 5 × 5m plots, est. 1991; one 30 x 30m "megaplot", est. 2003). We track C and N dynamics in heated and control plots to consider positive and negative feedbacks to the climate system (i.e., C fluxes to and from the atmosphere). Warming accelerates soil organic matter decay and CO_2 fluxes but responses are short-lived due to the small labile C pool. Warming increases plant N availability, which may stimulate enough C storage to compensate for soil losses (Melillo et al. 2002). These results challenge climate models that forecast large releases of soil C with warming (e.g., Cox et al. 2000). The megaplot addresses the resulting questions: (1) Has the increase in N stimulated C storage? (2) What is the balance between C lost from soils and stored in vegetation? (3) Does warming affect tree regeneration and composition with implications for ecosystem productivity? Results for 12 species document a 50% increase in seedling and sapling productivity, especially of slow-growing taxa. Consequently, studies of rapidly growing species may overestimate C uptake and projections of biotic feedbacks to the global C cycle may require revision. These results have refined regional and global models and are extensively incorporated in policy documents (Melillo et al. 1996; NAST 2001).

The ***Chronic N Addition Experiment*** (est. 1988) studies the responses of N-limited ecosystems to increased N deposition and tests hypotheses that responses will be nonlinear: positive (e.g., increases in net primary production) in the short-term, but negative (e.g., increased nitrate leaching, reduced NPP) over the long-term (Aber et al. 1989). Three 30 x 30 m plots were established in pine and hardwood stands and treated annually with 0, 5, or 15 g N m^{-2} as NH_4NO_3. Results from the first 15 years (Aber and Magill 2004) prompted revisions of N cycling theories (Aber et al. 1989): foliar and fine root N concentrations were significantly elevated with N additions; pine showed substantial reduction in leaf longevity, cessation of biomass accumulation, and 56% mortality with high-N; high-N hardwoods showed increased ANPP, but excess N availability and a severe drought led to 72% mortality in red maple; the role

of soil N retention was underscored as plants diminished as net sinks for N (Magill et al. 2004); and soil respiration, though initially stimulated, was suppressed by 40% after 13 years (Bowden et al. 2004), concomitant with reduced microbial, primarily fungi, biomass (Frey et al. 2004).

Comparisons of Ecosystem Response to Natural Disturbance vs. Anthropogenic Stress showed that following hurricanes many key ecosystem processes remain intact and recovery is rapid, in keeping with natural cycles of disturbance (Foster et al. 1997; Foster and Aber 2004). In contrast, N addition and warming generate delayed visible impacts but serious imbalances of ecosystem function with long-term implications for ecosystem health.

The ***Detritus Input and Removal (DIRT) Experiment*** (est. 1990) employs chronic manipulations of leaf litter and root inputs to investigate how quantities and sources of plant inputs influence soil biogeochemistry and carbon balances. DIRT treatments are applied to 3 replicate, 25 m^2 plots: NO LITTER, DOUBLE LITTER, NO ROOTS, and NO INPUTS (no leaf or root inputs). The DIRT Network includes sugar maple (1991, Bousson Exp. Forest), Douglas fir (1997, AND LTER), oak (2000, IBP site in Síkfőkút, Hungary), and mixed hardwood-pine forests (2004, Univ. of Mich. Biol. Station), enabling us to estimate fine root production (Bowden et al.1993b; Sulzman et al. 2005), document temperature sensitivity of live roots vs. soil heterotrophs (Boone et al. 1998), and establish linkages between litter input, soil C and N accumulation, microbial communities and soil solution chemistry (Nadelhoffer et al. 2004).

Long-Term Measurements of Water and Carbon Fluxes at three eddy-flux towers (EMS, est. 1990; Little Prospect Hill, 2000; Hemlock Stand, 2002) and permanent plots are used to assess ecosystem responses to long-term climatic variation and historical and future disturbance (e.g., hemlock decline)**.** Over 13 years, net storage for hardwood forests averaged 2.2 Mg C ha^{-1} y^{-1} (0.8 to 4.2 Mg C ha^{-1} y^{-1}) with long-term increases in gross C uptake, total ecosystem respiration, soil respiration and net exchange. Inter-annual variation in soil respiration, due largely to summer droughts (Borken et al. 2006), results in an important transient source and sink of C in the forest floor (Gaudinski et al. 2000; Davidson et al. 2006). However, the dominant C sink is regrowth of aboveground biomass following 19th C. cutting, 1938 hurricane, and 1980s gypsy moth defoliation. The long-term record of carbon exchange and stand biometrics provide an invaluable data set that quantifies ecosystem dynamics at time scales relevant to succession and response to disturbances and climatic variation. Growth increment, recruitment and tree mortality in permanent plots indicate that gross C fluxes of aboveground biomass have little inter-annual variability whereas net fluxes vary primarily with mortality. Much lower (≈50%) maximum rates of C storage and water loss occur in hemlock forests, which constitute about 20% of HFR (Barford et al. 2001, Hadley and Schedlbauer 2002). Hemlock's low ET is associated with high soil moisture. Photosynthetically active radiation (PAR) exerted strong influence on ET in all forests, with the slope of this relationship in early summer twice as high for hardwood than hemlock forests. HFR eddy flux data were used in an NSF-ITR project to develop *analytic webs* – novel cyberinfrastructure tools that generate process metadata to accompany the more familiar descriptive metadata incorporated into ecological metadata language (EML; Osterweil et al. 2005; Ellison et al. 2006).

HFR measurements contribute to quantifying C budgets for the northeastern US. The CO_2 Boundary-layer and Regional Airborne (COBRA) study (NSF Biocomplexity, DoE and NASA funding) acquired data for diverse time/space scales using aircraft, flux towers, tall towers, remote sensing, and forest inventories. Data were assimilated to compute regional and continental carbon budgets, and to attribute C fluxes to specific processes. Matross et al. (2006) and Pathmathevan et al. (2006) showed that strong uptake of CO_2 by northeastern forests

provided an atmospheric signal that could be linked to ecosystem scales using flux tower and remote sensing data. Albani et al. (2006a) used the Ecosystem Demography model to quantify contributions of land-use recovery, forest harvesting, and CO_2 fertilization to the size of past, current, and future carbon fluxes in the eastern US. Model predictions indicate that, in the absence of CO_2 fertilization, the C sink will approach zero by mid-21st century. Large inter-annual variation in regional fluxes confirm that long-term measurements (LTER, AmeriFlux, and NOAA networks) are necessary to document CO_2 uptake processes by North American ecosystems.

Measurements of Atmospheric Exchanges of Reactive Trace Gases at the EMS include dry deposition for nitrogen oxides, deposition of ozone, and emission of hydrocarbons (isoprene and terpenes) that influence ozone and nitrogen oxides in the regional and global atmosphere. These observations help define how biogenic hydrocarbons mediate N deposition by the formation of hydroxyalkylnitrates and elucidate the mechanisms that facilitate the escape of nitrogen oxides from regional sources to continental and global scales (Munger et al. 1998; Horii et al. 2004, 2005).

Other Collaborative and Intersite Modeling in LTER II-III expanded the PnET model to include integration with eddy covariance CO_2 flux measurements (Aber et al. 1996) and extrapolation to New England (Ollinger et al. 1998). PnET was used in the U.S. **National Climate Change Assessment** to estimate the importance of land use history versus atmospheric factors in regional C sequestration. In the process: (1) important environmental drivers were addressed through new algorithms that simulate full feedbacks between C, water and N cycles as influenced by land-use history, N deposition, tropospheric ozone and rising CO_2 (Aber et al. 1997, 2003; Ollinger et al. 2002a), and (2) critical sources of spatial variation in C assimilation by vegetation (factors affecting soil N availability and canopy N concentrations) were addressed through integration of the model with remote sensing of foliar N concentrations and species composition (Martin and Aber 1997; Ollinger et al. 2002b; Plourde et al. 2006) using high spectral resolution sensors (e.g., Ustin et al. 2004; Smith et al. 2002; Ollinger and Smith 2005). Using HFR as a core test site, we derived canopy N coverages and improved model predictions for C flux at sites from Maine to Florida. These results provide improved C assimilation estimates for individual sites and allowed for rigorous validation of global estimates generated by remote-sensing-based light-use efficiency models (e.g., Turner et al. 2004). We are extending this approach across the Northeast by examining our ability to detect canopy N with existing broad-scale satellite sensors.

Information Management and Technology. During LTER III our network was expanded to include additional buildings and field sites, local servers were installed to host the HFR web page and provide central storage and backup, the HFR web page and online Data Archive were completely re-designed and updated, and discovery-level metadata for online datasets were converted to EML (see section IV for more details).

II. Proposed Research

Program Development, Conceptual Framework and Research Thrusts

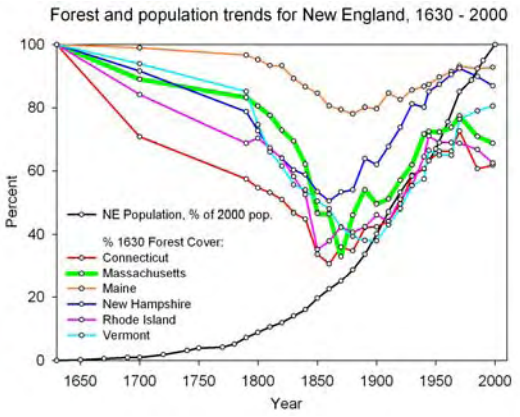


Figure 1. Historical changes in population and forest cover for the six New England states. Except for Maine, where the northern forest region was never settled and remained forested, the states share a common history of deforestation for agriculture followed by farm abandonment and natural reforestation. Forest cover has once again begun to decline in most states, primarily as a result of suburbanization. Population data compiled from U.S. censuses; forest cover data from Baldwin (1942) and U.S. Forest Service (1958, 1965, 1973, 1990, 2003).

The temperate forests of eastern North America represent dynamic ecosystems of global significance, supporting high biodiversity and critical ecosystem functions while providing natural resources and cultural benefits to an expanding human population. The region has experienced a broadly similar history of landscape change, including: major shifts in climate, vegetation, and disturbance at millennial time scales; extensive deforestation for agriculture in the 17th-19th centuries; abandonment of farmlands, natural reforestation, and increasing urbanization from the mid-19th to mid-20th centuries; and increasing forest fragmentation with widespread suburbanization in recent decades (Hansen and Brown 2005; Fig. 1). At the dawn of the 21st century, we are confronted with rapidly increasing rates of land conversion (Brown et al. 2005), steady to increasing rates of atmospheric deposition of pollutants, continued increase in temperature and atmospheric CO_2 (CCRC 1998), and the potential for more frequent *and* more intense hurricanes (Webster et al. 2005). Although these are global trends, the forests of eastern North America are being (sub)urbanized and fragmented more rapidly than elsewhere in the U.S. (Brown et al. 2005), and regional impacts of pollution and climate change may be especially dramatic due to New England's location at the end of the nation's "tail-pipe". **Our proposed work for LTER IV focuses on the impacts of the changes in rates and magnitudes of these key drivers of landscape change in New England and explores their consequences for regional populations, communities and ecosystems.**

Based on the successful synthesis activities carried out during LTER III, we recognize that:

1. A range of historical legacies have persistent but varying influences on modern ecological conditions, including species distributions, biotic interactions, biogeochemical functions, and response to disturbance (Ollinger et al. 2002a, b; Foster et al. 2003; Wofsy 2004);
2. Accurate interpretation of ecological patterns requires research addressing coupled human and natural systems (Turner et al. 2004; Redman and Foster 2006) and linking decadal-scale observations and sentinel measurements with long-term experiments (Melillo et al. 2002; Aber and Magill 2004; Munger et al. 2004);
3. Fundamental changes in biological and physical processes may result from the loss of a single "foundation" species that exerts strong control on biotic and environmental conditions (Orwig et al. 2002; Ellison et al. 2005a);

4. Successful conservation, management, and policy initiatives need to be based on a detailed understanding of historical legacies, human-environment interactions, and the drivers of landscape change (Foster et al. 2005; Foster and Orwig 2006; Lindenmeyer et al. 2004).

The transition from LTER I-III to LTER IV therefore represents a shift in focus from the impacts of the primary, physical drivers of forest change examined largely at a single site or landscape to a comprehensive analysis of both primary and secondary forces and responses operating across the entire New England region. This mandates a greater emphasis on the biological components of landscape change such as invasive species and pests, and the contributions of individual taxa to ecosystem processes. In LTER IV, we will explore the ecological impacts of changes in rates and magnitudes of drivers of landscape change in New England in the context of the four conclusions resulting from the synthetic activities of LTER III. In addition to considering drivers we have explored in LTER I-III (see Prior Results), we will incorporate new mensurative and experimental studies of land-cover change (resulting from forest harvesting, conversion, and land protection) and the spread of invasive species (plants, pests, and pathogens) and native ungulates that are (re)colonizing our region. Our broadened research agenda (Fig. 2) is a consequence of an increasing regional perspective (Fig. 3), greater interdisciplinary participation, a strong commitment to inform conservation, management, and policy efforts through collaboration with mission-oriented agencies and non-profit organizations (e.g., The Nature Conservancy), and a commitment to position the HFR LTER program for inter-site and emerging research opportunities outlined by the LTER Strategic Task Force (STF; Collins et al. 2005) and NEON planning processes (Michener et al. 2005).

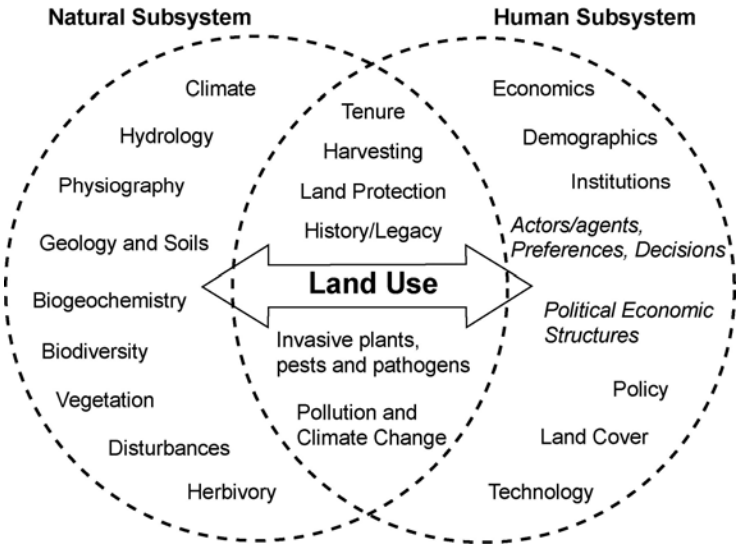


Figure 2. The HFR LTER program began in 1988 with a strong emphasis on components and processes within the natural subsystem. With expansion to regional scales, increased interaction with mission-oriented agencies, and substantial evidence of the ecological importance of land-use legacies, the research program now increasingly emphasizes land use and the coupled human-environment system. Modified from the Boston Report of the NEON Land Use Committee (http://www.neoninc.org/documents/LUC_Boston_Report.pdf).

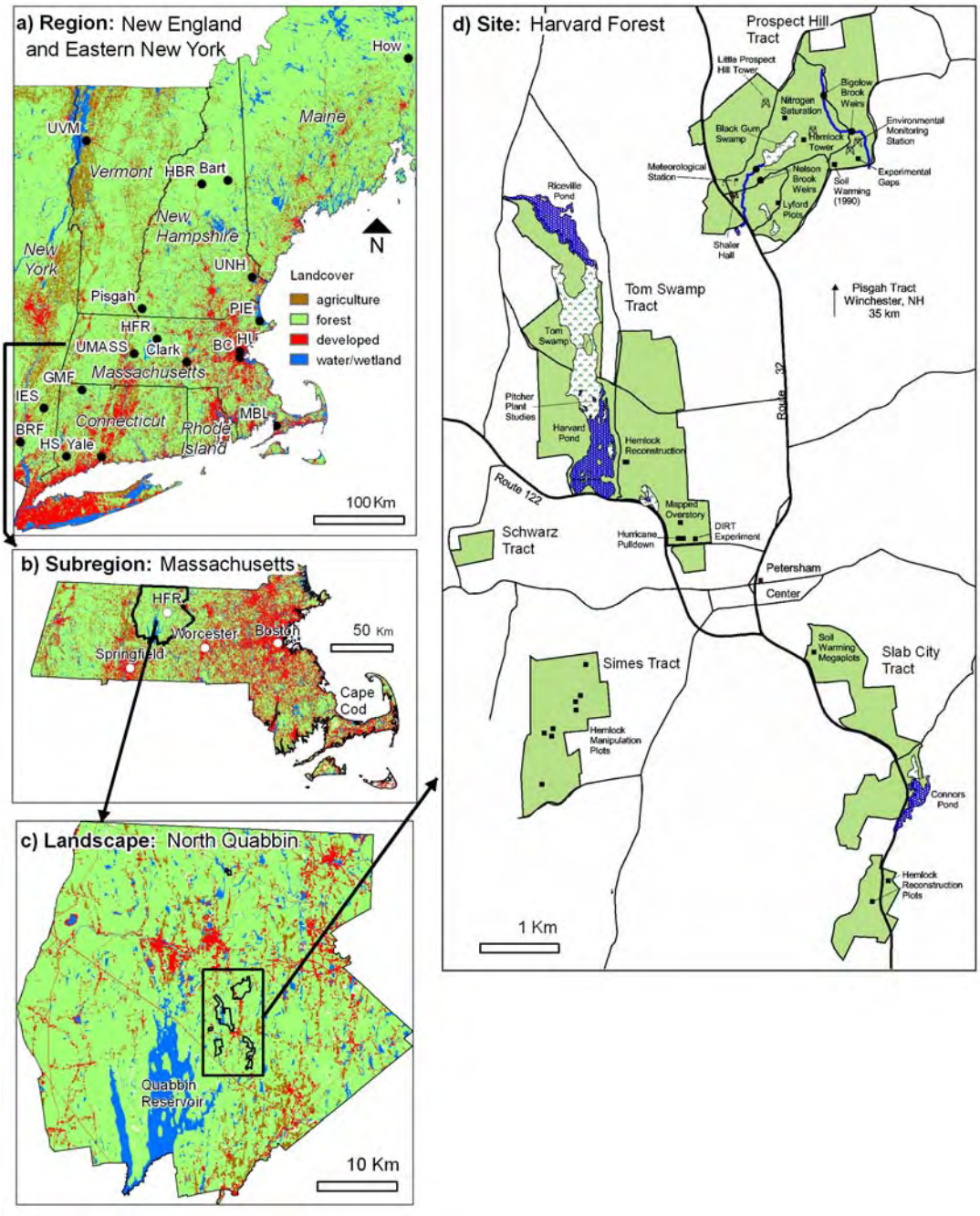


Figure 3. Harvard Forest Long Term Ecological Research program studies address a range of spatial scales. During LTER I and LTER II, we examined the response of forest ecosystem patterns and functions to natural and anthropogenic disturbances at site- and multiple landscape-levels. In LTER III and LTER IV we expanded our efforts to include subregional and regional-scales as part of collaborative efforts to examine the patterns, drivers, and consequences of forest change over time. Abbreviations: How = Howland Forest; Bart = Bartlett Experimental Forest; HBR = Hubbard Brook LTER; UVM = University of Vermont; UNH = University of New Hampshire; PIE = Plum Island LTER; HU = Harvard University; BC = Boston College; MBL = Marine Biological Laboratory; Clark = Clark University; GMF = Great Mountain Forest; IES = Institute of Ecosystem Studies; BRF = Black Rock Forest; HS = Highstead Arboretum.

LTER IV also presents new opportunities for HFR researchers to integrate and synthesize many efforts: long-term studies initiated in 1988, new complementary thrusts, and research initiated under funding from other grants and agencies. Table 1 summarizes this array of studies, topics and scales of analysis while distinguishing new, ongoing, modified, and related efforts. The research is presented below in the following sections:

A. Patterns, Drivers, and Consequences of Ecological Change. Focused studies integrating regional analyses, long-term measurements, and experimental manipulations to explore the primary drivers of change in New England forests: land conversion and protection, meteorological disturbances, climate warming, nitrogen deposition, forest harvesting, invasive pests and pathogens, and expansion of ungulate populations.

B. Regionalization, Modeling and Synthesis. A range of synthesis activities including comparative research, cross-site and regional studies, modeling, and major new synthetic volumes.

C. New Instrumentation and Infrastructure. The equipment and facilities planned to serve HFR and the broader ecological community, including: a synthesis center for integrated research and education using long-term ecological data, a sensor network to make HFR a wireless laboratory and classroom, and state-of-the-art nutrient analysis equipment.

A. Patterns, Drivers, and Consequences of Ecological Change in Southern New England.

Our studies will investigate the primary drivers of landscape change in the northeastern U.S., explicitly recognizing that these processes interact and are strongly conditioned by both the modern environmental setting and the history of human and natural disturbances. Through regional analyses, long-term measurements, large manipulations, field experiments, and extensive sampling we will: document the spatial and temporal patterns of these major human and natural processes; interpret their physical and biotic drivers and correlates; assess their impacts on forest structure, composition and function; develop hypotheses for future site-based measurements and experiments; develop critical groundwork for new collaborative studies across the LTER Network and through LTER STF and NEON programs; and provide essential information to our partners in public agencies and NGOs. Below, we present these studies beginning with continued long-term, site-based manipulations and measurements followed by proposed regional and mechanistic studies of important human and biotic processes:

1. Decadal Studies of Long-term Experiments
2. Carbon Exchange and Hydrology: Long-term Dynamics in Temperate Forests
3. Regional Patterns of Land Development, Forest Harvesting, and Land Protection
4. Hemlock Woolly Adelgid (HWA) and Loss of Foundation Species
5. Invasive Plants – Population-to-Landscape Studies and Experiments
6. Dynamics of Expanding Native Ungulate Populations

Table 1. HFR LTER study matrix, highlighting the suite of drivers and study approaches employed in examining the impacts of these key ecological processes on landscape change in New England and the consequences for regional populations, communities and ecosystems. Color = initiated in LTER I, LTER II, LTER III, LTER IV.

Ecological Process	Reconstruction (landscape to regional)	Long-term Measurement (site to regional)	Experiment (site-based)	Modeling (site to regional)	Broader Impacts (regional to global)
Carbon and Water Dynamics	1) Influence of land-use history on carbon stocks 2) CWD dynamics – above and below ground	1)Eddy-flux towers: EMS, Hemlock Tower, Little Prospect Hill 2) Gauged watersheds 3) Phenology study 4)Long-term soil respiration plots	1)Soil warming study 2) Soil waming megaplots 3) Warming x Nitrogen study 4) DIRT study 5) Hemlock manipulation	1) Modeling carbon dynamics: PnET TEM RAMS-ED2 2) Hydrological reconstruction	Global warming policy & models; watershed management
Wind Disturbance	Hurricane histories of New England, Puerto Rico and Yucatan	Permanent plots established after 1938 hurricane and Pisgah Tract	Hurricane simulation	Historical hurricane intensity: HURRECON	Forest management (e.g. Quabbin, USFS)
Atmospheric Deposition of Nitrogen and Pollutants	Specific pollutant histories	EMS tower	1) N Saturation 2) Warming x Nitrogen study	Modeling the regional N budget: PnET and other models	Air and water pollution policies; climate change models
Forest Harvesting, Development, or Protection	1) Historical maps of land cover 2) forest harvesting, land protection, housing	1) Statewide survey plots 2) Hemlock harvest transect	Hemlock manipulation	Changes in land use as a result of socioeconomic factors	Land conservation and management policy (e.g. *Wildlands and Woodlands*)
Invasive Pest Expansion	Paleoecological analysis of the 5500 y bp hemlock decline	1) Stand to landscape patterns of HWA spread, hemlock decline and logging 2) Hydrology of hemlock vs. deciduous watersheds 3) Hemlock vs. deciduous forest water and carbon exchange with the atmosphere	Hemlock manipulation	Modeling patterns of HWA spread, harvesting and consequences of forest-type change	Forest management options (e.g. Silvicultural options for managing hemlock forests brochure)
Invasive Plant Expansion	1) 19th century land use as a predictor of exotic species distributions 2) Comparison of modern vs. historical floras	Metapopulation and population monitoring of garlic mustard and Japanese barberry	1)Experimental eradications 2) Reciprocal transplant study 3) Soil manipulations	Species-specific distribution predictions	Management recommendat-ions to mission-oriented organizations
Ungulate Range Expansion	Historical wildlife study	Radio-collared moose Browse study	Deer exclosures	Range and population models	Vegetation and wildlife management strategies

1. Decadal Studies of Long-term Experiments

The suite of long-term experiments begun in LTER I represents an invaluable scientific legacy as it continually attracts additional researchers, provides fundamental and novel insights into unfolding ecological processes, and yields critical results for the development of sound management and policy. The experiments also present a mixture of challenges and opportunities, including: long-term maintenance, administration, financing, and opportunities for melding old experiments with new treatments (e.g., crossing treatments; investigating recovery when treatments stop; or phasing in new replications with additional treatments). Each of our original experiments is in a different situation regarding these respective opportunities and yet each grows in value with succeeding measurements. Thus, we intend to continue monitoring the long-term effects of what we have identified as primary physical drivers of forest change: physical disturbances and chemical and climatic stresses. As we develop new directions for our long-term studies in LTER IV, we will place a stronger emphasis on biological responses to these drivers, and the respective roles that they play in forest structure and function.

Ecosystem Response to Climate Change - Soil Warming

Due to the small size of the original warming plots (5m × 5m), we could not answer two key questions related to soil warming effects on ecosystem processes: (1) Has the increase in available N increased C storage in the vegetation? And (2) What is the balance between the C lost from the soil and C stored in the vegetation? These questions are being addressed in the 30 × 30 m megaplot, established in 2003.

We also will address three new questions with both sets of plots:

(1) *Has long-term soil warming exhausted the labile C pool?* This will be the first time that the labile C pool has been quantified in field experiments and we want to understand the biogeochemistry underlying this phenomenon. Results will be used to develop a multiple-box soil C and N module for the whole-ecosystem biogeochemistry model TEM (Terrestrial Ecosystem Model; Melillo et al. 1993, McGuire et al. 1997, Tian et al. 1999, Felzer et al. 2004). To assist these interpretations, we will measure: CO_2 and $^{14}CO_2$ soil efflux; C of the bulk soil and the LD and HD soil fractions; and ^{14}C of the bulk soil and fractions.

(2) We will link this experiment with the chronic N experiment by asking: *can soil warming change ecosystem N distribution and the capacity of forests to store C?* We will make a series of plant and soil measurements to quantify changes in C storage and provide insight into the relationship between these changes and N cycling in heated plots. In trees we will measure: 1) annual woody increment; 2) the C:N ratio in the increment, roots, and leaves; and 3)^{15}N content in the various plant parts. In soils we will make a series of measurements of: 1) C and N stocks in bulk soil and in light density (LD) and heavy density (HD) soil fractions; 2) ^{14}C and ^{15}N content of the bulk soil and fractions; 3) CO_2 and $^{14}CO_2$ efflux from the soil surface; 4) liginase enzyme activity in various soil horizons; and (5) net N mineralization and nitrification rates.

(3) In tandem with studies at the eddy flux towers, we ask: *how will climate change influence the capacity of mid-latitude forests to store C?* We will use TEM to explore the consequences of warming for net C storage at the stand level. The model will be calibrated with data from the eddy flux towers to model net C flux between the land and the atmosphere from 1900 to the present using the reconstructed temperature and precipitation record for HFR.

Adding N to Soil Warming: Microbial Community Structure and Function.

Long-term N enrichment significantly alters ectomycorrhizal community structure and reduces the fungal component and its ability to degrade many common sources of soil C (Frey et

al. 2004). Soil warming reduces labile C, microbial biomass, and microbial substrate utilization (Fig. 4; Smith 2005). These results raise four new questions:

1. Is the shift in microbial community composition and function in heated soil due to the warming or to changes in moisture, N availability, or other mechanisms?
2. What is the relative importance of abiotic vs. biotic N immobilization in N enriched soils?
3. What is the importance of denitrification to N loss in controls and treatments?
4. Is acclimation of soil respiration with warming due to a loss of labile C or other factors?

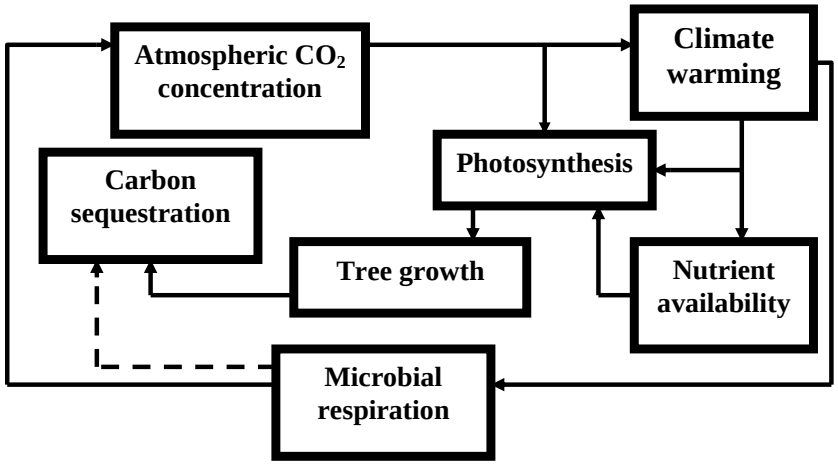


Figure 4. Schematic diagram of major feedbacks in the coupled climate-carbon cycle system. Solid arrows indicate positive feedbacks and dashed arrows indicate negative feedbacks. Over the short term (6 years), warming increases both microbial respiration and nitrogen availability. Increased nitrogen availability in temperate forests can lead to increased photosynthesis, tree growth and carbon sequestration in long-lived plant tissue such as wood. The net effects of warming on the atmospheric concentration of CO_2, a dominant greenhouse gas, depend on the relative magnitudes of the loss of carbon as CO_2 from the soil and the storage of carbon in new plant tissues such as wood.

Supported by a 5-year NSF CAREER award, Serita Frey will use a new set of 3 × 3 plots (est. 2005) to examine the interactive effects of warming and N additions (control, heated, heated +N, +N only) on microbial community dynamics and to identify microbial communities that regulate C and N cycles (e.g., denitrifiers responsible for N_2 and N_2O emissions). Soil respiration, microbial metabolism, microbial community composition, and soil C and N pools will be measured regularly.

Chronic Nitrogen Addition Plots

Inputs to the terrestrial nitrogen cycle have more than doubled in the past century due to anthropogenic activities, resulting in significant increases in N deposition to forests in the northeastern U.S. and Europe (Vitousek et al. 1997). Since most temperate plants evolved under low N conditions, chronic N enrichment alters ecosystem properties and processes in fundamental ways. Over two decades the chronic N addition plots have provided a unique platform for research on ecosystem response to chemical stress (Fig. 5). Because of the recent termination of the European NITREX experiments, the HFR LTER experiment is one of

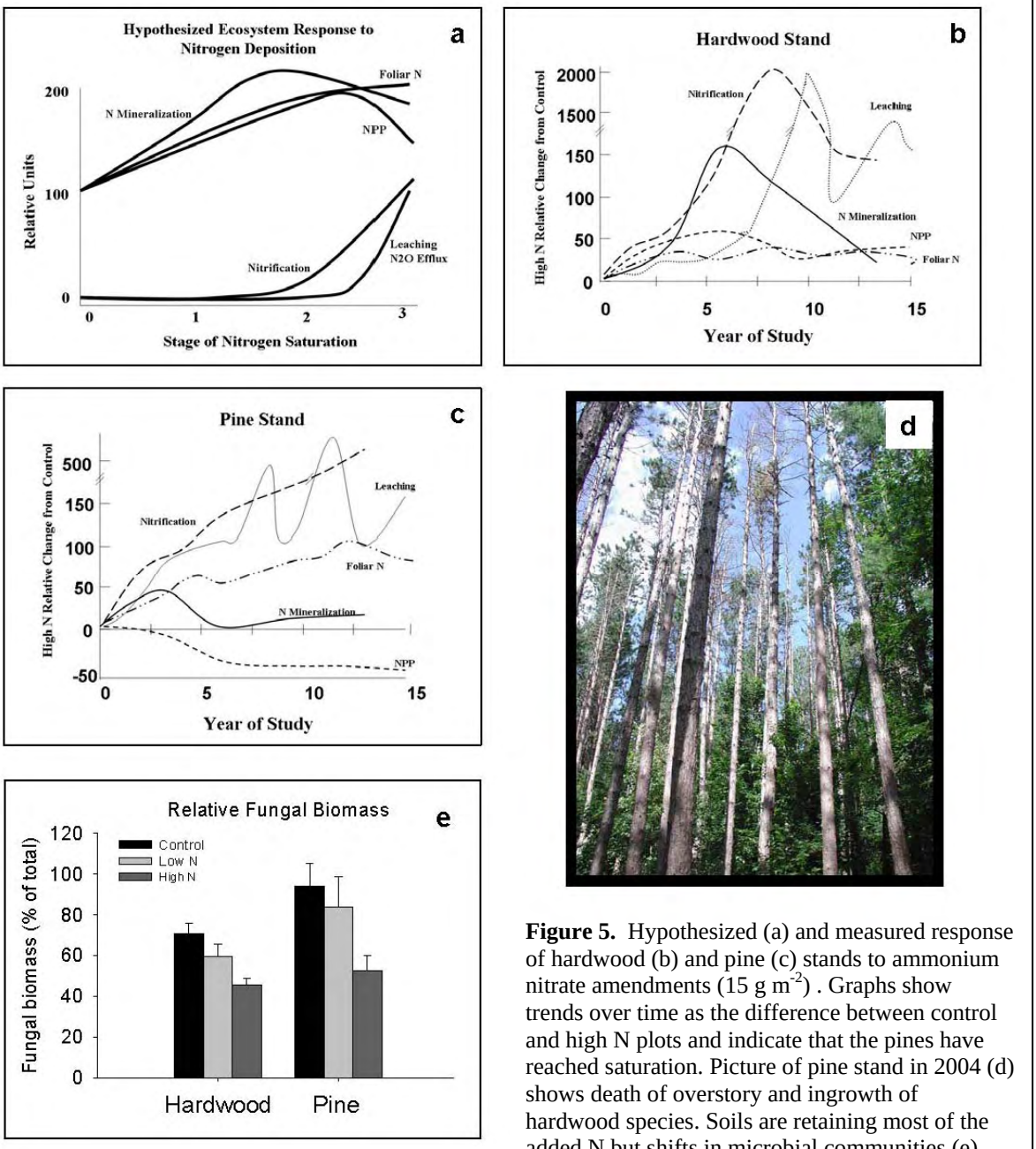


Figure 5. Hypothesized (a) and measured response of hardwood (b) and pine (c) stands to ammonium nitrate amendments (15 g m^{-2}) . Graphs show trends over time as the difference between control and high N plots and indicate that the pines have reached saturation. Picture of pine stand in 2004 (d) shows death of overstory and ingrowth of hardwood species. Soils are retaining most of the added N but shifts in microbial communities (e) suggest major changes in retention mechanisms.

the last remaining N saturation studies (e.g. Wright and van Breeman 1995; Wright and Rasmussen 1998). Despite numerous publications and revisions to early N cycling theories, substantial uncertainties remain regarding the pathways of reactive N. Surprises from our early work include: the near total collapse of the high-N pine stand; the large amounts of N sequestered in soils or remaining unaccounted for in the oak forest (Magill et al. 2004); and the potential importance of denitrification (e.g., Venterea et al. 2004) and abiotic immobilization (Berntson and Aber 2000; Davidson et al. 2003). Resolving the importance of these mechanisms

is critical because each has different implications for long-term patterns of N transfer in the environment.

We will continue treatments and measurements (except in the high-N pine plot) with three principal goals, to: (1) determine if the hardwood and low-N pine stands become saturated and exhibit decline, (2) resolve the mechanisms through which N becomes sequestered in soils or lost in gaseous forms, and (3) monitor recovery of the high-N pine plot after the cessation of N inputs. In hardwood and pine plots we plan to investigate the role of mycorrhizae in organic N use by plants under a separate NSF proposal (Hobbie, Ollinger and Frey). We are exploring abiotic N immobilization (cf., Berntson and Aber 2000; Dail et al. 2001; Davidson et al. 2003) through a NSF grant to E. Davidson and gaseous N losses as NO and N_2 (cf., Groffman 2006; Venterea 2003, 2004) through a proposal to EPA by Ollinger.

In addition, students working with R. Vilgalys (Duke) and T. Bruns (UC Berkeley) are examining responses of ectomycorrhizal fungi to chronic N. E. Hobbie (UNH) and J. Hobbie (MBL and ARC LTER) are using ectomycorrhizal fruiting bodies from the Chronic N plots for isotopic analyses and examining whether shifts in community composition reflect underlying shifts in the abundance of fungi possessing proteolytic capabilities.

Detritus Input and Removal (DIRT) Experiment

HFR DIRT plots will be continued through annually excluding or transferring litter. Temperature and soil moisture data are logged continuously and soil solution samplers are located beneath the O horizon (zero-tension collectors) and at approx. 60cm depth. Soil respiration and soil solution measurements (non-destructive) are made regularly and soil chemical analyses, C and N mineralization potentials, and microbial characterizations occur every five or more years. In LTER IV we will actively collaborate with the inter-site DIRT Network to link soil biogeochemical, microbial, and trophic structures to variation in litter loading across sites and along litter input gradients within sites (Nadelhoffer et al. 2003, 2004).

Hurricane Manipulation

The hurricane manipulation is one of our original experiments contrasting ecosystem response to natural disturbance and anthropogenic stress. The study has yielded many surprises, notably high initial survival by uprooted trees and great resiliency in ecosystem process, environmental conditions, and composition (Cooper-Ellis et al. 1999; Fig. 6). The forest is now in an intermediate phase of stand development, which has been largely ignored by ecologists. To interpret these long-term trends we are replacing annual sampling regimes with a 3-5 year interval for tree canopy and understory dynamics. We will continue to collect annual litterfall and encourage participation by new investigators (cf. Weishampel unpubl. data) as we address ongoing questions:

1. *How does the importance of different mechanisms of tree regeneration vary over time?* Despite the key role of sprouting in the initial stabilization of ecosystem processes, advanced regeneration of seedlings/saplings now comprise the bulk of the new canopy. Post-manipulation regeneration (Carlton and Bazzaz 1998a, b) has played a minor role, but may become important as the forest matures and gaps develop. To follow these dynamics we will track all tree cohorts and understory vegetation and continue to monitor long-term changes in pit and mound complexes as factors controlling microenvironments and regeneration.

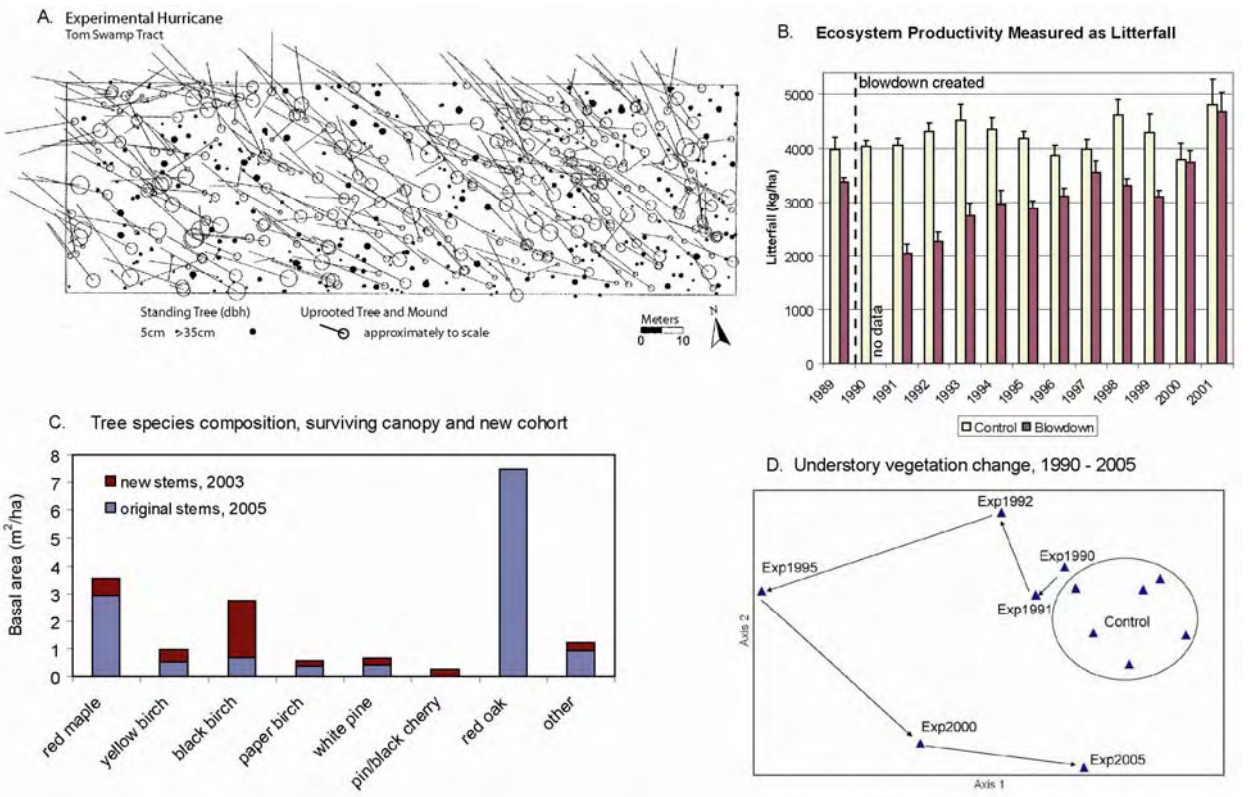


Figure 6. Long-term vegetation recovery in the hurricane study (A) continues to be a focus of investigation. (B) While basal area is still only 63% of the pre-disturbance value, litterfall recovered within 10 years. (C) The forest canopy is two-tiered, with survivors emerging above a thick canopy of new trees. (D) As analyzed using principal components analysis, the understory composition shifted modestly and is returning to an assemblage similar to the pre-disturbance community.

2. *What are the interactions between new tree cohorts and the remnant canopy?* The forest has a two-tiered canopy, with compositional changes buffered by the persistence of surviving overstory trees. To interpret the interactions between the young canopy and survivors we will conduct detailed spatial analyses of three-dimensional canopy structure with a ground-based LIDAR to better characterize this complex arrangement (Weishampel unpubl. data).

3. *How persistent are changes in herb and shrub communities and do they parallel canopy dynamics?* The understory composition changed modestly following the manipulation, but has been reverting to prior conditons through mortality of new species and recovery of former ones. We will measure these dynamics focusing on spatial relationships between understory vegetation and the heterogeneous post-disturbance environment.

2. Carbon Exchange and Hydrology: Long-term Dynamics in Temperate Forests

Three components of the HFR LTER infrastructure, the meteorological station, three eddy-flux towers, and the new array of headwater streams gauges, provide a unique ability to track long-term C dynamics and hydrological processes in hardwood and conifer forests, and assess changes resulting from hemlock mortality (see subsection 4, below). The proposed work builds on our decadal record of C, water, and energy exchange and will enable us to close the water balance for the small watersheds and develop a coupled terrestrial-aquatic-atmospheric

research program. This effort will position us well for the LTER STF, NEON, and DOE NICCR programs and for cross-site activities with HBR and PIE, which have strong watershed studies.

Long-term Records of Carbon Dynamics and Water Use

The EMS tower (80-120 year-old hardwood forest), Hemlock tower (100-200 year-old hemlock forest), Little Prospect Hill tower (50-year-old aggrading hardwood forest) and associated biometry plots (est. 1993) and soil studies provide detailed measures of ecosystem-scale C, water, energy, and pollutant exchanges between the forest and atmosphere on hourly to decadal time scales. Through the towers, HFR will continue to be an anchor point for C budget estimation supported by other programs (NSF-Biocomplexity, NOAA, DoE) seeking to derive regional to continental-scale budgets by merging site-based flux data with remote sensing data, meteorology, and atmospheric studies. In addition, 10+ years of soil respiration data at EMS (Savage and Davidson 2001; Davidson et al. 2006), two years of soil respiration data for hemlock stands, and measurements at contrasting deciduous and coniferous sites provide critical control for regional and comparative studies, experiments, and modeling. For instance, data from the hemlock tower indicate that hemlock and deciduous forests differ greatly in biosphere-atmosphere C and water exchange. In the mature hemlock forest, maximum rates of net ecosystem carbon uptake (12 µmol C m^{-2} s^{-1}) were only half of those in deciduous forest (Fig. 7). Although the evergreen hemlocks have a longer photosynthetic season, their annual C storage was ~ 1.2 Mg C/ha less than the deciduous forest (Hadley and Schedlbauer 2002; ftp://ftp.as.harvard.edu/pub/nigec/HU/Wofsy/hf_data/).

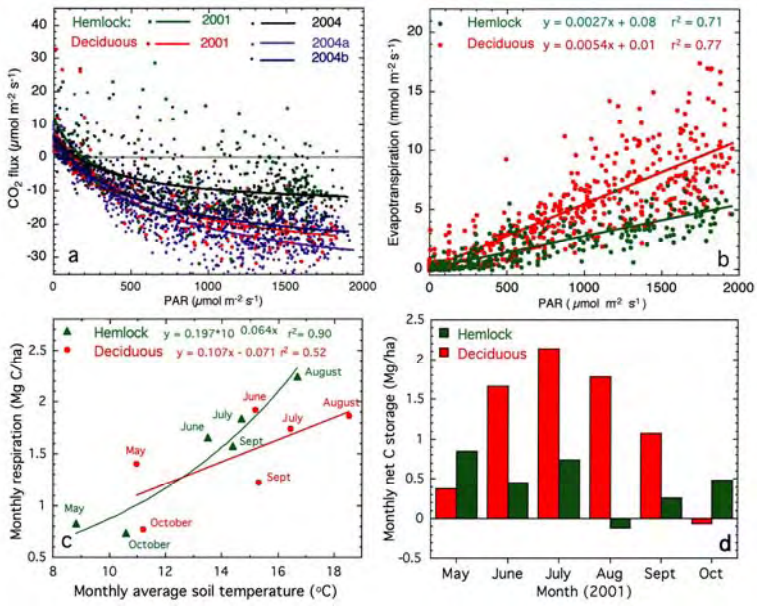
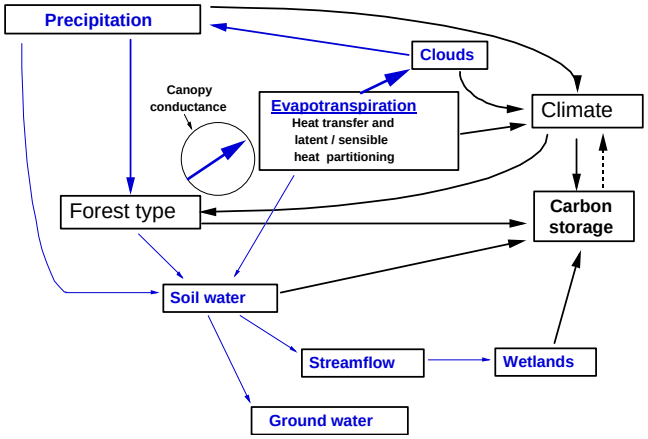


Figure 7. Carbon and water exchange of hemlock and deciduous forests as determined from eddy covariance data. Mature (100-220 year old) hemlock forest reached a maximum rate of net ecosystem carbon uptake of 12 µmol C m^{-2} s^{-1} during July and August of 2001 and 2004. This was about 50% of the highest rate of C uptake for deciduous forests. (**a**; negative numbers in this figure indicate carbon storage by the forest. For deciduous forests, 2001 and 2004a indicate forest measured by the HFR EMS tower, and 2004b indicates measurements from the LPH tower.) The hemlock forest also had much lower water use than deciduous forests in summer. The ratio of evapotranspiration to PAR in July 2004 was only half as great for the hemlock forest as for deciduous forest at LPH (**b**). The hemlock forest in 2001 also showed stronger sensitivity of ecosystem respiration to soil temperature (**c**), which combined with low C uptake capacity to cause relatively little C storage by the hemlock forest during the summer of 2001 (**d**). The evergreen hemlocks have a longer photosynthetic season, but annual C storage was ≈1.2 Mg C/ha less than for deciduous forest in 2001 (Hadley and Schedlbauer 2002; ftp://ftp.as.harvard.edu/pub/nigec/HU/Wofsy/hf_data/**)**

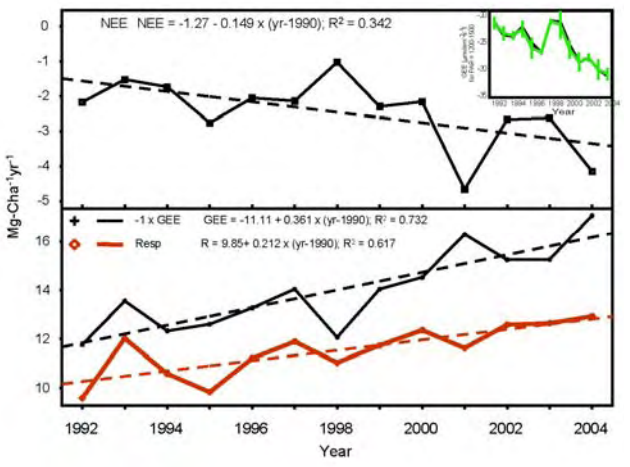
Ongoing measurements will focus on the following objectives: (i) to extend the spatial, temporal and mechanistic understanding of C dynamics; (ii) to examine the influence of canopy composition on C dynamics and hydrology; and (iii) to identify the consequences of the loss of a foundation species (hemlock) on both processes (Fig. 8). Carbon and water exchange

Figure 8. Effects of forest type and evapotranspiration on quantities and flows of water in and between atmospheric, terrestrial and aquatic environments. In closed-canopy forests, transpiration by the canopy during the growing season is the major source of water vapor entering the atmosphere. Transpiration reduces soil water recharge, ground water recharge, and streamflow. Thus a change in forest type from a dominant species that transpires large amounts of water to a species that uses much less water, or vice-versa, will have large effects on soil and aquatic environments. The availability of soil water and the presence of wetlands in turn influence carbon storage. Local climate, which is affected by moisture in clouds partly generated by evapotranspiration, affects carbon storage in the short term; global climate is affected by global carbon storage through its impact on atmospheric CO_2 over longer timescales.



measurements in the hemlock and aggrading hardwood forests, for which we currently have only three years of data, will clarify inter-annual response to climate variation, similar to our studies at EMS (13 years). At the EMS site, we will determine whether the increasing trend in annual net C storage continues, a question of great importance for predictions of future C storage by northeastern deciduous forests. Extending the record from the aggrading forest will examine whether there are long-term trends resulting from forest development, similar to those at the EMS site (Fig. 9). Further measurements at the hemlock site will allow us to detect effects on ecosystem C and water fluxes of hemlock decline due to the hemlock woolly adelgid (HWA), which is currently expanding its range into HFR (see HWA studies in subsection 4, below).

Figure 9. (Upper panel) Annual net ecosystem exchange (NEE) of deciduous forest measured at the HFR EMS tower from 1992 through 2004. Negative numbers indicate 0.8 to 4.6 Mg of annual carbon storage by the forest each year, with a trend toward increasing C storage. (Lower panel) The components of annual net ecosystem exchange: ecosystem respiration (Resp) and gross ecosystem exchange (GEE) which is equivalent to total photosynthesis. (Inset) Average gross ecosystem exchange at PAR values between 1200 and 1500 µmol m^{-2} s^{-1} during July of each year. The negative trend indicates that the forest has become increasingly efficient at using light to capture atmospheric CO_2. Therefore, the negative trend in NEE, indicating increased annual carbon storage, is not simply due to a climatic shift toward more favorable weather for photosynthesis.



Hydrology of Small Forested Watersheds

Headwater streams and wetlands provide natural flood control, recharge groundwater, trap sediments, recycle nutrients, support biological diversity, and sustain the productivity of downstream rivers, lakes, and estuaries. Such streams also comprise at least 80% of the nation's

stream network and offer the greatest opportunity for exchange between terrestrial and aquatic systems (Meyer et al. 2003). Despite providing essential ecosystem services that are increasingly threatened, headwater streams are relatively poorly studied and receive limited regulatory protection.

To better understand the critical role of headwater streams and wetlands in forest ecosystems, we initiated long-term measurements on two small watersheds in 2004 (Fig. 10). On Nelson Brook, weirs were installed on outlet streams of an 11-ha spruce-hemlock wetland (watershed = 44 ha). On Bigelow Brook, pipes measure flow above (watershed = 24 ha) and below (watershed area = 65 ha) a 3-ha shrub-dominated beaver swamp. Measurements of stream discharge, water temperature and wetland water levels were initiated in April 2005. A future wireless network will enable near-real-time posting of hydrological data. The gauged watersheds, though adjacent and comparable in size, differ significantly in topography, soils, wetlands, stream chemistry, stream biota, land-use history, and forest vegetation (including hemlock abundance). Thus, they provide an extraordinary opportunity to study the impacts of these factors on small watershed hydrology and ecology, and to contribute to regional and LTER Network hydrological studies.

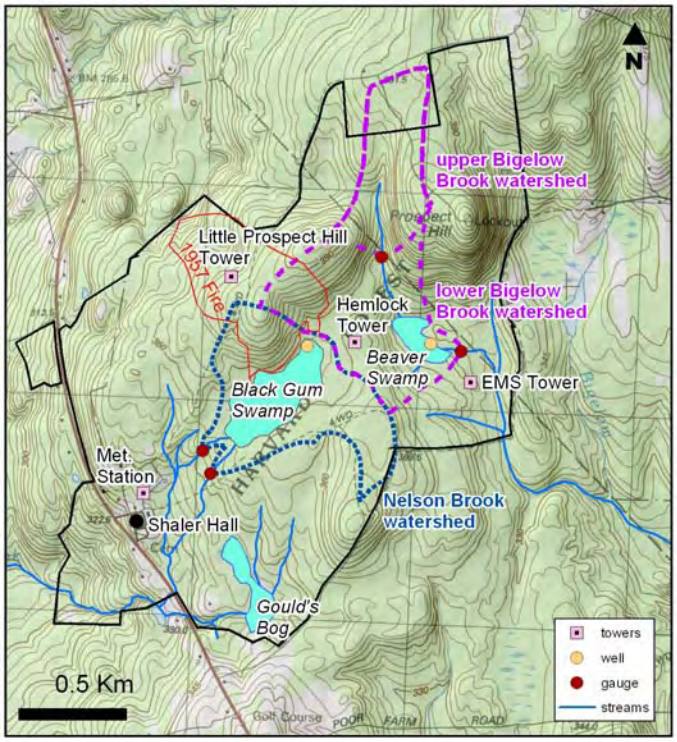


Figure 10. Study design for long-term hydrological measurements on the Prospect Hill Tract of Harvard Forest, showing the Nelson Brook watershed (44 ha) outlined in blue and the Upper and Lower Bigelow Brook watersheds (24 ha, 65 ha) outlined in purple.

We will develop near-real-time water budgets for the watersheds by integrating eddy flux, meteorological, and hydrological measurements. This effort will have several innovative features: (1) Direct measurements of all major terms in the water budget (including ET) will provide greater accuracy, especially for estimates of soil and ground water storage. While few sites can measure ET directly, we do so at all three eddy flux towers. (2) Frequent and automated sampling will support analysis at a wide range of temporal scales, from daily to synoptic to seasonal to annual. (3) Near-real-time analysis and display will reduce instrument down-time, provide exciting educational opportunities for both local and remote students, and serve as a prototype for future ecosystem diagnostic and forecasting tools. A pilot project to calculate water budgets in late spring/early summer 2005 yielded promising results and confirmed the important role of wetlands in retaining water during the transition from spring to summer (Fig. 11). Further refinements and estimation of year-round water budgets will require snow pack measurements, better sampling of ground water levels, piezometer studies of stream and ground water exchange, and integration with sap flow and other tree physiology measurements.

In addition to streamflow measurements, our hydrological design is ideally suited to study the role of small wetlands in forested watersheds. Preliminary results suggest that wetland

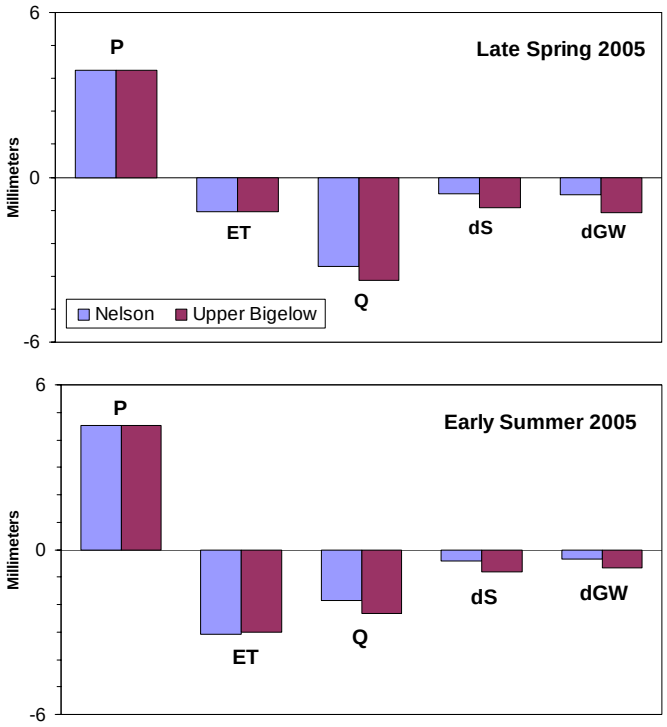


Figure 11. Water budgets for Nelson and Upper Bigelow watersheds for late spring (Apr 20–Jun 5) and early summer (Jun 6–Jul 26) 2005. Values are daily averages. Positive values represent a gain and negative values a loss of water to the forest ecosystem. **P** = precipitation measured at Fisher Meteorological Station. **ET** = evapotranspiration measured at Hemlock and Little Prospect Hill eddy flux towers, with values weighted according to the proportion of hemlock and hardwoods in each watershed. **Q** = yield measured at stream gauges, with gaps in data filled by a simple runoff model. **dS** = change in ecosystem water storage, calculated as dS = P + ET + Q. **dGW** = change in ground water storage measured at two nearby wells chosen to represent poorly-drained and well-drained soils, with values weighted according to the percentage of wet and dry soils in each watershed. Results show the expected seasonal decline in water storage from late spring through early summer. The relative loss of water to ET increased significantly after leaf-out in early June. Nelson watershed, with its much higher percentage of wetland area (60% vs. 10%), retained significantly more water than Upper Bigelow. In all cases the change in water storage calculated from P, ET, and Q closely matched the estimated change in ground water storage (Boose and Hadley, *unpublished data*).

water levels are closely coupled to stream discharge rates and that wetlands buffer storm flow and enhance water loss through evapotranspiration, in relationship to their contribution to total watershed area. Many questions remain, including: (1) how wetland hydrology varies with water level, vegetation phenology, and snow and ice accumulation, (2) how wetlands exchange water with the groundwater system and surface flow, and (3) how beavers (which will return to one watershed only) influence wetland hydrology.

Preliminary studies with a simple runoff model suggest that discharge rates can be predicted quite accurately for these watersheds. More comprehensive models will be developed to include water flux and storage in various components of the hydrological system, verified by empirical measurements. Hydrological models will be integrated with meteorological and tree physiological models to describe water flux through the coupled ecosystems. Novel cyber-infrastructure tools for this effort derive from our work with analytic webs (Ellison et al. 2006); support to further develop such tools and apply them to water-budget modeling is being sought through the NSF CEO:P initiative.

3. Regional Patterns of Land Development, Forest Harvesting, and Land Protection

Land-use change is the main transformative ecological process worldwide that determines the land-cover template upon which all other processes, including climate change work (Urban et al. 2001). Profound changes in land cover are occurring across the eastern U.S., dominated by three interacting processes: forest harvesting, land (forest and agriculture) conversion to developed uses, and land conservation (USDA 2004; Brown et al. 2005; McDonald and Urban 2006). Our exploratory work suggests that development and forest harvesting are inversely correlated, with proximity to urban regions strongly decreasing the probability of harvesting and increasing the probability of development (Fig. 12; Wear

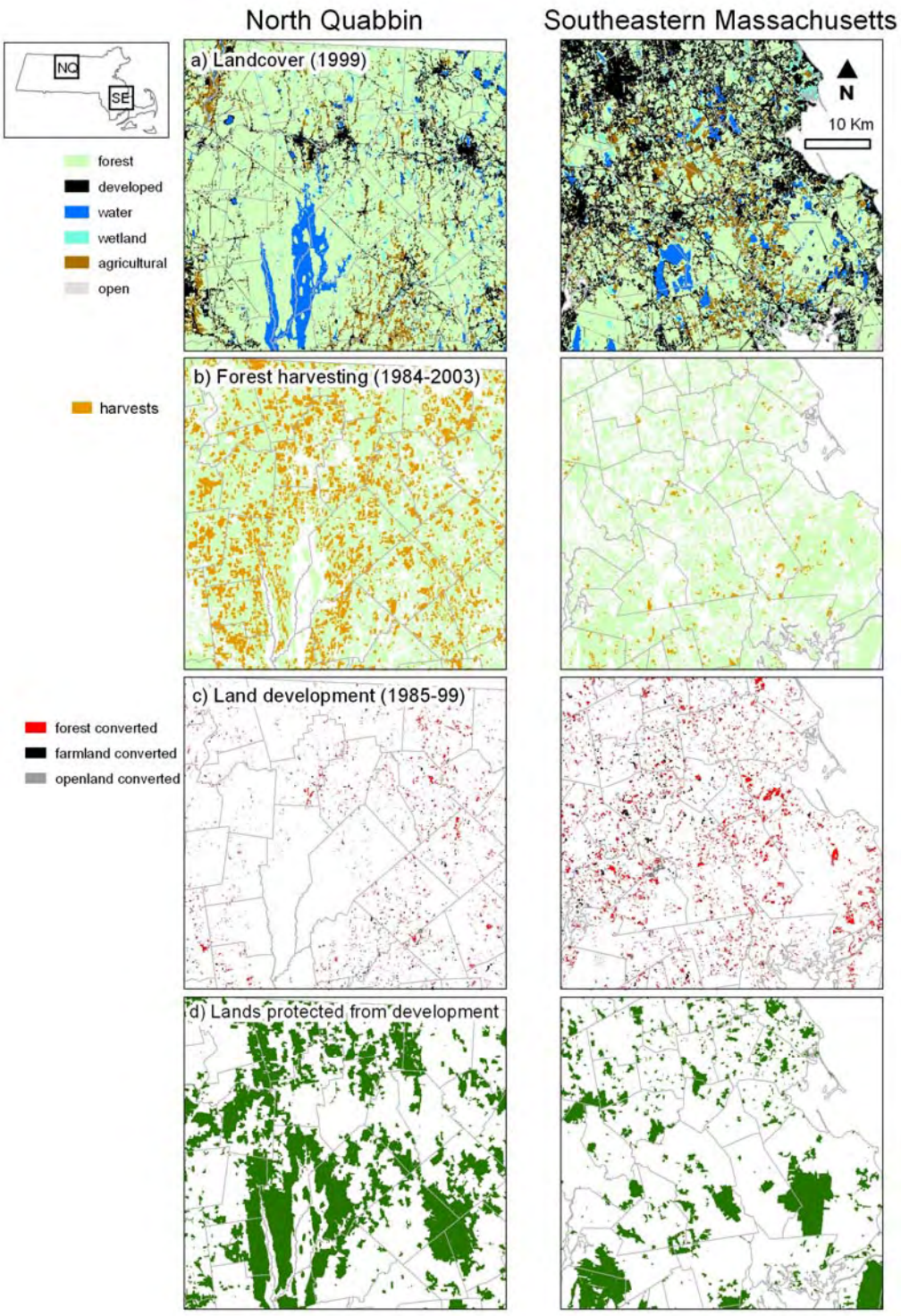


Figure 12. Details from statewide coverages illustrating contrasting landcover and transformative processes in two Massachusetts landscapes: the North Quabbin area (left column) and southeastern Massachusetts (right column). The North Quabbin area is predominantly forested (a), and has undergone a great amount of forest harvesting in the past 20 years (b). Southeastern Massachusetts is predominantly developed, with much forest loss since 1985 (c) and continued rapid rates of development. Land protection is an important process occuring in the state (d) although the long-term impacts of protection on surrounding lands are unclear and will be investigated in LTER IV.

et al. 1999; McDonald et al. 2006b). Simultaneously, growing awareness of the ecological, economic, and social consequences of landscape fragmentation by development has increased efforts to protect land (Ritters 2005; MAS 2003). Massachusetts has the greatest concentration of land trusts in the U.S. and is a leader in coordinated conservation efforts involving public agencies, NGOs, and academic organizations, including HFR (Pidot 2005). Thus, land protection must be considered an important ecological process that interacts with and constrains other land uses (Foster et al. 2005).

In LTER IV, we will conduct regional analyses to: (1) document the spatial and temporal patterns of development, forest harvesting, and land protection; (2) interpret the environmental, historical, and socioeconomic drivers of these patterns; and (3) assess their influence on forest composition and structure, including invasive species and expanding ungulate populations. This analysis takes advantage of unique geospatial databases developed in LTER I-III, the Cross-LTER Ag-Trans Biocomplexity project (e.g., McDonald et al. 2006c), and our collaborations with The Nature Conservancy (TNC), USDA Forest Service, and Massachusetts state agencies.

Documenting patterns and drivers of landscape change

Critical databases developed in LTER I-III will be used to describe statewide patterns of landscape change. These data include: (1) historical land cover and land use (1830, 1930s, 1951, 1971, 1990 and modern), (2) development 1970-1999; (3) forest harvesting (1984-2003); (4) land protection (1880s; and 1970-2005); and (5) socio-economic information. For instance, the 1830 database allows us to assess the historical legacies of 19th century agriculture on modern forest pattern and process (Motzkin et al. 1999; Hall et al. 2002; Bellemare et al. 2002; Eberhardt et al. 2003), whereas the harvesting database is nationally unique as it captures geospatial data on all commercial harvesting for the past two decades on public and private lands (Kittredge et al. 1996, 2003; McDonald et al. 2006b). Changes in forest distribution in recent decades will be examined using landscape metrics that represent the major dimensions of change in landscape patterns. In collaboration with TNC scientists, we will expand our geographical analysis of forest harvesting (McDonald et al. 2006b) utilizing FIA data for southern New England, and quantify patterns of land protection, which are highly variable over time and space (Malizia et al. 2006).

We will explicitly investigate relationships between patterns of land-cover change and socioeconomic factors that are likely to drive patterns of land use, particularly human population and economic growth (Fig. 13). Data on population and household density (1990, 2000) derived from the U.S. Census, and at approximately the census block level (Radeloff et al. 2005), will be correlated with land-cover patterns in order to select explanatory variables to include in a model of landscape change. The probability of deforestation will be modeled to generate three scenarios of change (i.e., a realization of the underlying probability distribution) for the future two decades: a "Status Quo" scenario based on demographic and economic predictions from the U.S. Census Bureau and Commerce Department; a "land protection" scenario based on the 50% forest protection scheme outlined in *Wildlands and Woodlands* (Foster et al. 2005); and a "clustered development" scenario that increases the spatial autocorrelation of development without increasing the overall amount of land developed.

Ecological consequences of landscape change

Our work evaluating the ecological consequences of landscape change includes modeling and GIS analyses to evaluate the effects of forest fragmentation on wildlife habitat and field studies focused on the effect of fragmentation on forest structure and composition (including invasive species).

Modeling and GIS analyses: We will evaluate each of our statewide scenarios of landscape change from the perspective of habitat loss, degradation, and isolation and their effect on different sets of organisms. The goal is not to reproduce the metapopulation dynamics of any particular species, but to represent the range of variability in organism response to landscape change. For this study we will consider two definitions of habitat: all forests and unharvested forests; we will vary systematically the minimum usable patch size, the maximum dispersal distance, and the distance of sensitivity to edge effects over a range of realistic values. For each of the habitat types, we will measure habitat loss in each of our scenarios by the number of hectares of habitat (in patches larger than the minimum usable patch size) lost to development. Similarly, habitat degradation due to edge effects will be calculated as the number of hectares of habitat lost due to edge effects. Habitat isolation will be calculated using a graph theoretic approach, where patches of available habitat will be connected by the edges of the graph. Loss of different habitat patches will affect the overall graph diameter (Urban and Keitt, 2001), which we will use as a metric of habitat connectivity. Our analysis of scenarios of future development will relate to conservation planning efforts at broader spatial scales (e.g., the Massachusetts to New Hampshire "Quabbin to Cardigan" project (http://www.spnhf.org/landconservation/q2c.asp) and will contribute substantially to the Ag-Trans BioComplexity program. We will continue to work closely with local to national conservation and planning agencies and NGOs to develop products that address their conservation and policy applications (e.g., Foster et al. 2005; Orwig and Kittredge 2005).

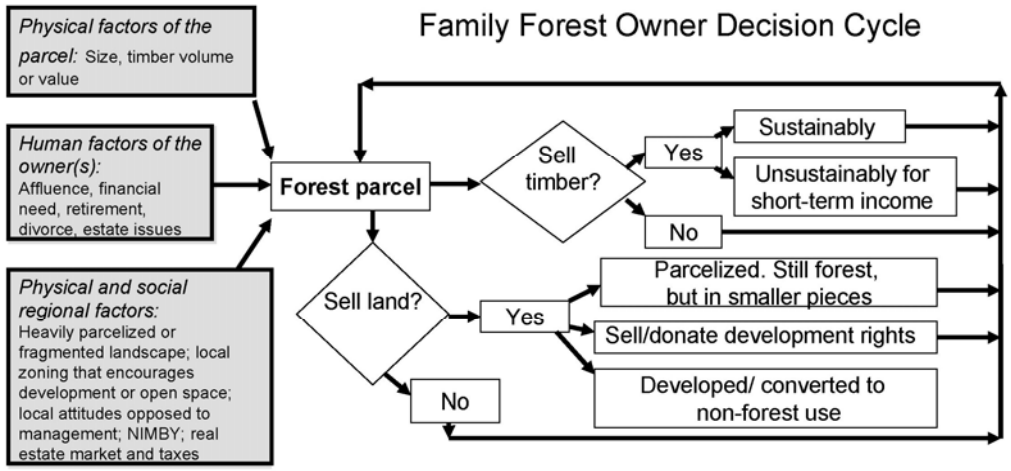


Figure 13. Flowchart illustrating the decision process for private forest landowners regarding the long-term management, conservation, and disposition of land. This process plays out regularly in tens of thousands of households and collectively determines forest condition and regional patterns of land cover. The process is cyclic but becomes terminal when land is converted to developed use. We hypothesize that the decisions highlighted are influenced by characteristics of individual owners (e.g., environmental ethics or attitudes, relative affluence, age and thus likelihood of selling or moving, circumstances of heirs (e.g., many or few, in residence or absentee)) as well as landscape or community context (e.g., physically parcelized / fragmented vs. largely intact; prevailing suburban vs. rural public attitudes). These factors are all dynamic. In some cases, the decision cycle operates slowly, with landowners not making active decisions for decades, whereas in other circumstances the cycle turns quickly, e.g., when landowners receive numerous offers for timber or land. There may also be interacting effects, e.g., situations in which owners first liquidate timber value and subsequently develop. These processes will be investigated in a parallel study by Co-I Kittredge.

Field studies: Building on our pilot studies, we will conduct extensive statewide sampling to evaluate the influence of environmental variation, land-use history, current landscape conditions, and human and natural disturbances on forest structure and composition, including invasive plant species. Sampling locations will be stratified by historical land-use (pasture, cropland, continuous woodland) and recent harvesting across the major ecoregions statewide. Regional analyses of the extent and spread of invasive plant species will be combined with comparisons of demographic performance and metapopulation dynamics to determine the potential roles of land-use history and habitat on the distribution, abundance, and further incursion of invasive species into forests across the region (see below). One goal will be to quantify the effect of existing and past landscape structure on modern forest composition, wildlife habitat, and invasive species in order to estimate the likely ecological effects of different scenarios of future development.

4. Hemlock Woolly Adelgid (HWA) and Loss of Foundation Species

Eastern hemlock (*Tsuga canadensis*) is a long-lived and shade-tolerant tree that dominates *ca*. 1×10^6 ha of forest in eastern North America (McWilliams and Schmidt 2000). Hemlock is a foundation species (Dayton 1972), whose architecture and functional characteristics define forest structure and microclimates and dominate ecosystem processes (Ellison et al. 2005a). Consequently, its widespread loss to an exotic insect and pre-emptive harvesting serves as a model system for investigating natural-human interactions and ecosystem consequences of the loss of foundation species.

Hemlock's deep shade and acidic, slowly-decomposing litter result in a cool, damp microclimate, slow rates of nitrogen cycling, and nutrient-poor soils (Jenkins et al. 1999) hostile to the establishment of other species. Hemlock canopies have lower rates of C and water exchange with the atmosphere than hardwoods (Catovsky et al. 2002; Hadley, 2000a, b; see also subsection 2, above). Hemlock forests also create unique aquatic habitats by maintaining high soil moisture levels, stabilizing base-flows, and decreasing diel temperature variation (Snyder et al. 2002). Deep shade and low litter quality from hemlock limit in-stream productivity and periphyton growth. Shifts in annual streamflow patterns, and in the amounts and quality of C inputs to streams, are predicted to accompany the shift from hemlock to deciduous forest (Ellison et al. 2005a).

Hemlock could functionally disappear in a few decades from the outbreak of HWA (*Adelges tsugae*), a rapidly spreading Asian insect that kills hemlocks of all sizes within 4-15 years of infestation, and associated increases in hemlock harvesting. As hemlock declines, it is replaced by hardwoods especially birch (*Betula* spp.), oaks (*Quercus* spp.) and maples (*Acer* spp.; Orwig et al. 2002). This compositional shift is leading to substantial changes in wildlife populations (Tingley et al. 2002; Ellison et al. 2005b), regional homogenization of floral and faunal assemblages (Ellison et al. 2005b), and altered soil ecosystem processes (Jenkins et al. 1999; Jefts and Orwig 2005) and hydrological regimes. Hemlock logging, which has increased in response to HWA, initiates more rapid and greater ecosystem changes than HWA because of the abrupt structural and environmental changes, removal of wood products including other tree species, soil scarification, and extensive slash (Kizlinski et al. 2002).

We have developed a comprehensive approach to examining forest response to the loss of a foundation species like hemlock (Table 2**)**. Building on studies supported by USDA and NSF (Orwig and Foster 1998; Kizlinksi et al. 2002; Orwig et al. 2002; Tingley et al. 2002; Jefts and

Table 2. Experimental space x measurement matrix for studies on the decline of hemlock from the hemlock woolly adelgid. Shading indicates that projects (rows) will occur in that observational experimental space (columns), and the collaborating institutions (HFR= Harvard Forest; HU = Harvard Univ.; UMass = Univ. of Massachusetts; UNH = Univ. of New Hampshire; UTenn = Univ. of Tennessee; UVM = Univ. of Vermont; WHRC = Woods Hole Research Center).

	Extensive (space-for-time transect)	Intensive (Prospect Hill)	Experimental manipulations	Temporal scale
Retrospective studies	HFR	HFR	HFR, Hampshire College	Decades to millenia
Patterns of insect dispersal and logging	UMass, HFR	UMass, HFR		Years to decades
Insect physiology and effect on trees	HFR, UMass, UVM	HFR, UMass, UVM	HFR, UMass, UVM	Days to years
Soil ecosystem processes	HFR	HFR, WHRC	HFR, WHRC	Months to decades
Atmospheric CO_2 and H_2O flux	HFR, HU	HFR, HU		Instants to years
Forest structure and environmental variables	HFR	HFR	HFR	Months to years
Structure of associated biota	HFR, UMass	HFR, Holy Cross	HFR, UTenn, Coweeta	Years to decades
ED and PnET models	HFR, HU, UNH	HFR, HU, UNH	HFR, HU, UNH	Decades to centuries

Orwig 2005; Stadler et al. 2005, 2006) and DOE (E. Davidson unpubl.), and leveraged by LTER, this approach uses paleoecological, observational and experimental studies at both regional and stand scales to evaluate:

- Biological attributes of hemlock that control compositional, structural, and functional characteristics of hemlock-dominated forests, including biogeochemistry and the physical linkages between terrestrial and aquatic ecosystems and the atmosphere;
- Environmental and biotic drivers, and dynamics of prehistoric declines in hemlock;
- Historical and environmental factors influencing: the current distribution, composition, and ecosystem characteristics of hemlock forests; rates and distances of HWA spread; patterns of hemlock decline and mortality; and rates and distribution of salvage logging;
- Mechanisms by which HWA disperses, alters hemlock physiology, and kills hemlock;
- Major changes in forest community characteristics and ecosystem functions resulting from hemlock loss and its replacement by deciduous trees as a result of HWA and logging.

From these studies, we will develop general mechanistic and process-based models of *coupled biological-physical system* response to the loss of foundation species (cf. Ellison et al. 2005a).

Evaluating the Pre-historical Decline and Dynamics of Hemlock. The abrupt, range-wide hemlock decline 5500 years ago is cited as the sole North American example of a pre-historical forest pest outbreak and an analogue for recent declines of chestnut and hemlock (Allison et al. 1986, Foster et al. 2006). Initial results from our investigations of the drivers of the mid-Holocene decline suggest that it involved interactions between pests/pathogens and a rapidly changing climate (Foster et al. 2006). In 17 sites across a climatic and vegetation gradient from northwest MA, where hemlock was abundant, to the coast where it was rare, the inland hemlock decline was paralleled by a decline in coastal oak (Fig. 14). High-resolution sediment

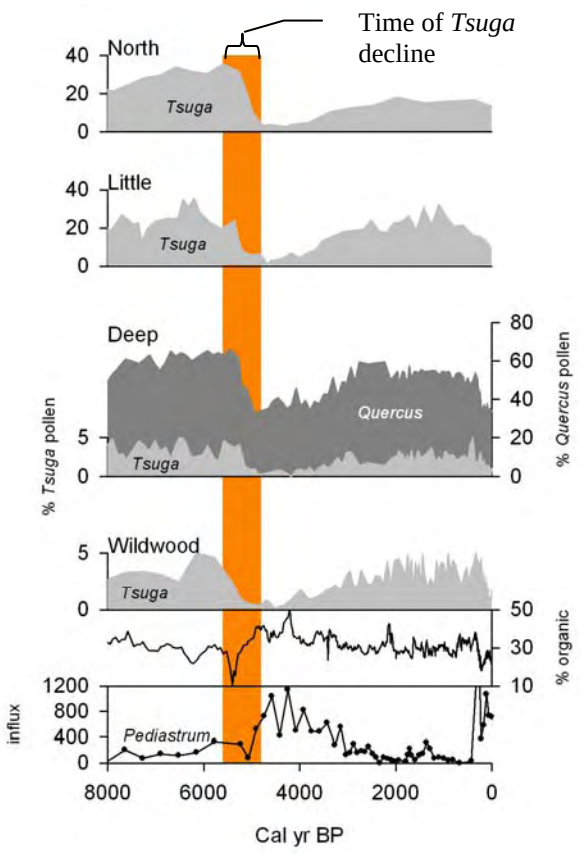


Figure 14. Paleoecological and paleoclimatic data from sites in New England: North (northwestern MA, Whitehead and Crisman 1978), Little (north-central MA, Oswald et al. 2006), Deep (Cape Cod), and Wildwood (Long Island NY, Foster et al. 2006). All sites show a prominent decline in *Tsuga* abundance at 5500 cal yr BP. However, coastal sites such as Deep feature a coincident (orange bar) drop in *Quercus* percentages. This dynamic is of the same magnitude and duration as the *Tsuga* decline, but involves a taxon that is different in terms of ecological and climatic preferences, perhaps indicating an abrupt climate change at the time of the *Tsuga* decline. The sharp drop in organic content at 5500 cal yr BP in the Wildwood record may indicate reduced water levels in response to severe drought. Lake-level data (e.g., Shuman et al. 2001) and increased abundance of *Pediastrum* algae, an indicator of low lake levels, at Wildwood suggest that the *Tsuga* decline was coincident with an interval of dry climate. We will analyze additional paleoenvironmental proxies at these and other sites to better understand mid-Holocene ecological dynamics.

analyses indicate that these dynamics coincided with intense droughts within an extended period of drought (Foster et al. 2006; Oswald et al. 2006), suggesting that the mid-Holocene decline in both species was driven at least in part by climate. This situation has modern parallels as HWA impacts appear to be mediated by climate, especially in the Northeast.

We will analyze key paleoclimatic and paleoecological proxies across southern New England to determine the relative importance of climate versus biotic factors in driving mid-Holocene forest dynamics. These include: (1) high-resolution analyses of pollen, organics, and compound-specific isotope geochemistry in sediments 6000-4000 years old to determine the relationship between hemlock and oak dynamics and abrupt climate changes; (2) identical analyses for the interval 9000 to 7000 years ago to determine whether similar ecological dynamics occurred in response to abrupt climatic changes 8200 years ago (Alley and Ágústsdóttir 2005); initial analyses reveal parallel declines in both species; (3) analyses of sediments in small lakes and vernal pools for insect remains and charcoal to see whether pest outbreaks or fires were associated with the declines and drier climate; and (4) ^{14}C analyses for chronological control. The results will provide historical context for modern hemlock dynamics from HWA in a rapidly changing climate.

Stand to Landscape Patterns of Spread and Damage. HWA reached southern New England in 1985 and currently occurs in every town in CT and half of MA. Results from CT suggest that infested hemlocks die over a ~10 year period and are rapidly replaced by black birch and other hardwoods. Preliminary studies of a 7500 km^2 area document HWA in over 90% of

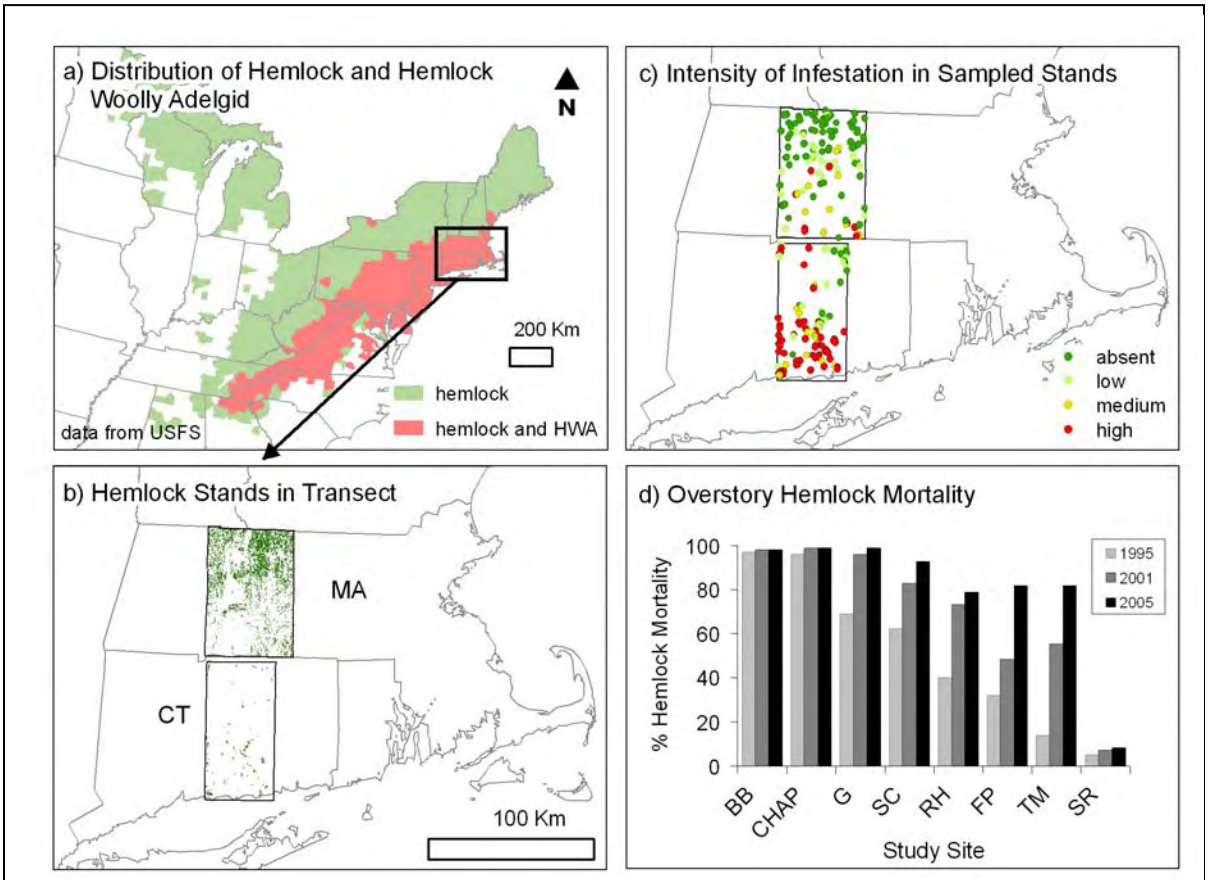


Figure 15. Distribution of hemlock and the hemlock woolly adelgid (HWA) in the eastern United States (a). A latitudinal transect through Massachusetts and Connecticut is used to sample the northward spread and impact of HWA (b). Individual hemlock stands were mapped from aerial photographs with ground truthing; HWA presence and decline/mortality of hemlocks were sampled in 237 stands. A series of permanent plots in 15 stands is being used to evaluate long-term changes in forest structure, compostion, microenvironments, and nitrogen cycling as hemlock decline and mortality occurs. Modified from Orwig et al. (2002 and 2006). Hemlock stands sampled within the latitudinal transect depicting intensity of HWA infestation (c). From Orwig et al. (2006). Hemlock mortality trends over the past ten years (1995-2005) at sites arrayed along the latitudinal transect in Connecticut (d). Hemlock trees at all southern sites exhibit progressive decline and mortality with no evidence of recovery. Salmon River (SR) was the last site to be infested by HWA, which was detected there in 1999. Modified from Orwig (2002).

CT hemlock stands and 40% of MA stands (Fig. 15). Tree damage parallels the northward spread of HWA, with heavy mortality in the south and little damage in the north. Mortality is not strongly related to stand or site factors, although the low damage in northern MA may be related to cold winter temperatures that reduce HWA populations (Paradis and Elkinton 2005). Many questions remain concerning the factors affecting HWA population dynamics and tree damage and mortality. We will extend our permanent plot network into Massachusetts and compare dynamics there with our extensive measurements of healthy hemlock stands and the new hemlock manipulation study (see below).

Comparison of HWA-induced Decline and Hemlock Logging. We have shown that thinning crowns due to HWA result in increased soil temperatures, moisture, N availability (Jefts and Orwig 2005), and litter decomposition (Cobb et al. 2006), even before widespread mortality. Intensive pre-emptive logging, the primary management response to HWA (Orwig et al. 2002;

Brooks 2004) leads to more abrupt microenvironmental and vegetation changes than HWA. We hypothesize that logging will result in greater abundance of shade-intolerant and invasive species, higher soil pH and nitrification rates, and reduced forest floor mass (Kizlinksi et al. 2002). To test this, we will expand our studies of vegetation and ecosystem dynamics in permanent plots in infested and logged hemlock forests. We will assess the long-term trajectory of decline in relation to regional and landscape position and environment, and will incorporate results into widely-distributed outreach materials to assist decision making for managers and landowners (cf. Orwig and Kittredge 2005).

Hemlock Manipulation Study. We will adopt a new experiment (est. 2003) in LTER IV that assesses the biotic and biogeochemical responses of hemlock-dominated ecosystems to slow and rapid removal of hemlock. Eight 90 x 90 m (0.8 ha) plots are grouped in two blocks, each consisting of one hardwood control plot and three hemlock-dominated plots: a hemlock control, a plot in which all hemlocks were girdled to simulate slow death-by-adelgid, and a commercially logged plot (Table 2). Data collection began in May 2003, two years prior to logging and girdling (Jan.-May 2005). This before-after-control-impact (BACI) design allows for good statistical power in the analysis of results, despite the fact that there are only two replicates of each treatment (Underwood 1994; Stewart-Oaten and Bence 2001; Gotelli and Ellison 2004).

All the trees in each plot have been identified, measured (DBH), and mapped (*x*- and *y*-coordinates and elevations relative to topographic relief of each plot). Cores have been taken from 30 trees in each plot to reconstruct stand ages and responses to historical climate events (e.g., 1938 hurricane) and pest outbreaks (e.g., chestnut blight, gypsy moth). Response variables measured in each plot include: temperature (air and soil) and light (grid of hemispherical canopy photographs); tree physiology (sap flow); soil respiration; N availability and N mineralization rates; primary production (litterfall) and decay of coarse woody debris; biodiversity assessment (understory vegetation); seed bank composition; and regeneration rates. Measurements are concentrated in the center 30 × 30 m of each plot, with the surrounding area of each plot being a buffer to account for edge effects. Locations for measurements are randomized while controlling for conflicts with other measurements and logistical constraints. All data are maintained in a set of GIS layers.

Three parallel experiments provide comparisons among social contexts, latitude, and focal foundation species. First, we initiated a study in a heavily infested hemlock stand in urban Boston at Harvard's Arnold Arboretum. We employ identical sampling methods as at HFR to examine the impacts of adelgid and logging in a setting where human safety drives management responses to invasive species. Second, to compare forest responses across regions, we are collaborating in experimental design and measurement protocols of a hemlock girdling experiment at the Coweeta LTER at the southern edge of the HWA invasion front. Third, we are collaborating on an analogous red oak removal experiment at the Black Rock Forest (eastern NY). Collectively we are establishing a network of long-term, large-scale experiments focused on the impact of the loss of foundation species from forest ecosystems (Ellison et al. 2005a).

5. Invasive Plants – Population-to-Landscape Studies and Experiments

Invasive plants are major biotic drivers of forest change in the Northeast and the subject of new HFR research initiatives. Despite widespread concern that exotic species fundamentally alter forest ecosystems, we know little about the mechanisms underlying their regional distribution, abundance and impacts (Levine et al. 2003). Drawing on our expertise linking historical land-use to modern vegetation patterns (e.g., Foster 1992; Motzkin et al. 1996, 1999)

and recent subregional (Von Holle et al. 2006) and population (Stinson et al. 2006c) studies, we are uniquely poised for long-term studies addressing the relative contribution of historical vs. modern disturbances and environmental variation in controlling: (i) patterns of invasion and spread; and (ii) impacts of invasive plants on forest ecosystems. In LTER IV, landscape-to-population-level observations, historical studies, and controlled experiments will examine how invasive plants respond to and drive forest change. We will combine broad multi-species analyses with focused studies of two important exotic species: the Eurasian biennial herb, *Alliaria petiolata*, and the shrub, *Berberis thunbergii*, both of which present major management concerns (Nuzzo 1993; Silander and Klepeis 1999), alter native plant performance (Stinson et al. 2006a, b), may change soil biogeochemistry and biota (Stinson et al. 2006b), and impact forest dynamics (Nuzzo 1993; Silander and Klepeis 1999, McDonald et al. 2006a). ***Landscape-level analyses*** will test whether current and historical factors are associated with invasive species presence and abundance, and investigate impacts of exotic plant abundances on native community structure and diversity. ***Metapopulation studies***, including experimental eradications, will determine whether populations are demographically self-sustaining and characterize responses of native organisms to invasive plant removals. ***Population-level studies*** will quantify contributions of environmental and genetic variation to invasive species distributions, and the responses of native organisms to above- and below-ground environmental alterations associated with invasion and land-use histories.

Landscape-level Historical Analyses – Regional Invasion Patterns and Impacts. Our recent work demonstrates that 19th-century land-use strongly influences exotic species distributions, in addition to modern disturbances such as logging (Fig. 16), providing some of the first evidence that past land-use influences invasive species distributions across broad spatial scales. Utilizing statewide historical and modern data on past and present land-use and current vegetation, soils, and environment (Hall et al. 2002; Kittredge et al. 2003; see subsection 3, above), we will: (a) document the history of introduction and spread of the invasive species of greatest management concern in northeastern forests; (b) evaluate the relative influence of historical and modern land-use and environment on invasive species distributions in a 10,000 km^2 study area; and (c) document landscape-level variation in relationships between native and invasive species. Our initial studies lead us to hypothesize that: (i) the influence of logging on invasive species is largely dependent on prior land-use and (ii) environmental factors influence invasive plant distributions at sub-regional scales, but prior land-use, interacting with recent logging, increasingly drive distributions and impacts at finer scales. We will quantify the presence, population sizes, spatial extent, and densities of our focal species and collect detailed environmental data in sites with known past and present land-use. We will use multivariate spatial analyses to assess landscape-level variation in the distribution and abundance of invasive plants.

Metapopulation Studies – Identifying Sources of Invasion and Impacts of Removal. We will characterize the degree of demographic self-sustainability of invasive plant populations and evaluate the relative contribution of populations in specific habitats to invasion in similar and different habitats. First, we will intensively monitor natural metapopulations. The first annual survey by 30+ undergraduates in our REU summer program generated population maps demonstrating strong relationships between historical agriculture and current distribution of invasives at HFR. We will expand these long-term surveys to monitor metapopulation dynamics of six species: *A. petiolata*, the shrubs *B. thunbergii, Rhamnus cathartica, R. frangula, Lonicera spp.* and the vine, *Celastrus orbiculatus.* Documentation of colonization, extinction, and

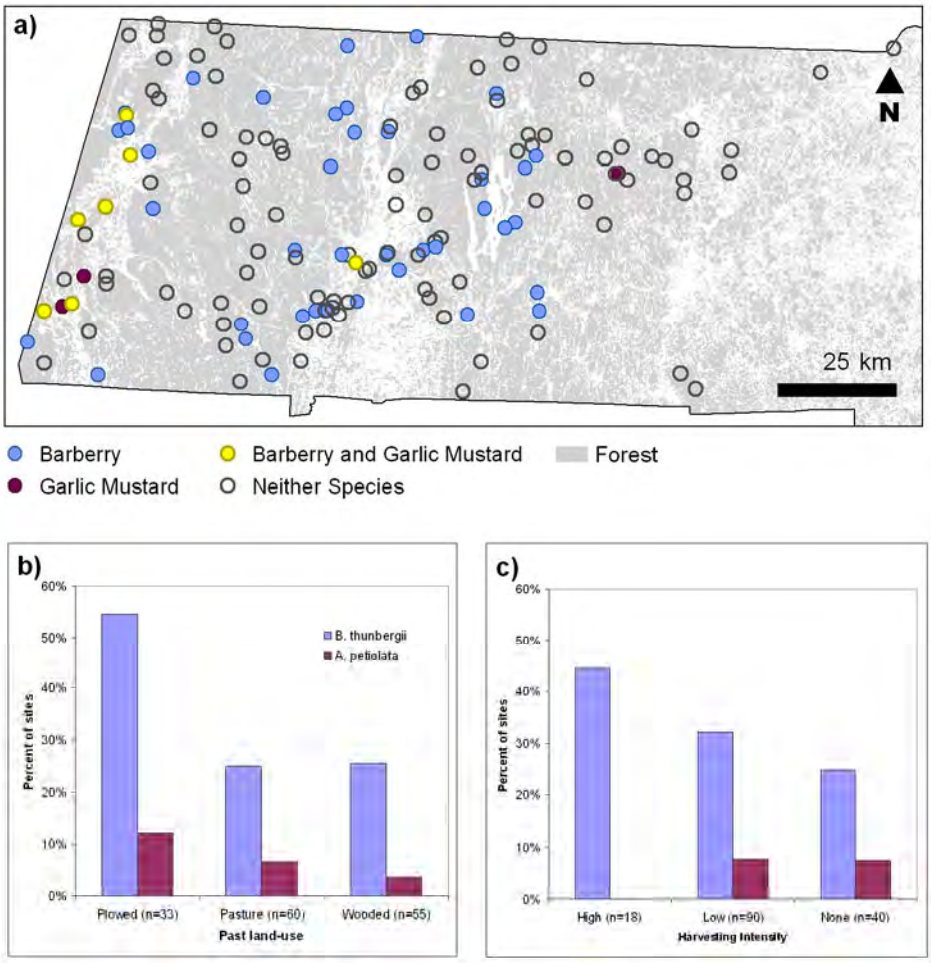


Figure 16. Preliminary data on invasive species distribution in central and western Massachusetts (a). There was increased abundance of *B. thunbergii* and *A. petiolata* in sites that were plowed for historical agriculture (b) and increased abundance of *B. thunbergii* in areas of modern forest harvesting (c). We plan to expand these investigations in LTER IV for several important exotic species, and to conduct additional, intensive studies of these two focal species to further establish the influence of historical and modern landuse on their modern distributions.

population growth will provide a historical context for interpreting ongoing and future patterns of invasion. Changes in invasive plant distribution and abundance will also be compared with overall floristic change as determined by a recent floristic inventory of the 1200-ha HFR. Intensive floristic inventories in the 1930s and 1940s provide the basis for detailed evaluations of changes over 75 years (Raup 1938; Smith 1948, 1949).

Second, we will determine the degree to which populations in specific habitats are self-sustaining by conducting experimental eradications of putative source populations of invading populations. Initial data for *A. petiolata* and *B. thunbergii* suggest that net dispersal and success of propagules from highly disturbed "source" habitats may be critical for invasion of forested sites (Fig. 17). In particular, post-agricultural sites may be the primary sources of invasion into continuously wooded and recently disturbed areas. Experimental eradications will test for demographic self-sustainability of populations in different historical and modern habitats (Donohue et al. 2000a; Griffith et al. 1994; Foster 1992; Kittredge et al. 2003) and identify source habitats that support invasion into other habitats. Combined with demographic field observations, these studies will identify key sources of invasion pressure and estimate the degree

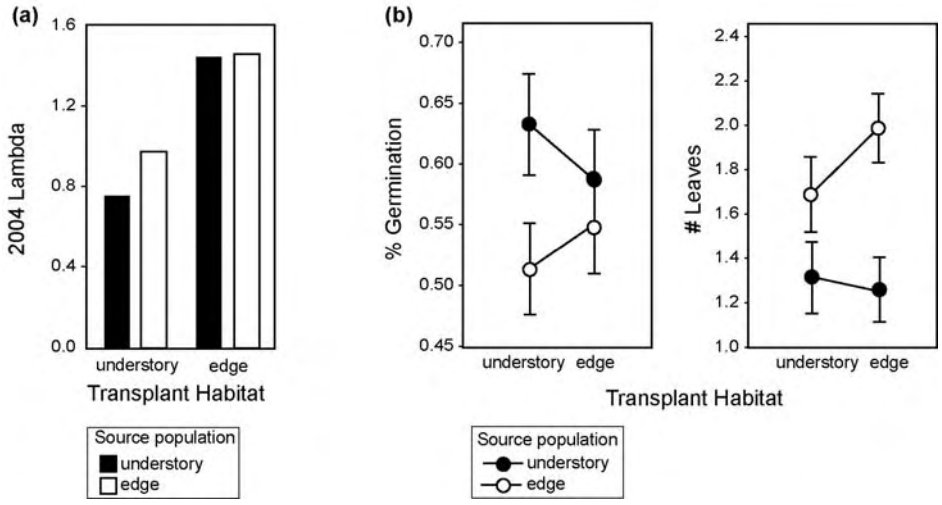


Figure 17. Preliminary work with *A. petiolata* has motivated questions about metapopulation dynamics and evolutionary potential within invading populations. (a) 2004 Projected population growth rates (lambda) in forest edge and understory habitats at Harvard Forest. Immigrant seeds from edge habitats have higher population growth rates than native seeds in the forest understory, suggesting that populations in recently (and possible historically) open sites act as sources of propagules for forest invasions; (b) Results from 2004 Reciprocal Habitat Transplant study demonstrating source-population effects on seedling performance in local HFR populations. The source of seeds determined germination success and plant size in the forest understory; seeds matured in the forest had higher germination success than immigrant seeds from the edge, but immigrant seeds from the edge grew more than those from the forest.

to which history and environment determine the frequency and conditions of new colonization and extinction of invasive species across differing landscapes.

Our experimental eradications will also provide direct tests for impacts of *A. petiolata* and *B. thunbergii* on native organisms. We will measure impacts on plant and soil microbial communities in eradication sites and in adjacent sites with populations that are potentially maintained by the manipulated source population. These data will quantify indirect effects of population eradications on native plant communities that operate through effects on dependent invasive populations.

Population-level Studies – Direct Mechanisms and Impacts of Invasion. Variation within and among populations in the source and timing of colonization, phenotypic expression, and genetic makeup may also contribute to landscape distributional patterns and metapopulation dynamics of invasion. We will directly test for intrinsic population characteristics that may interact with environmental and historical factors to control these larger-scale processes. We have identified subregional and habitat-specific variation in individual plant performance in our focal species. In *A. petiolata*, seeds matured in forest habitats have survival advantages in forests compared to those matured in open habitats. However, the higher fitness of plants in open sites nevertheless rendered those populations the primary contributor to invasion in forests (Fig. 17). Thus, environmental effects of multiple habitats influence the demography of interacting populations growing in different habitats. To distinguish between environmental and genetic

effects on variation in invasive species performance in different regions, reciprocal transplant experiments using *A. petiolata* will be conducted in approved sites. We will thereby characterize how environmental and genetic variation influence regional and local variation in plant performance and determine the degree of local adaptation and the potential for further evolution of this species. In addition, life-history and physiological traits associated with fitness in different habitats will be identified using phenotypic and genotypic selection analyses (Lande and Arnold 1983). We will also acquire accessions of *A. petiolata* populations for future phylogeographic studies of the history of invasion.

Finally, we plan a series of soil manipulation experiments to (a) focus on recent evidence that *A. petiolata* suppresses tree seedling growth by disrupting mycorrhizal fungi symbioses (Fig. 18); and (b) compare native plant performance on soils from distinct subregions with differing histories of land-use (crop cultivation, pasturing, or continually forested) and invasion. We will measure native plant performance and microbial activity at invaded and uninvaded sites and in uninvaded soils that have been experimentally conditioned with seedlings of *A. petiolata* and/or *B. thunbergii*, including physiological and growth responses and compositional responses of species mixtures. We will quantify the responses of soil microbes, including mycorrhizal fungi, to these treatments and relate microbial processes to native plant performance. Combined with the experimental eradications and landscape studies, these experiments will provide broad opportunities for collaboration on evolutionary, physiological, community, and ecosystem responses to invasion, and new insights into population-level processes controlling native-invasive species interactions.

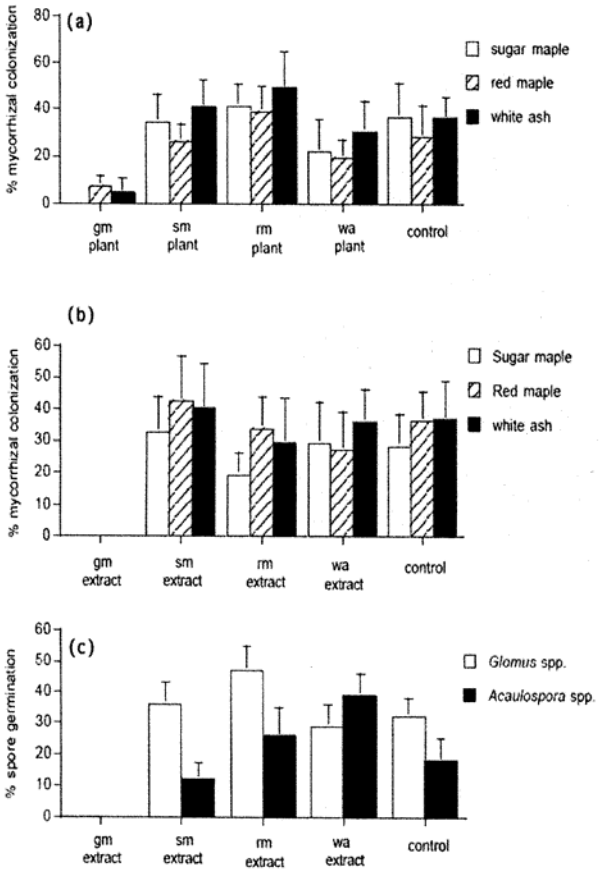


Figure 18. Novel evidence that garlic mustard (*A. petiolata*) suppresses native tree seedling growth by disrupting symbiosis with arbuscular mycorrhizal fungi has motivated new research directions on the biotic impacts of invasive plants. Figures show the effects of: (a) soils conditioned with garlic mustard (gm), sugar maple (sm), red maple (rm), white ash (wa), or a no-species control treatment on mycorrhizal colonization of native tree seedlings; (b) extracts of the above plants or a water control on mycorrhizal colonization of native tree seedlings; (c) extracts or water control on percent germination of native arbuscular mycorrhizal fungal spores.

6. Dynamics of Expanding Native Ungulate Populations

As a consequence of reforestation and changing social attitudes, New England is experiencing a resurgence of forest wildlife, including deer and moose (Fig. 19). Moose recolonized Massachusetts in the last 15 years, are expanding rapidly in the absence of predators

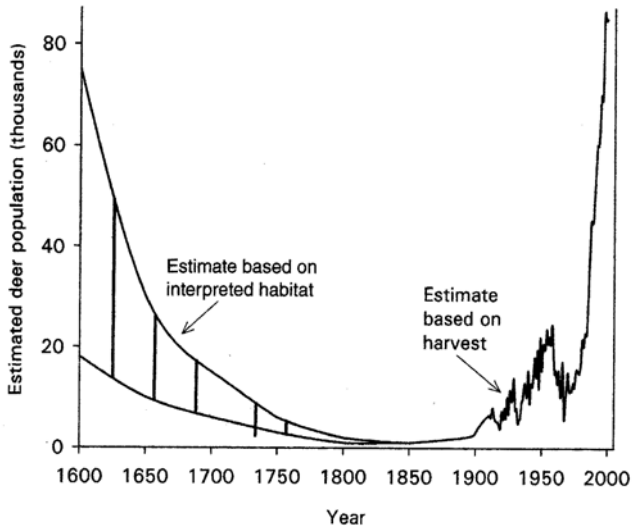
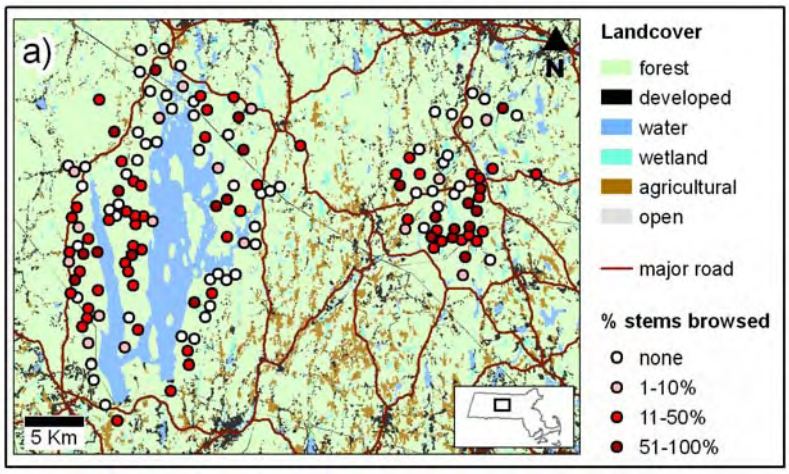


Figure 19. Estimated white-tailed deer populations in Massachusetts for the past 400 years. Following 300 years of decline, the populations have rapidly increased due to reforestation and declines in the number of hunters and huntable land. The dramatic increase in deer since the 1950s has important ecological implications for the state's forests which will be more fully explored in LTER IV (Foster et al., 2002).

or hunting, and have a population of ca. 800 individuals (B. Woytek, pers. comm.). Locally they are reducing tree regeneration and understory and aquatic vegetation. Because they were extirpated historically from the southern portion of their range, there is no information on moose behavior or ecology in temperate forests at their southern range limit, but studies from boreal and subarctic regions indicate that they exert long-lasting effects on ecosystem processes, especially nitrogen dynamics and forest productivity, structure and composition (Pastor et al. 1993). In similar fashion to our early studies on HWA with its arrival in the region, we plan long-term studies of moose in their arrival and growth phase.

These expanding populations of large herbivores are a potent biological driver of ecosystem dynamics and a major challenge for land managers (Foster et al. 2002). Preliminary studies indicate that selective browsing by these ungulates exerts substantial impacts on forest structure and composition (Fig. 20), with a high degree of regional variability and interactions with other processes, especially forest harvesting and land conversion. In LTER IV, through collaboration with scientists at U.S. Fish and Wildlife, MA Fish and Wildlife, and the University of Massachusetts, we will initiate studies of the effects of these expanding



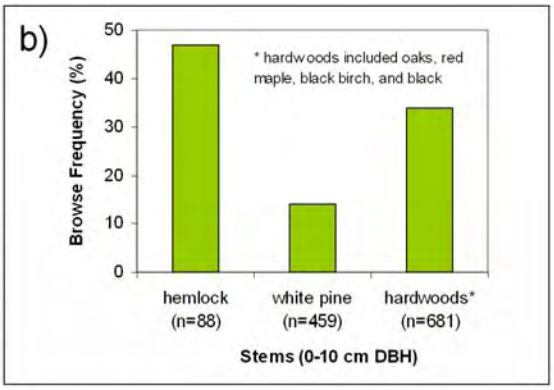


Figure 20. Moose browse intensity in the Quabbin and Ware River watershed forests (a) and seedling and sapling preference in harvested and unharvested forests (b). As part of a collaborative effort with federal, and state agencies, and the Univ. of Massachusetts, we will determine the spatial distribution of moose populations in central Massachusetts, identify preferred browse species and size, and determine the relationship between moose browsing and timber-harvesting (Faison 2006).

populations on New England forests. This work will address hypotheses that moose: (1) density and activity is inversely related to human activity centers; (2) are preferentially browsing and altering forest composition in recent (<10 year-old) intensively logged areas; and (3) are selectively removing hardwoods and hemlock and shifting forest composition to white pine.

This work will include three thrusts: (1) Spatial analysis and modeling of moose home range and movement to provide the first insights into activity patterns of moose in temperate forest landscapes; (2) Quantification of moose and deer browse in regional sampling of harvested and intact forests (see subsection 3, above) to clarify browse preferences (species and size class of material) and the landscape distribution of browsing with relationship to harvesting; and (3) Focused study of impacts by individual collared moose in harvested and unharvested forests to directly relate impact patterns to particular animals and specific durations of habitat use. This study will leverage state and federal agency plans to continuously track 15 moose in our region with GPS radio collars. The agencies and UMass personnel will compile information on moose location and movement and HFR researchers will conduct ground and vegetation analyses. Both groups will conduct home range and spatial analyses of moose activity using contrasting approaches. The HFR group will utilize the mechanistic home range analytical approach developed by collaborator P. Moorcroft (Moorcroft et al. 1999, 2006a, b).

B. Regionalization, Modeling and Synthesis

1. Cross-site and Regional Studies

LTER IV is designed geographically, thematically and disciplinarily to: (i) enhance collaborations with the HBR and PIE LTERs, and other regional groups (e.g., Geography Dept. at Clark University; Institute for Urban Studies at Boston College) and LTER sites (e.g., BES, CAP) that emphasize social sciences and human dimensions and (ii) position our research for opportunities emerging through the LTER STF and NEON programs. We have begun discussions and held workshops with many of these groups and currently coordinate the Northeastern NEON domain. We have also begun to identify other regional collaborators and satellite institutions including Bartlett and Howland Experimental Forests, Black Rock Forest, Institute for Ecosystem Studies, Great Mountain Forest, and Highstead Arboretum (Fig. 3).

Regional collaborations allow for parallel measurements and experiments under different environmental or historical settings. The three New England LTER sites represent important points on a regional hydrological gradient from mountains (HBR) to central highlands (HFR) to coastal plain (PIE), with additional differences in topography, geology, wetlands, stream chemistry, vegetation, and history. Together they provide an opportunity to evaluate the range of stream hydrology in New England. An important step in enhancing these efforts will be assembling information on historical differences across sites. Here, too, the New England LTERs offer a valuable contrast. Historical land use at HBR and other mountain sites across northern New England has been dominated by pulses of intensive timber harvesting and slash fires, with intervals of recovery that lacked agriculture. HFR and the surrounding central highlands were also subjected to extensive clearing, but much of the land was kept clear for long periods of time and used for pasture or crop cultivation. Although the same is true for lands surrounding PIE, New England's coastal plains have also been influenced by extensive and ongoing industrial development and urbanization. These historical patterns have left imprints on ecosystem composition, structure and function and have ongoing effects on cultural, economic, and conservation activities of the region's inhabitants (Fig. 21). We will use our regional studies across New England as the basis for collaborating with PIE and HBR colleagues (Cogbill,

Hamburg, Pontius) to synthesize narrative histories and data that depict the variation in land-use, landscape dynamics, and land-protection activities.

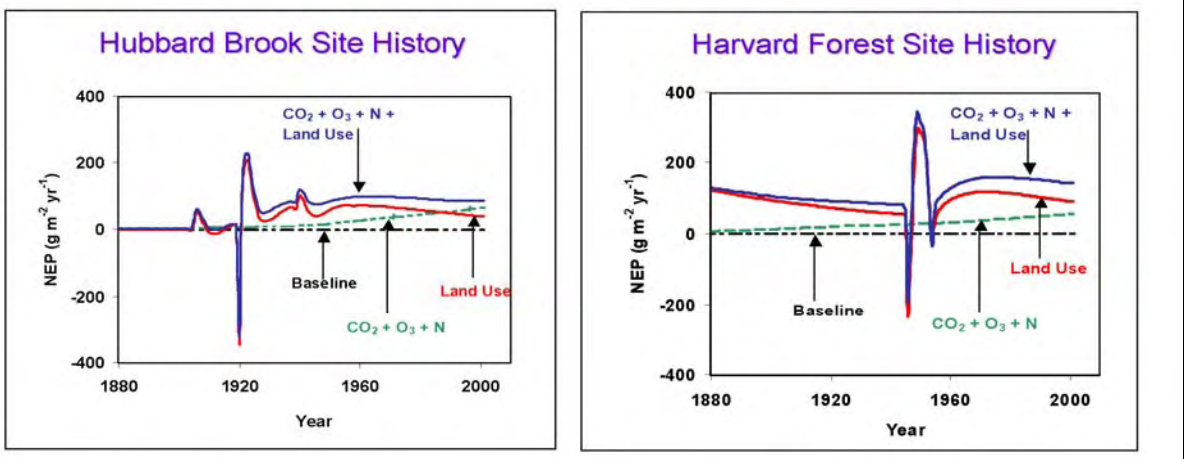


Figure 21. Transient effects on predicted carbon balances for two LTER sites: HBR (**left**) and HFR (**right**). The implication is that the influence of atmospheric change and land use history on present day C balances are roughly equal in magnitude.

2. Modeling

We will continue to synthesize our data and those of regional collaborators through modeling of spatial environmental patterns, invasive species, climate, vegetation, and ecosystem processes. For example, in HF LTERs I-III the PnET ecosystem model, (e.g., Aber et al. 1995, 1997; Ollinger et al. 1997, 2002a) provided a means of linking process studies to regional climatic drivers (Ollinger et al. 1993, 1998, 2002a). Similarly, validation of model estimates (Aber et al. 1995; Ollinger et al. 1998) against site-specific measurements of NPP and ecosystem CO_2 fluxes (Wofsy et al. 1993; Goulden et al. 1996) provided confidence in extending simulations to the regional level.

Modeling Carbon and Nitrogen Dynamics. In LTER IV, we plan to continue to regionalize our work to understand the role of northeastern ecosystems in the C and N cycles, and the degree to which ongoing changes in regional land use, climate and chemistry of the atmosphere and precipitation influence ecosystem-atmosphere feedbacks. Research on the regional C and N cycles will build on the current modeling activities of three of the Co-PIs and their collaborators – Ollinger (UNH), Wofsy (Harvard) and Melillo (MBL).

Ollinger and the UNH Team – In LTER II –III research, we identified the need for spatial information concerning N availability and N cycling mechanisms as factors limiting the accuracy with which we can model regional budgets of C and N. We have initiated an effort to characterize spatial patterns in N availability, and its effect on C uptake, through integration of field measurements from biometry plots and eddy covariance towers, high spatial and spectral resolution remote sensing data, and coarse-resolution global remote sensing data from several orbital platforms. Preliminary results using data from multiple sites across the eastern U.S. showed good success relating field-measured canopy N concentrations to high spectral resolution

scenes using relatively simple vegetation indices and a single standardized prediction equation (Figs. 22 and 23). Application of this work to the entire Northeast now appears feasible with

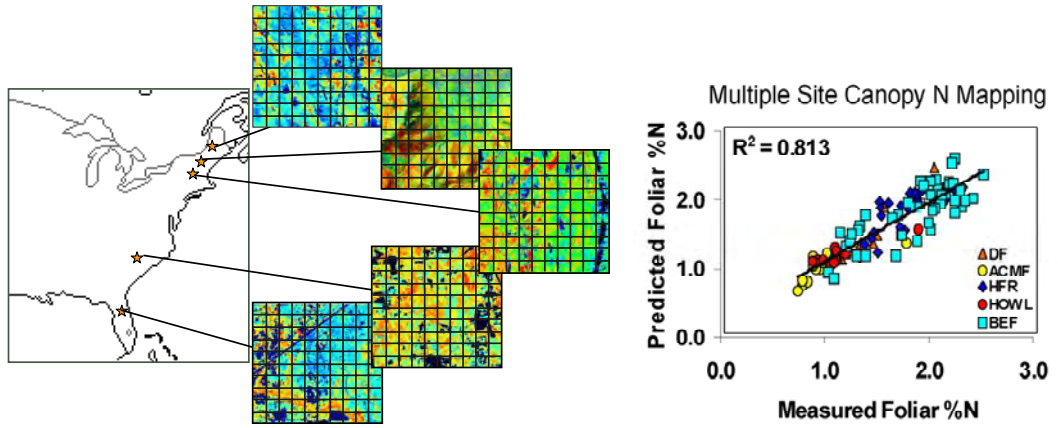


Figure 22. Canopy N mapping across five eastern U.S. AmeriFlux sites. The sites include a range of forest types along a gradient from Maine to Florida. From south to north, the sites are: Gainesville, FL (Austin Cary Memorial Forest, ACMF); Duke Forest, NC (DF); Harvard Forest (HFR); Bartlett Forest, NH (BEF); and Howland Forest, ME (HOWL). **(Left)** Mapped estimates of canopy N concentrations for landscapes surrounding the five sites. **(Right)** Predicted versus observed foliar N concentrations at 130 plots across the five sites. Predictions were generated using a single, PLS regression applied to AVIRIS spectral data after all images underwent a standardized atmospheric correction.

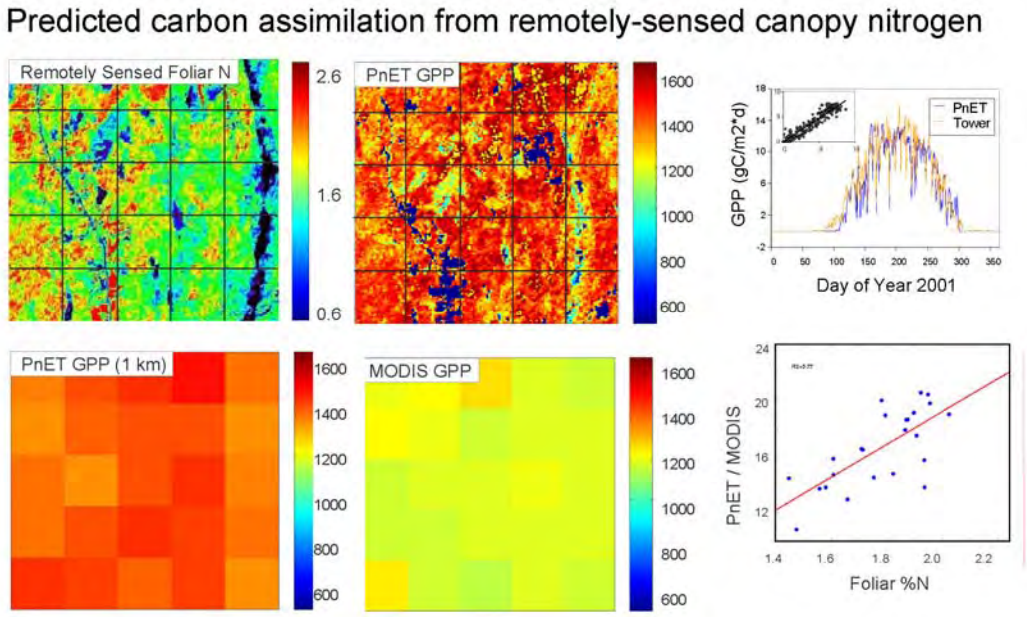


Figure 23. Spatial patterns in canopy nitrogen and foliar nitrogen concentration for a 5x5 km landscape at HFR, as estimated by NASA's AVIRIS sensor and AVIRIS integration with the PnET-Day ecosystem model (**top left and top center**). Validation of model estimates with measurements from the HFR EMS tower (**top right**) showed good correspondence between measured and modeled values. Degrading the resolution of PnET predications provided an opportunity to compare foliar N-based GPP predictions with those being generated by the global MODIS satellite (**bottom panels**). Overall, MODIS estimates were found to be low with respect to PnET with a degree of deviation that corresponded to estimated canopy N.

relatively modest additional effort. Once completed, the next step will involve extending predictions of forest C dynamics under scenarios of altered climate, atmospheric chemistry and land use with the PnET model (Fig. 24). PnET is a well-validated site-to-regional model of ecosystem C, N and H_2O fluxes designed to capture important controls on net primary productivity, C exchange and N retention using a minimal number of parameters and without reliance on calibration. It has been modified to predict the effects of multiple atmospheric pollutants (tropospheric ozone and nitrogen deposition) and disturbance history and has been tested against C, N and H_2O flux data at sites across North America and Europe (e.g. Aber et al. 1995, 1997, 2003; Goodale et al. 2002; Law et al. 2000; Li et al. 2000; Ollinger et al. 1997, 1998, 2002a; Ollinger and Smith 2005; Reich et al. 1999). With this model we can also explore the effects of changes in atmospheric CO_2 concentration, climate and land cover and use on carbon cycling in terrestrial ecosystems.

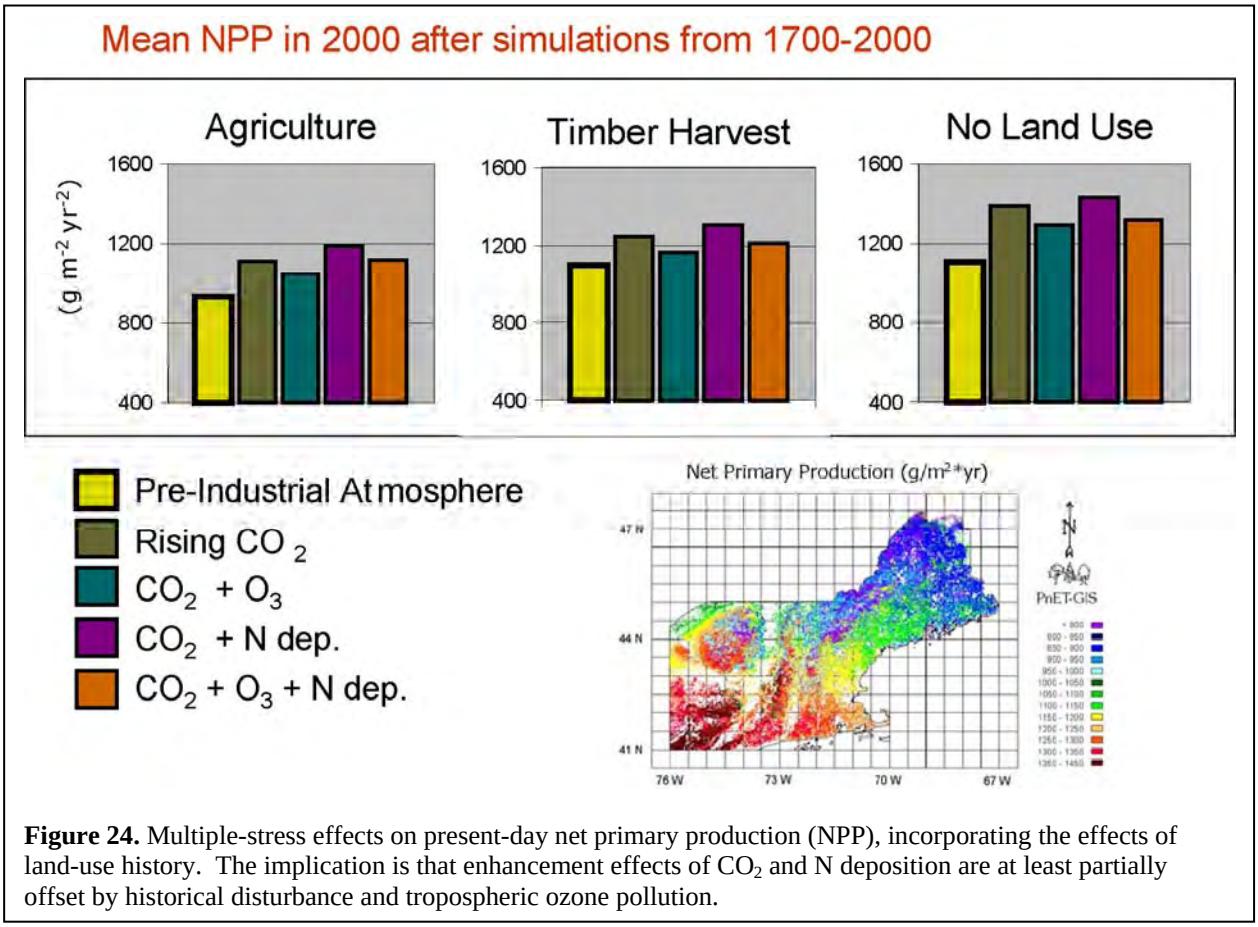


Figure 24. Multiple-stress effects on present-day net primary production (NPP), incorporating the effects of land-use history. The implication is that enhancement effects of CO_2 and N deposition are at least partially offset by historical disturbance and tropospheric ozone pollution.

We also plan to use PnET to examine the degree to which several poorly quantified N cycling mechanisms contribute to the "missing N" in current northeastern N balances. The need for improved modeling of the N cycle is highlighted by the fact that N budget estimates frequently contain discrepancies, with inputs from atmospheric deposition and fertilizer exceeding hydrologic outputs, often by sizeable amounts. In a synthesis of data for N inputs, losses and internal transfers among 16 large northeastern river basins, riverine outputs represented just 49% of the total N loss needed to produce balanced N budgets (van Breemen et al. 2002). The unaccounted fraction of N exports has been attributed to denitrification and sequestration in soils,

although their relative roles are unknown and neither mechanism has been quantified at the appropriate spatial scales. We plan to address this question by including these mechanisms in a series of revised northeastern U.S. N budget simulations.

Wofsy and Moorcroft (Harvard) – To provide a regional context for our site-based carbon measurements, Wofsy and Moorcroft are engaged in an NSF-Biocomplexity effort to relate regional carbon fluxes to climate variability, land-use change and CO_2 fertilization. This effort involves developing a constrained implementation of the Regional Atmospheric Modeling System-Ecosystem Demography Model Version 2 (RAMS-ED2) for the New England region (Moorcroft et al. 2001; Moorcroft 2003; Medvigy et al. 2005, 2006). RAMS-ED2 is a coupled atmosphere-ecosystem model that synthesizes the fast timescale responses of individual plants to the atmosphere and the long-term, regional-scale dynamics of heterogeneous ecosystems subject to land-use change and harvesting. It is designed to predict carbon fluxes on spatial scales of hectares to thousands of square kilometers that are consistent with fast timescale flux-tower measurements of CO_2 fluxes, seasonal measurements of canopy phenology from remote sensing data, and decadal scale forest inventory measurements and land-use history forcing. The ecosystem state variables and environmental response functions of the optimized model provide a comprehensive description of short- and long-term factors regulating fluxes in the regional carbon cycle.

In preliminary tests ED2 was jointly constrained using eddy-flux measurements and forest-inventory measurements from HFR to yield accurate short- and long-term ecosystem dynamics. Furthermore, with additional input of only initial canopy composition for a dissimilar forest in Maine, it successfully reproduced the dynamics of that site as well. The optimized model will provide a unique tool for quantifying the contributions of environmental forcing, ecosystem recovery from land-use change, forest harvesting and CO_2 fertilization to current and future patterns of terrestrial carbon fluxes and resulting patterns of atmospheric CO_2 concentrations in North America. The constrained ED2 model is now being used in coupled regional RAMS-ED2 simulations in which the ED2 model is initialized with forest inventory measurements across the region and then used to simulate decadal–scale forest dynamics, CO_2 fluxes and atmospheric CO_2 patterns across New England.

Melillo and the MBL Team – We will use MBL's Terrestrial Ecosystem Model, TEM, to provide a third approach to simulating regional carbon dynamics. The Terrestrial Ecosystem Model (TEM) is a process-based model that uses spatially referenced information on climate, elevation, soils, vegetation and water availability to make monthly estimates of vegetation and soil carbon and nitrogen fluxes and pool sizes. TEM is well-documented and has been used to examine patterns of terrestrial carbon dynamics in the Northeast and across the globe. The model is structured to consider the influence of multiple factors such as CO_2 fertilization, climate change and variability, land-use change and ozone pollution (Melillo et al. 1993; VEMAP Members 1995; McGuire et al. 1997, 2000a, b, 2001; Tian et al. 1998, 1999, 2000, 2003; Xiao et al. 1998; Prinn et al. 1999; Reilly et al. 1999; Clein et al. 2000; Zhuang et al. 2003, 2004; Felzer et al. 2004, 2005). Recently, TEM has undergone two important changes. First, it was modified to better account for the influence of nitrogen inputs from nitrogen fixation and atmospheric nitrogen deposition as well as losses of carbon and nitrogen due to leaching of nitrate, dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) from terrestrial ecosystems and trace gas emissions of nitric oxide (NO), nitrous oxide (N_2O) and dinitrogen (N_2). Second, the water balance module in TEM was modified to incorporate more detailed plant physiology. Studies of the carbon, nitrogen and water cycles at HFR, including eddy flux studies, provided

data for the parameterization and testing of TEM. In LTER-IV, we will run TEM in both diagnostic and prognostic modes for the region.

Common databases – The MBL, UNH and Harvard modeling teams will work together to develop a common set of drivers (land use, climate, N deposition, tropospheric ozone and so on) for our regional modeling studies. For land-use change, we will make extensive use of new data we will develop to document patterns of landscape change (see II.A.3) to update and refine existing data sets already in use by the three modeling groups. We will take advantage of some new work being done in support of a Northeast climate-change impacts assessment (Hayhoe et al. 2006) to improve and extend our regional climate databases. The UNH Team (Ollinger et al. 2002a) has developed a spatially explicit nitrogen deposition database that we will use as a foundation for our modeling work. Likewise, the MBL Team (Felzer et al. 2004) has developed a model-generated spatially explicit database for tropospheric ozone (1900 to the present) that we will use, at least initially, for our diagnostic simulations. We will use county-level historical land-use and forest harvesting scenario developed by the Harvard Team (Albani et al. 2006a).

The three modeling groups associated with HFR have extensive experience with creating, managing and using large spatially-explicit databases. Our challenge in the proposed work will be to construct internally consistent databases that meet the temporal and spatial demands of the three parallel models. This will facilitate model intercomparisons.

Modeling Patterns of HWA Spread, Harvesting and Forest Damage. Invasive species like HWA, with rapid population growth and the potential for rapid spread, provide exceptional opportunities to investigate synergistic interactions between dispersal and demography, especially at invasion "fronts." Nonetheless, collecting the necessary data and parameterizing realistic regional-scale models of invasion present significant logistical challenges, and few studies have rigorously tested the relative roles of dispersal and population dynamics on invasions (Holt and Keitt 2005; Moller 1996). Assessment of HWA spread by HFR and federal and state agencies and demographic data on HWA lineages by collaborators at the University of Massachusetts (Elkinton et al. unpubl.) provide the geographically extensive data necessary to explore the factors determining rates of HWA range expansion. Albani et al. (2006b) used the ED model in conjunction with an empirically-calibrated HWA spread model to predict the regional-scale consequences of HWA infestation for forest composition and terrestrial carbon fluxes in the region. With Paul Moorcroft (Harvard) and Adam Porter (UMass) we are developing scalable models that project HWA regional dispersal and invasion rates from demographic and short-range dispersal data collected within individual forest stands, and from town-level HWA data. We model range expansion as a combination of population growth and the propensity to disperse over different spatial scales. Related models with non-hierarchical structure include reaction-diffusion models (Flather and Bevers 2002; Skalski and Gilliam 2003), telegraph models (Holmes 1993), wave-front models (Fisher 1937; Harris 2004), and velocity-jump models (Hillen and Othmer 2000). Our hierarchical, patch-based model is inspired by these, but designed for empirical studies of patchily-distributed organisms.

3. Major New Synthetic Volumes

We plan three new volumes as part of the LTER Network synthesis series, focusing on the integration of long-term research and conservation planning; statistical approaches for large ecosystem experiments; and cross-site LTER studies addressing transitions in agrarian systems.

Coastal Lands Through Time. Historical Insights into the Conservation of Natural and Cultural Landscapes. D. R. Foster and G. Motzkin (HFR). Written in an accessible style this case-study

of the region extending from Cape Cod and the islands of Massachusetts and Rhode Island to Long Island, will present new approaches to conservation based on a decade of integrated studies in archaeology, history, geography and ecology. Major themes include: history of the people, land and environment; changing disturbance regimes (fire, wind, coastal processes, and land use); long-term changes of globally important plant and animal species; and ecological-historical insights for protecting and conserving landscapes.

Statistics for Ecosystem Experiments: How to Analyze Data when the Time-series are too Short or There are too Few Replicates - A. M. Ellison (HFR) and N. J. Gotelli (Univ. of Vermont). This volume will provide how-to solutions and computer code for analyzing "typical" ecosystem experiments with examples drawn from studies at LTER sites. Because of their large spatial extent, these experiments often have few replicates or inadequate temporal depth to be analyzed with standard statistical tools. Topics include: the perils of pseudoreplication; hypothesis testing in the "standard" statistical framework and Bayesian alternatives; model-based vs. design-based experiments and statistics; exploratory analysis and graphical displays for spatial and temporal data; dealing with spatial, temporal, and spatiotemporal autocorrelation; time series modeling; BACI designs and analysis; spatiotemporal modeling; and dataset synthesis (including cross-site syntheses).

Agrarian Landscapes in Transition: Contrasting Social and Ecological Dynamics and Conservation Responses. C. Redman (CAP LTER) and D. Foster (HFR). The Agrarian Landscapes in Transition BioComplexity project involves six LTER sites (CWT, CAP, HFR, KNZ, KBS, SGS) representing differing biogeographic regions and contrasting agrarian transformations. With their institutional partner The Nature Conservancy, they are quantifying the ways in which landscape transformations differ spatially and temporally and help explain cross-scale patterns. This volume of case studies will: describe social, technological, and ecological drivers of agricultural and land-use change; their ecological consequences; the influence of legacies in social and ecological response; and emerging major conservation issues and strategies for these regions.

C. New Instrumentation and Infrastructure

1. A Wireless Sensor Network for Prospect Hill. Quantifying spatial and temporal variability of the physical environment and ecosystem processes is of critical importance but many projects are limited to manual measurements in remote plots or automated measurements adjacent to data acquisition and control modules. We will leverage LTER support by seeking additional funds from NSF, DOE and USDA to install wireless networking and small, low-power autonomous sensors on the Prospect Hill tract, the site of many core LTER experiments (stream gauges, eddy flux towers and biometry plots, soil warming plots, N addition plots). This will enable direct measurements of ecosystem processes operating on local scales and network connectivity for ongoing studies.

2. Nutrient Analysis Equipment. *CHN Autoanalyzer.* There is growing demand for C and N analyses by LTER, REU, other NSF and TNC-funded scientists and students who annually analyze over 4000 soil, foliage and water samples. We plan to replace our disabled Fisons CHN with equipment to handle larger sample volumes and to complement our recently acquired (with NSF MUE funds) Lachat 8500 autoanalyzer. The equipment will be maintained and run by HFR but available to all visitors, collaborators and students. We will also have access to new IMS

and ICP-MS facilities at the University of New Hampshire. At The Ecosystems Center two new Continuous Flow Isotope Ratio Mass Spectrometer Systems (CF- IRMS) have the capability to measure the natural abundance or enriched isotopic ratios of C, N, O and H in individual components of complex mixtures such as phospholipid fatty acids, amino acids and fatty acids, isotopic ratios of C, O and H in water, dissolved inorganic and organic compounds and C, N, O and H isotopic ratios of the greenhouse gases CO_2, CH_4 and N_2O from environmental samples and tracer manipulations.

3. Synthesis Center – Integrated Research and Education with Long-term Ecological Data. Ecology and conservation integrate a spectrum of biological, physical and social sciences, span broad scales of time and space, and rely on diverse resources including digital data bases, physical archives, and library collections. Reports from the LTER and NEON programs, IPCC (Intergovernmental Panel on Climate Change) and IHDP (International Human Dimensions Program on Global Environmental Change) highlight the need for facilities that promote the teaching and pursuit of interdisciplinary environmental research. These centers, ranging from national hubs (e.g., NCEAS) to regional, institution-based facilities, will provide integrated access to diverse information and tools for analysis and development. HFR plans to develop a facility (Center for Synthesis in Ecology and Conservation) that fuses its unique digital and archival collections on the New England landscape in an integrated resource that serves as a regional and national center and a model for synthetic research and education. The Center, which will be both a building and a platform accessible to distant users through the internet, will include:

- Quantitative, cartographic, photographic, and descriptive materials from HFR's 100-year history of field, laboratory, and controlled experiments;
- Historical and pre-historical records of ecological and cultural change centering on southern New England and the northeastern U.S.;
- 20,000 volumes on the history, ecology, conservation and environment of New England;
- A comprehensive information system of all research over the past 20 years;
- Real-time access to on-going observations and measurements of physical and biological processes in the 1200-ha HFR field laboratory and classroom.

Section III. Management of the Harvard Forest and LTER Program

Administration. The HFR LTER program is unusual within the LTER Network as it is administered at the research site, which is the base for: the PI, many Co-Is and students; the major experiments and research facilities; data management and archives; and the financial office. HFR is a department in the Faculty of Arts and Sciences of Harvard University, administers the Masters in Forest Science, and offers courses and the Ph.D. degree through various departments. Partial funding for HFR is derived from endowments; most research activities are supported with grants. As PI and Director, David Foster is responsible for project administration, coordination of science meetings and the HFR research group, and site representation in the LTER Coordinating Committee, a task shared with Co-I Aaron Ellison. John O'Keefe oversees informal education and outreach programs through his position as Coordinator of the Fisher Museum. LTER Co-Is focus much of their research on HFR-based projects and the Science Team is responsible for policy decisions, developing research directions and inter-site collaborations, data management policies, and representing HFR LTER in the scientific community. Emery Boose, Information Manager, serves as LTER Data Manager, assisted by Julie Pallant and Archivist John Burk. Edythe Ellin, Director of Administration, oversees facilities and financial staff and coordinates the summer undergraduate research program. The skilled Facilities staff assists with research implementation and is equipped for experimental manipulations, forestry operations, and construction and maintenance of research projects.

Enhancing Collaborations. The emergence of the integrated research and education program at HFR has been accompanied by a growing user group of national and international scholars; more than 100 outside scientists, representing more than 40 institutions, conduct research at HFR annually. To enhance collaboration and research by non-LTER scientists, we advertise opportunities including Bullard Fellowships, the Summer Research Program for Undergraduates, our Annual Ecology Symposium, facilities, and long-term measurements and experiments through our web page, mailings and venues such as *Science*, *ESA and BES Bulletins*, and *BioScience*. A new web-based research application process facilitates submission and review of proposals for new studies as well as updates of long-term projects. Since launching this system in 2005, we have reviewed 75 research applications, 15 by new investigators. Initial review is completed by the Site Coordinator, Director of Administration, Data Manager, and Director, with further review by the LTER science team as appropriate. A new forest land-use plan, emphasizing research, conservation and educational uses is being developed this year.

The **Annual HFR Ecology Symposium** integrates the LTER and NIGEC/NICCR (DOE) programs and provides a forum for all researchers working at HFR to discuss progress and new directions. The symposium is widely advertised and open to all scientists, students, and professionals in the northeastern U.S. and is a major venue for new collaborations. The symposium is well attended by agency representatives, policy makers, and collaborators. Abstracts are published on-line for the public and broader community. The schedule emphasizes synthesis, critical review of program development, and opportunities for interdisciplinary interactions (e.g., historical ecologists, atmospheric scientists, and population biologists).

Land Base. The 1200-ha HFR (Fig. 3) has operated as Harvard University's main ecological research and educational facility since 1907, and its records on historical land use and vegetation dynamics are unsurpassed by any site in the US. HFR also owns the Pisgah old-growth tract

within Pisgah State Park, NH, which blew down in the 1938 hurricane and is the site of much historical and ongoing research.

Research Facilities and Resources. The HFR provides a complete base for research in forest, ecosystem and historical ecology and biosphere-atmosphere interactions. The historical land records, long-term experiments and three eddy flux towers attract many innovative collaborative studies. The Fisher Meteorological Station records 15-minute and daily values in near-real time. Shaler Hall, completely renovated in 2004-2005, provides offices, seminar rooms, a 20,000-volume library, dining facilities for up to 100, laboratories for paleoecological, tree-ring, morphological, computational and GIS studies, and a complete herbarium of the local flora. The John G. Torrey Laboratory includes physiology and nutrient analysis laboratories with fume hoods, gas chromatograph, Lachat autoanalyzer, nano-pure water, balances, and drying ovens. Two recently upgraded (2004) greenhouses, two shade houses and a common garden provide controlled research conditions. A mobile lift provides access for up to four researchers to 20-m forest canopies. The Archive (300 m^2) houses 100 years of data on the land and research, sample storage including cold facilities, and air photo interpretation systems. Researchers also make extensive use of laboratory, controlled environment, and computing facilities in the Division of Applied Sciences and Biological Laboratories at Harvard, The Ecosystems Center at the Marine Biological Laboratory, the Complex Systems Research Center at University of New Hampshire, and the University of Massachusetts.

The **Fisher Museum** and lecture hall (1000 m^2) is devoted to public and formal education, seats 100, and displays the Harvard Forest Dioramas that depict the history and conservation of New England forests. Group housing is provided at Fisher and Raup Houses, (36 max.) plus 12 apartments/houses for visiting researchers, graduate students, and post-doctoral fellows. Equipment for experimental manipulations, construction, and maintenance includes a back-hoe, bulldozer, crawler, skidder, tractor, dump truck, flat bed truck, vehicles including pick-ups, a van, SUVs and a sedan, a wood-working shop, maintenance garage and a sawmill.

Section IV. Information Management and Technology

1. Purpose & Scope

The Harvard Forest Information Management System (IMS) is designed to store and deliver scientific information (data and metadata) resulting from research at the HFR. In its current form it includes most data collected over the last 20 years (both LTER and non-LTER) as well as selected data from earlier studies recorded in the HFR Archives. Datasets include both long-term and short-term field measurements as well as historical, paleoecological, and modeling studies. As a general rule, datasets are included in the IMS if they support a publication or are deemed to have long-term scientific value, regardless of the source of funding.

2. Online Data Archive

The design of the Harvard Forest IMS has evolved rapidly in recent years with steady improvements in cyberinfrastructure at HFR (Tables 1 and 2). In its current form the online Data Archive consists of a series of static web pages accessed from the Data Archive home page:
http://harvardforest.fas.harvard.edu/data/archive.html
From this page users can find datasets by research category or by dataset ID (if known), or by searching the LTER Data Catalog. Each dataset has two associated web pages: an Overview page that contains discovery-level metadata (generated directly from EML via an XSL stylesheet), and a Data page that contains links to data files and associated attribute-level metadata. Tabular data are stored as comma-delimited text files while spatial data are stored as ArcView or Idrisi files. Large files are stored in a standard compressed format (zip).

3. Web Page

While the Data Archive contains much information on past and ongoing projects, other sections of the HFR web page provide information on recent, current, and upcoming projects:

The Major Research Topics section (http://harvardforest.fas.harvard.edu/research.html) provides a comprehensive overview of all research activities at the Forest, updated annually.

The Annual Harvard Forest Ecology Symposium Abstracts (and Summer Student Research Abstracts) (http://harvardforest.fas.harvard.edu/research.html) provide summaries of all current research projects at HFR (with preliminary results and often with figures), updated annually.

All researchers who wish to work at HFR are required to submit a Research Project Application (http://harvardforest.fas.harvard.edu/research/conducting.html). Applications are reviewed for their scientific merit, compatibility with HFR goals, and logistical feasibility (the team of reviewers includes the Information Manager). Information from the online forms is stored in a MySQL database and can be accessed from the HFR Intranet web page (password protected).

The HFR Publications page (http://harvardforest.fas.harvard.edu/publications.html) contains a complete bibliography of HFR as well as a growing list of journal articles available for download in pdf format.

4. Security & Backup

The current hardware base includes four Dell servers (Windows 2000) and about 100 individual desktop and laptop computers (mostly Windows XP; includes about 30 computers in summer for REU students and visiting researchers). The servers are backed up daily onto tape. A tape rotation system retains three weekly, three monthly, and one annual tape backup. Individual desktop and laptop computers are backed up to the server over the Internet using GetConnected software. Servers and individual computers are kept up to date with antivirus software and operating system patches. The Data Archive is copied to CD annually and copies stored offsite.

The HFR is connected via a T1 line to the Harvard University campus network. The University provides e-mail services and strong support for the network connection and network-level security.

5. Policies & Data Submission

Harvard Forest information management policies are posted on the Policies and Guidelines web page (http://harvardforest.fas.harvard.edu/data/policies.html). HFR endorses the new LTER Network policy for data release. After recent improvements in cyberinfrastructure, we are now in the process of implementing the new policies for data access and use, including user tracking and a standard use agreement.

As mentioned above, a Research Project Application must be submitted annually for every new and continuing research project at HFR. This information allows us to track new and ongoing projects and ensure that data and metadata are submitted to the Information Manager in a timely fashion. Individual scientists prepare their own data and metadata files, which are checked, reformatted, and posted by the Information Manager. Primary responsibility for quality control rests with the individual scientist. Every effort is made to update the Data Archive annually in conjunction with the Harvard Forest Ecology Symposium in later winter or early spring.

6. Related Materials

In addition to online scientific data, HFR also maintains extensive document and sample collections. The Harvard Forest Archives contains document records for nearly 100 years of research at HFR, including more than 1700 published and unpublished studies as well as extensive collections of maps and photographs. The Harvard Forest Sample Archives contains over 200 boxes of soil, litter, and tree core specimens. Both Archives are fully cataloged. Information on these and other resources for research are listed on the Site and Facilities web page (http://harvardforest.fas.harvard.edu/research/site.html).

7. Future Plans

In LTER IV we expect that cyberinfrastructure and IMS capability will continue to develop rapidly at the HFR. We view the following goals as particularly important for this period:

- During LTER III we used the creation of discovery-level EML as an opportunity to update the metadata for all of our datasets. Direct coding and maintenance of such metadata in EML was found to be a satisfactory short-term solution. However it is not a good solution for encoding attribute-level metadata or for updating information that changes frequently (such as individual contact data). We plan to migrate our metadata to a relational database that can exchange content directly with EML. HFR has joined a recent LTER Network initiative to develop a generic database design for this purpose.

- Once we have such a relational database in place, we plan to develop online forms so that researchers can enter their metadata directly online. Though we anticipate that the metadata so entered will require some follow-up editing by the Information Manager, we also expect that a system of this type will make dataset submission considerably easier for everyone.

- We also plan to begin migration of our core long-term datasets to a relational database for better access, quality control, and online query capability. Though the broad scope of our IMS may preclude the inclusion of all datasets, we would like to move ahead with datasets deemed to have the greatest long-term scientific value.

- As described above, the HFR web page contains a wealth of information on past, current, and upcoming research projects. However this information could be better integrated for the user. We plan to develop a consistent list of research categories to use throughout, to make selected information from the Research Project Applications available on our public web page, and to provide additional links to direct users to the proper section.

- We also plan to better integrate the Data Archive with other local information resources, including the Research Project Applications, the publication list, and catalogs of the HFR Archives, Sample Archives, and Library.

- The Data Archive contains a few spatial datasets of general utility (e.g., HF014. HF055, HF110), but most are incorporated directly into larger datasets for the specific projects that used them. We would like to increase the number of spatial datasets (GIS and remote sensing) available on our web page and add better metadata and search capability.

Table 1. Cyberinfrastructure Development at Harvard Forest

Year	LTER	Internet Access	Ethernet (buildings)	Computers	Servers	Datasets Online	EML
1988	I	none	0	6	0	0	0
1991	I.5	9.6k	0	10	0	0	0
1994	II	14.4k	0	30	0	0	0
1997	II.5	56k	3	45	0	30	0
2000	III	T1	3	60	0	47	0
2003	III.5	T1	6	100	4	66	66
2006	IV	T1	6	100	4	95	95

The location of HFR headquarters and core researchers on the field site (65 miles from the main Harvard campus) offers many scientific and logistical advantages, but also presents numerous challenges for developing the cyberinfrastructure required for an LTER site. Since 1988, considerable effort and resources (from NSF and the University) have been devoted to installing and maintaining wiring, telecommunications, computers, servers, and software at HFR (numbers of computers and number of datasets online in 1997 are estimates).

Table 2. Cyberinfrastructure Milestones in LTER III

2000. Fisher, Raup & Community Houses wired for Ethernet
2000. High-speed DSL connection to EMS (HF004)
2001. Automated weather station (HF001)
2002. Four servers, centralized storage, tape backup system
2002. HF web page moved from LNO to local server
2002. HF Intranet web page
2003. HF web page redesigned
2003. Data Archive redesigned, metadata converted to EML
2003. Centralized backup system (GetConnected)
2004. Wireless network access (Shaler Hall & Archives buildings)
2005. Online application system with MySQL (visiting researchers, etc)
2005. Schoolyard LTER web page

During LTER III our local network was expanded to include additional buildings, the EMS, and wireless access. Local servers were installed to host the HFR web page and to provide server-based software, storage, and backup. Information resources, including the HFR web page and online Data Archive, were completely revised and updated. An online database system was created to handle applications from researchers, students, and visiting fellows.

Section V. Outreach Program

Since 1985, the Harvard Forest **Summer Program in Ecology** has provided outstanding research experience for a diverse and talented group of up to 36 students (selected from >200 applicants each year) centered on an NSF REU site grant (12 students) with additional support from other grants, including Mellon Foundation-UNCF Minorities in Ecology program. Program administration emphasizes advertisement and recruitment; selection of diverse and productive students; one-on-one student-mentor relationships within research groups comprised of faculty, graduate students, post-doctoral associates and undergraduate students; weekly seminars and workshops on research topics, ecological career opportunities, graduate studies, and ethics in science; field trips to research sites and other institutions including participation in the IES Ecology Careers Workshop; an **Annual Student Symposium** with student presentations on research results; program evaluation and discussion; and follow-up including publication, professional presentation, thesis development, and career tracking, including a formal follow-up study of past participants. Recruitment of traditionally under-represented groups has been strongly emphasized and a new initiative to have senior research personnel visit UNCF colleges is yielding excellent results; in 2005, 27% of summer students were from traditionally under-represented groups.

A total of six to eight **Bullard Fellowships** are awarded annually to mid-career scientists and professionals seeking to synthesize past work, initiate new studies, or collaborate with HFR researchers. Beyond engendering new collaborations this program has greatly facilitated the exchange of LTER scientists across the Network including: AND (T. Spies, M. Harmon, F. Swanson, J. Jones. J. Franklin), LUQ (R. Waide, N. Brokaw, J. Thompson), HBR (J. Aber), and KNZ-NWT (J. Briggs).

Harvard Forest provides training to both Masters and PhD level graduate students. The Masters in Forest Science (MFS), a thesis-oriented program based at HFR offered through the Harvard University Graduate School of Arts and Sciences, provides an exceptional opportunity for students with strong backgrounds in biology, forestry, environmental sciences, geography or related fields to pursue independent research in ecology, conservation, forestry and environmental science. The program is strongly oriented towards innovative research that will lead to published results in major research journals. Following graduation, previous students have entered doctoral programs or pursued careers in conservation, natural resource management, consulting, and public education. In addition, each year 5-10 PhD students from other departments within Harvard University as well as other institutions from across the country conduct their research using the extensive facilities at HFR.

The Fisher Museum attracts approximately 6,000 visitors annually to view its world-renowned dioramas, displays, and videos presenting our LTER research as well as posters from scientific meetings. Among these visitors each year are more than 90 groups (including K-12 classes, professional groups, and university classes) that receive interpreted programs on HFR LTER research. John O'Keefe, Coordinator, also provides six to eight presentations annually on HFR LTER research to professional and community groups throughout New England. The Museum also hosts more than a dozen professional meetings each year.

Through the Schoolyard LTER program (SLTER), HFR set a goal of reaching out to the K-to-12 population in a comprehensive manner by utilizing our scientists, research protocols, and web-based data resources to enhance hands-on science and outdoor inquiry-based learning. The Schoolyard LTER, augmented by grants from the NSF EdEn Venture fund, GreenLeaf Foundation, and Massachusetts Environmental Trust, has allowed us to expand our HFR-SLTER

program into a significant ecology education model that includes a two-day Summer Institute for Teachers, academic-year teacher seminars, and professional environmental education support throughout the school-year. Protocols and background information on each of 4 research themes, field materials, and related books and resources are provided to each teacher in our program. Twenty-eight teachers and approximately 750 students participated actively in developing an educational model based on HFR field research protocols. Collaboration with 4 regional environmental organizations has effectively enabled us to reach a wide range of schools across the region.

Demand for our research-based, hands-on approach continues to grow each year, and we plan to offer continued support to existing schools while expanding our outreach to under-served students in our region. We are currently seeking additional funding to support eight teachers in urban Worcester, Massachusetts, which has the highest level of cultural and racial diversity in central Massachusetts.

Each year at least one local high school student intern has been supported to work in the laboratory on HWA research and these interns have achieved outstanding success in their science coursework, science fair projects, and continuing academic careers.

HFR scientists make direct and indirect contributions to improved natural resource policy and management. HFR research on hurricane disturbance in southern New England has influenced overall policy and specific management of the state's Quabbin Reservation (~20,000 ha), which serves as the watershed for metropolitan Boston. The 10-year forest management plan and scheduled silvicultural activities are directly influenced by an improved knowledge of hurricane periodicity and impacts to forests resulting from HFR LTER studies. HFR research results on HWA as a disturbance vector and silvicultural management implications have been incorporated into a chapter in a published proceedings as well as an Extension fact sheet for practitioners on silvicultural options for stands that are either infested or at risk of infestation. The fact sheet is available on-line in pdf format, and was distributed via direct mail to all practicing foresters and loggers in Massachusetts through the office of the state Extension Forester. HFR statewide data on timber harvesting as a form of disturbance will be used by the state's Department of Conservation and Recreation in developing ecosystem assessments for the state's 13 ecoregions and forest and park management plans for public lands across the state. Further analysis of these statewide or regional data will be used to inform foresters and woodland owners about the role that their individual properties play at broader ecosystem scales, placing individual management decisions into habitat and watershed contexts. The HFR Wildlands and Woodlands white paper has been distributed to conservation organizations throughout Massachusetts and beyond, and serves as a catalyst for discussion of state and local land protection and management. Numerous land trusts, watershed associations, and conservation-oriented philanthropic organizations have expressed interest in applying HFR recommendations, and one of the co-authors has been invited to present Wildlands and Woodlands concepts in a plenary session at the 2006 national convention of the Society of American Foresters. Thus, through the development and analysis of data, and production of specific outreach products, Harvard Forest research influences a broad range of management and policy decisions of conservation agencies and non-governmental organizations, resource managers, and woodland owners.

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