

Experimentally testing the role of foundation species in forests: the Harvard Forest Hemlock Removal Experiment

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Summary

1. Problem statement – Foundation species define and structure ecological systems. In forests around the world, foundation tree species are declining due to overexploitation, pests and pathogens. Eastern hemlock (*Tsuga canadensis*), a foundation tree species in eastern North America, is threatened by an exotic insect, the hemlock woolly adelgid (*Adelges tsugae*). The loss of hemlock is hypothesized to result in dramatic changes in assemblages of associated species with cascading impacts on food webs and fluxes of energy and nutrients. We describe the setting, design and analytical framework of the Harvard Forest Hemlock Removal Experiment (HF-HeRE), a multi-hectare, long-term experiment that overcomes many of the major logistical and analytical challenges of studying system-wide consequences of foundation species loss.

2. Study design – HF-HeRE is a replicated and blocked Before-After-Control-Impact experiment that includes two hemlock removal treatments: girdling all hemlocks to simulate death by adelgid and logging all hemlocks > 20 cm diameter and other merchantable trees to simulate pre-emptive salvage operations. These treatments are paired with two control treatments: hemlock controls that are beginning to be infested in 2010 by the adelgid and hardwood controls that represent future conditions of most hemlock stands in eastern North America.

3. Ongoing measurements and monitoring – Ongoing long-term measurements to quantify the magnitude and direction of forest ecosystem change as hemlock declines include: air and soil temperature, light availability, leaf area and canopy closure; changes in species composition and abundance of the soil seed-bank, understorey vegetation, and soil-dwelling invertebrates; dynamics of coarse woody debris; soil nitrogen availability and net nitrogen mineralization; and soil carbon flux. Short-term or one-time-only measurements include initial tree ages, hemlock-decomposing fungi, wood-boring beetles and throughfall chemistry. Additional within-plot, replicated experiments include effects of ants and litter-dwelling microarthropods on ecosystem functioning, and responses of salamanders to canopy change.

4. Future directions and collaborations – HF-HeRE is part of an evolving network of retrospective studies, natural experiments, large manipulations and modelling efforts focused on identifying and understanding the role of single foundation species on ecological processes and dynamics. We invite colleagues from around the world who are interested in exploring complementary questions to take advantage of the HF-HeRE research infrastructure.

Key-words: biodiversity and ecosystem functioning, climatic change, ecosystem manipulation, foundation species, invasive species, *Tsuga canadensis*

Introduction

Foundation species (*sensu* Dayton 1972) are taxa that are locally abundant and regionally common, whose structural or

functional characteristics create habitat for a large number of associated species, and which modulate core ecosystem processes such as energy and nutrient fluxes or water balance (reviewed by Ellison *et al.* 2005a). Because foundation species are common and abundant, in most cases they are not in immediate threat of extinction and thus are rarely of conservation

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concern (Gaston & Fuller 2008). Nonetheless, in terrestrial ecosystems world-wide, a number of foundation tree species are declining as a result of introductions and outbreaks of non-indigenous pests and pathogens, irruptions of native pests and over-harvesting or high-intensity logging (see review in Ellison *et al.* 2005a for detailed case studies). Paleocological studies have shown that foundation tree species, such as eastern hemlock [*Tsuga canadensis* (L.) Carr.] have declined in the past due to insects and climate change (Allison, Moeller, & Davis 1986; Foster *et al.* 2006; Shuman, Donnelly, & Newby 2009). The occurrence and magnitude of these declines are expected to increase with future climate change and an increase in extreme climatic events (Gaston & Fuller 2007; Berggren *et al.* 2009). Such declines and the eventual local or regional extinction of foundation species may result in cascades of evolutionary, ecological and environmental changes (e.g. Smith & Knapp 2003; Whitham *et al.* 2008; Albani *et al.* 2010).

There are significant logistical and analytical challenges involved in experimentally assessing the system-wide consequences of the loss of foundation species for individual populations, multi-species assemblages and ecosystem dynamics. The spatial scale of manipulations must encompass at least substantial portions of entire ecosystems. The temporal duration of monitoring following experimental manipulation must encompass life spans of long-lived organisms and capture slow turnover in plant- and soil-bound nutrients and carbon; consequently, the time required to characterize effects fully requires at least decades, but can exceed centuries (Harmon 1992). At the same time, the frequency of monitoring also must be fast enough to identify the turnover and non-equilibrium dynamics of short-lived taxa and rapid biogeochemical cycles, along with the transient dynamics of long-lived taxa and fast changes in ecosystem processes (e.g. Smith & Shugart 1993; Hastings 2001). Finally, the necessarily large spatial grain, long duration, and intensity of instrumentation and measurements of these experiments preclude the comparatively high replication common in small-scale ecological studies (Witman & Roy 2009). Low replication and relatively short time series (generally < 50 observations) present significant challenges for data analysis and strong inference.

Here, we describe the Harvard Forest Hemlock Removal Experiment (HF-HeRE), a large-scale, long-term experiment designed to assess the consequences of the loss of a single foundation species, eastern hemlock (*T. canadensis* (L.) Carr.), from eastern North American forests. Eastern hemlock is declining throughout an increasing part of its range because of the rapid spread of an exotic insect, the hemlock woolly adelgid (*Adelges tsugae* Annand) and pre-emptive salvage logging (Orwig, Foster, & Mauseel 2002). We focus here on the experimental setting, design and layout of HF-HeRE, describe a statistical framework that can be used to analyse the data, and discuss provisions for long-term management of the experiment and curation of the data. Finally, we invite researchers interested in the general topic of foundation species and the ecology of hemlock forests to consider using this large-scale experimental infrastructure for complementary studies.

The hemlock – hemlock woolly adelgid – human system

Eastern hemlock (*T. canadensis*; Coniferophyta: Pinaceae) is a long-lived, late-successional conifer tree native to eastern North America, where it ranges from the southern Appalachian Mountains northward to southern Canada and westward to the central Lake states (McWilliams & Schmidt 2000; Fig. 1). In the northern part of its range, where HF-HeRE is sited, hemlock stands are characterized by > 50% basal area of this single species, and the understorey is species-poor and open (Foster & Zebryk 1993; McLachlan, Foster, & Menalled 2000). In these hemlock-dominated stands, the combination of deep shade and acidic, slowly decomposing litter results in a cool, damp microclimate, slow rate of nitrogen cycling and nutrient-poor soils (Jenkins, Aber, & Canham 1999; Orwig *et al.* 2008). Hemlock intercepts more snow and has a higher leaf area index and lower transpiration rates per unit leaf area than do co-occurring deciduous tree species (Catovsky, Holbrook, & Bazzaz 2002). Although hemlock continues to photosynthesize and store carbon in the spring and fall when deciduous trees are leafless, during the summer hemlock stands overall fix less carbon and transpire about 50% of the total water released by deciduous trees (Hadley 2000; Hadley & Schedlbauer 2002; Daley *et al.* 2007). As a result of all of these characteristics, eastern hemlock mediates soil moisture levels, stabilizes stream base-flows and decreases diel variation in stream temperatures (Ford & Vose 2007; Nuckolls *et al.* 2009). The environment created by this foundation tree species provides critical habitat for unique assemblages of associated animals, including birds, insects, salamanders and fish (Snyder *et al.* 2002; Tingley *et al.* 2002; Ellison *et al.* 2005b; Dilling *et al.* 2007; Mathewson 2009).

The hemlock woolly adelgid (*Adelges tsugae*; Hemiptera: Adelgidae) is a small (< 1-mm-long adult) flightless insect that was introduced to the United States from Japan in the early 1950s (Havill *et al.* 2006; Havill & Footitt 2007). Since the early 1980s, it has been spreading rapidly through both eastern hemlock and Carolina hemlock (*Tsuga caroliniana* Engelm.) stands in the eastern United States (Fig. 1). The adelgid attacks trees of all size classes and ages, from small seedlings and saplings to mature trees, eventually killing the tree within 5–15 years in hemlock's northern range and 1–3 years in its southern range.

The life cycle of the adelgid includes two parthenogenetic generations (the sexual generation is absent in North America; Havill & Footitt 2007) that are tied to the annual production of new hemlock needles (McClure 1987). The spring generation of adelgids (progreddiens) develops from March to June, whilst the fall/over-wintering generation (sistens) develops from June to March. As the sistens hatch, they crawl and disperse onto newly produced hemlock needles, where they settle and estivate (summer diapause). In early fall, sistens emerge from estivation and begin to feed on ray parenchyma cells at the base of the needle (Young, Shields, & Berlyn 1995). The sistens feed throughout the winter and produce progreddiens in early spring the following year. The progreddiens continue to

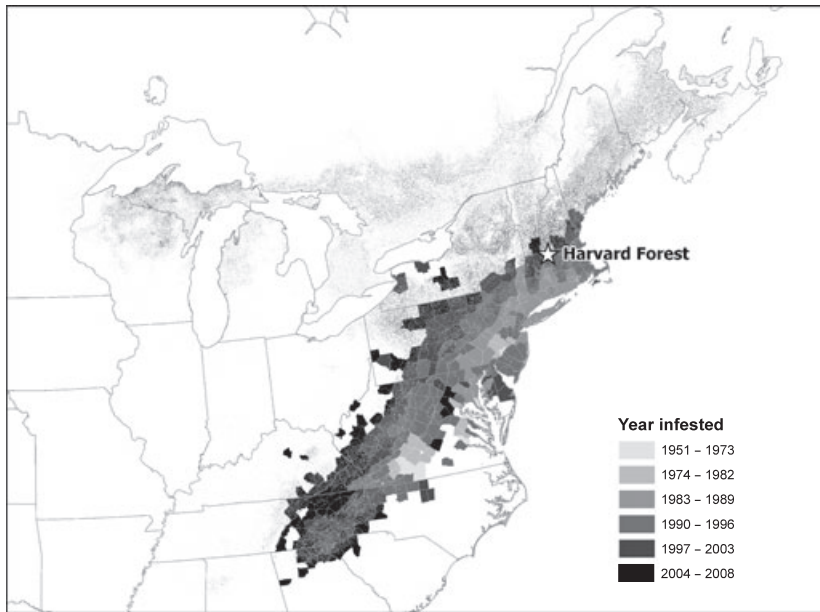


Fig. 1. Distribution of eastern hemlock (*Tsuga canadensis*) in eastern North America, based on U.S. Forest Service Forest Inventory Analysis plots (grey shading) and spread of the hemlock woolly adelgid (*Adelges tsugae*) since its initial introduction into Virginia in 1951 (polygons), based on data compiled by the U.S. Forest Service. The white star indicates the location of the Harvard Forest Hemlock Removal Experiment (HF-HeRE).

feed on the same branchlets and needles as their parent sisters; these needles are mature but generally are < 14 months old (Young, Shields, & Berlyn 1995; Lagalante *et al.* 2006). Needles live 2–4 years (Powell 1991), and as adelgid populations build, new needle production declines. In response, adelgid populations also may decline, but they rebound when new needle production again increases (McClure 1991).

As the adelgid has spread and hemlock declines throughout its range, landowners, including individuals and public agencies, have responded with a range of management strategies. Chemical control of the adelgid is expensive and is usually limited to specimen trees and small stands (Doccola *et al.* 2003). Systemic insecticides must be applied broadly because the adelgid feeds on all age and size classes of hemlock, but these chemicals may have significant non-target effects on soil fauna and nearby streams and other aquatic habitats (Cowles 2009). Biological control by the derodontid beetles *Laricobius nigrinus* Fender and *Laricobius rubidus* Le Conte (introduced from western North America) and the coccinellids *Scymnus sinuanodulus* Yu & Yao, *Scymnus ningshanensis* Yu & Yao, and *Sasajiscymnus tsugae* (Sasaji & McClure) introduced from Asia has not yet controlled this pest in forested settings (Cheah & McClure 2002; Mausel *et al.* 2008). To date, individuals or genetic lines of hemlock resistant to the adelgid have not been described although screening programmes are underway at Cornell University¹ and the University of Rhode Island² (Ingwell *et al.* 2009).

One of the most common management responses is to harvest hemlock stands before adelgid infestation kills the trees and decreases their generally modest economic value (Orwig, Foster, & Mausel 2002; Foster & Orwig 2006). In most of these commercial timber harvests, all of the merchantable hemlocks are removed along with many of the more valuable hardwoods.

Associated species such as white pine (*Pinus strobus* L.) are also removed to increase revenue from the logging operations (Kizlinski *et al.* 2002). In the northern parts of hemlock's range, both pre-emptive salvage logging and post-infestation clear-felling are removing hemlock from the landscape more rapidly than is the adelgid. As hemlock is removed, it is replaced by various early successional and fast-growing hardwood species, including black birch (*Betula lenta* L.) and red maple (*Acer rubrum* L.). These processes result in a progressive homogenization of the New England forested landscape (Foster & Orwig 2006; Albani *et al.* 2010), in which the extent of young and even-aged deciduous forests is increasing as older multi-aged and structurally diverse mixed evergreen and deciduous forest decline.

Conceptual framework and hypotheses

HF-HeRE is organized around a series of three broad, conceptual questions:

1. What are the processes by which forested ecosystems re-organize following loss of hemlock, and how is this re-organization related to the biology of hemlock and the adelgid?
2. Will the system reach new equilibria following this re-organization?
3. How does logging vs. the adelgid alter these transitions and equilibria?

We hypothesize that the re-organization of this forested ecosystem will occur at several levels of organization. First, we expect dramatic changes in both the mean and variance of seasonal light availability, air and soil temperature, soil moisture and other microclimatic variables as hemlock, which casts deep shade and has acidic needles that are slow to decompose, is replaced by deciduous species. These environmental changes should lead to the development of new soil microbial communities and concomitant changes in rates of soil nitrogen and carbon cycling, and soil formation. For example, in

¹<http://www.reeis.usda.gov/web/crisprojectpages/208986.html>.

²<http://cels.uri.edu/preisserlab/research/resistance.html>.

adelgid-infested stands, throughfall is enriched in nitrogen, causing transient increases in nutrient and energy cycling under declining hemlock canopies (Stadler *et al.* 2005; Stadler, Müller, & Orwig 2006). Soil respiration should decline dramatically when hemlock roots die, and there should be a short-term pulse of nutrients into the soil as needles are shed (Kizlinski *et al.* 2002; Orwig *et al.* 2008). Over decadal time-scales, models predict that rates of carbon uptake should decline regionally as hemlock disappears (Albani *et al.* 2010). But these models also forecast that over longer time-scales, carbon uptake by the re-assembled early- and mid-successional hardwood stands may equal or even exceed that of the lost hemlock stands (Albani *et al.* 2010).

Secondly, species that are dependent on hemlock or the habitat that it creates will disappear. As a new forest develops, other species, both native and exotic, will colonize and interact (Rohr, Mahan, & Kim 2009). Because black birch-dominated forests are not a common feature of the eastern U.S. landscape, the trajectory of this community re-assembly process is not easy to forecast. One already evident change is an increase in local diversity of ants as omnivores and decomposers in the genus *Formica*, normally absent from hemlock stands, colonize

early successional hardwood stands (Ellison *et al.* 2005b). Ants are known to have broad effects on soil ecosystem dynamics (Folgarait 1998). Disentangling the direct effects of hemlock loss on ecosystem processes from indirect effects caused by changes in biological diversity associated with hemlock loss is a key component of HF-HeRE (Fig. 2).

We hypothesize that the rate at which these re-organizations occur and the new equilibria that they reach will depend on the dynamics of adelgid populations and on how hemlock stands are managed. For example, pre-emptive salvage logging (Foster & Orwig 2006) changes canopy composition much more abruptly than does the adelgid, and logging machinery compacts soil, altering patterns of regeneration from the seed-bank. Nutrient pulses from slash piles should be larger and more rapid than pulses of nutrient-enriched throughfall associated with the adelgid (Stadler *et al.* 2005; Stadler, Müller, & Orwig 2006). All of these changes are likely to be mediated, even amplified, by changes in microclimate associated with hemlock loss. These and other differences between logged stands and stands that succumb slowly and more heterogeneously will feed back on and interact with changes caused by biotic responses to hemlock loss.

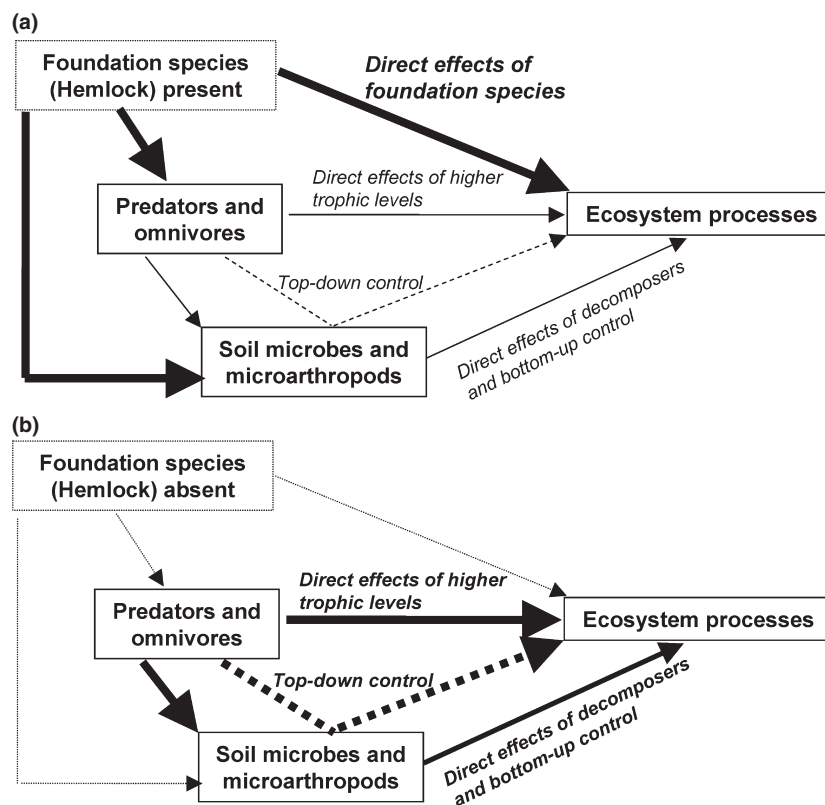


Fig. 2. Conceptual model for disentangling the direct effects on ecosystem processes of foundation species from indirect effects caused by changes in biological diversity associated with foundation species. (a) In intact hemlock stands, this single foundation species is the dominant controller on both the composition and abundance of associated species and on core ecosystem processes (strength of influence indicated by width of arrows). (b) When hemlock is lost, other taxa predominantly affect core ecosystem processes. For clarity, neither effects of hemlock on microclimate nor other primary producers, including understorey species, are shown. Hemlock creates a uniquely cool and dark microclimate in which decomposition proceeds slowly and soil organic matter accumulates relatively rapidly. As hemlock is replaced by hardwoods, there is less of a role for particular species in mediating microclimate. These deciduous species are also leafless for *ca.* 6 months in New England during which time microclimate is controlled more by regional weather systems than by local biota. The understorey is very sparse in the hemlock forests of New England, but the denser understorey vegetation of deciduous forests can alter rates of nutrient fluxes prior to spring bud-burst (Zak *et al.* 1990).

Site description

The HF-HeRE is located within the 121-ha Simes Tract (42°47'–42°48' N, 72°22'–72°21' W; elevation 215–300 m a.s.l.) at the Harvard Forest Long-Term Ecological Research Site in Petersham, MA, USA (Fig. 3). This tract lies within the Chicopee River watershed and extends up a valley in southern Petersham. A gentle slope (<10%) rises up the eastern side of the tract, and a moderate to steep slope (*c.* 30%) runs along the western edge of the tract where the tract abuts the 30 000-ha Quabbin Reservoir Reservation. Typical of hemlock forests throughout this region, much of the central portion of the tract is poorly drained or swampy; elevated areas have small hills and better drainage. The soils are predominantly coarse-loamy, mixed, active, mesic Typic Dystrudepts in the Charlton Series that are derived from glacial till (USDA n.d.). Eastern hemlock and red maple dominate the poorly drained soils, whereas red and white oaks (*Quercus rubra* L. and *Q. alba* L.), white pine, and eastern hemlock dominate the hills and slopes. Black birch and other hardwoods are common associates. Sugar maple (*Acer saccharum* Marsh.) grows in the southern part of the tract. Much of the tract was cleared for agricultural

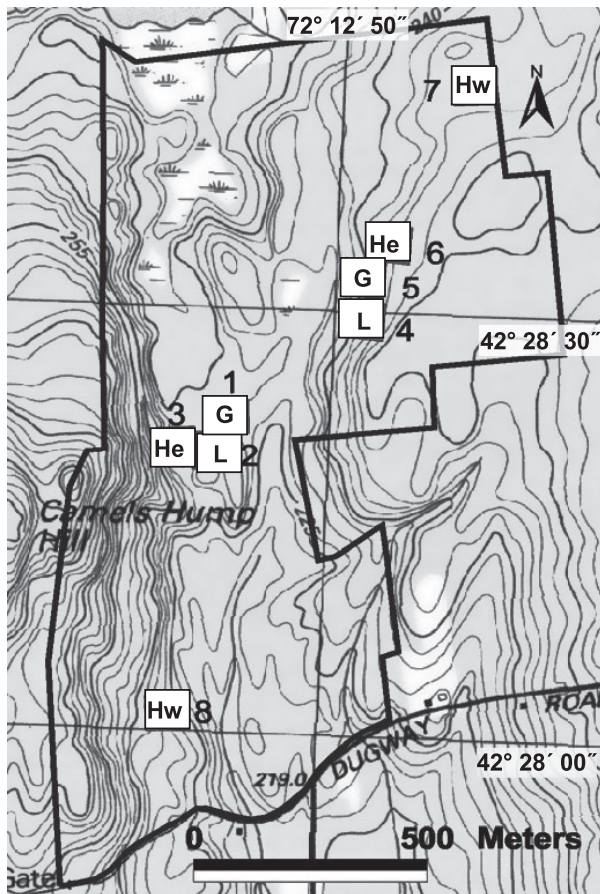


Fig. 3. Location of the blocks and treatments within the Simes Tract at the Harvard Forest. This Before-After-Control-Impact replicated block design has two blocks (plots 1, 2, 3 and 8 are the 'Valley' block, and plots 4–7 are the 'Ridge' block). Each of the four treatments – Girdled (G), Logged (L), Hemlock control (He) and Hardwood control (Hw) – were applied in 90 × 90 m plots within each block.

use or harvested for timber in the early and mid-1800s. The forest has been regenerating since the late 1800s and early 1900s (Kernan 1980). Tree-core samples have revealed that the trees in the experimental plots are 50–75 years old (Bettmann-Kerson 2007).

Experimental design and treatments

CANOPY MANIPULATION

The primary canopy-level manipulation – girdling or harvesting of standing hemlock – was done in large (90 × 90 m = 0.81 ha) plots using a replicated, blocked design with measurements collected both before and after treatments [analogous to an *experimental* before-after-control-impact (BACI) design]. Plots were identified in 2003 and sampled for two growing seasons (spring/summer in each of 2003 and 2004) prior to canopy manipulations. The eight plots comprising this experiment are grouped in two blocks (Fig. 3), each consisting of three plots initially dominated by hemlock and one plot of mixed northern hardwoods (Table 1). The 'Valley' block (plots 1–3 and 8 in Fig. 3) is in undulating terrain bordered on its northern edge by a *Sphagnum*-dominated wetland. The 'Ridge' block (plots 4–7 in Fig. 3) is on a forested ridge. The four treatments in each block include:

- 1. Girdling** to simulate the physical decline and mortality of hemlock resulting from its death by the hemlock woolly adelgid. Over a 2-day period in May 2005, the bark and cambium of all individual hemlocks were girdled using chain saws (on large trees) or hand knives (on small saplings and seedlings). No other species were girdled and there was no site disturbance. Girdling immediately reduced sap-flow by 50% (Fig. 4 – inset), and girdled trees died within 2 years (Fig. 4). Thus, an important characteristic of hemlock woolly adelgid infestation that is missing from this treatment is the very lengthy period of decline (especially in northern regions) during which the plant is undergoing physiological stress and metabolic imbalance that may induce biogeochemical and microbial changes on the site (cf. Stadler, Müller, & Orwig 2006). These additional (additive and/or interactive) impacts of the adelgid over and above (or with) the physical decline of trees can be assessed in the *hemlock control* treatment (see below).

- 2. Logging** to mimic the effects of a typical commercial hemlock salvage operation. All hemlock individuals > 20 cm d.b.h. and other commercially valuable trees, including larger hardwoods (primarily red oak) and white pine, were removed for saw logs. Other hardwoods (red maple, black birch) and smaller stems that a commercial logger might remove to improve future stand quality, facilitate log removal and general operation or initiate a new cohort of sprouts were also cut. Between 60% and 70% of the stand basal area was cut in these two plots (Fig. 4), using hand-felling by chainsaw. Logs were removed by dragging them with a rubber-tired skidder. Slash (small branches and damaged or rotted boles accumulating to ≤1.3 m high) was left on site as permitted by Massachusetts forest management laws. The intent was to harvest

Table 1. Initial (pre-treatment) overstorey composition (percent basal area of each species) of the eight plots of the Harvard Forest Hemlock Removal Experiment

	Valley block				Ridge block			
	Girdled	Logged	Hemlock control	Hardwood control	Girdled	Logged	Hemlock control	Hardwood control
Total basal area (m ² ha ⁻¹)	50.3	47.9	45.5	29.6	53.0	49.5	52.1	35.6
Percent basal area								
<i>Tsuga canadensis</i> (L.) Carr.	73	50	66	3	69	59	53	9
<i>Pinus strobus</i> L.	14	19	6	3	2	2	18	35
<i>Acer rubrum</i> L.	6	3	6	13	6	7	12	17
<i>Quercus rubra</i> L.	0	0	0	11	0	0	0	0
<i>Quercus alba</i> L.	2	22	7	36	8	12	3	15
<i>Betula lenta</i> L.	1	3	8	24	11	15	3	15
Other	5	4	7	10	4	5	11	9

The diameters of all trees in each plot were measured, so these data are a complete inventory, not a statistical sample. 'Other' species include *Betula alleghaniensis* Britt., *Betula papyrifera* Marsh., *Betula populifolia* Marsh., *Carpinus caroliniana* Walt., *Carya glabra* (Mill.) Sweet, *Carya ovata* (Mill.) K. Koch, *Castanea dentata* (Marsh) Borkh., *Fagus grandifolia* Ehrh., *Fraxinus americana* L., *Fraxinus nigra* Marsh., *Hamamelis virginiana* L., *Ostrya virginiana* (Miller) K. Koch., *Prunus serotina* Ehrh., *Quercus alba* L., *Quercus velutina* Lam. and *Sorbus americana* Marsh.

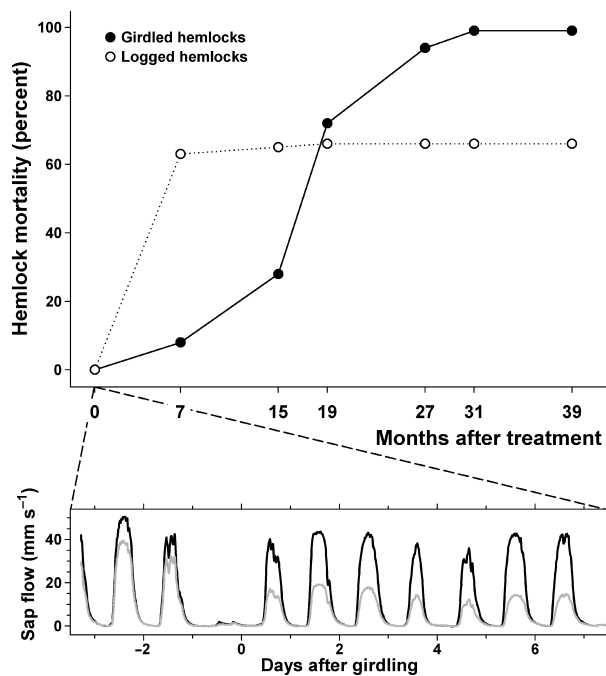


Fig. 4. Mortality rate of eastern hemlock (*Tsuga canadensis*) in the core 30 × 30 m sampling areas in the girdled (●) and logged (○) plots following treatment application in April–May 2005. **Inset** at bottom shows the average change in the rate of sap-flow in three girdled (grey lines) and three reference (non-girdled) hemlock trees (black lines) before and after girdling (girdling occurred at Day = 0). A single 20-mm-long Granier sapflow probe was installed at 1.4 m above-ground in each of the six trees. The day before trees were girdled, the site received 32 mm of rain (data from Harvard Forest weather station: <http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id=hf001>), and measured sap-flow velocity was near 0.

the stands following the approach of a commercial harvest. To minimize soil damage and following standard 'best management' harvesting procedures (Kittredge & Parker 1999), logging was done between February and April 2005, when

the soil was frozen. Nonetheless, there was scarification as well as damage to small remaining stems.

3. Hemlock control plots are hemlock-dominated and received no manipulation. At the start of this experiment, no adelgid was present at the Simes Tract. When we established this experiment in 2003, we anticipated that the hemlock control plots would eventually become infested by the adelgid. The adelgid was first observed at low densities in these control plots in 2008 and was widespread in the plots, but still at low densities, in 2009. Using data collected prior to 2010, contrasts of the hemlock control plots with the logged or girdled plots will reveal effects of hemlock that was physically deteriorating or removed. From 2010 onwards, the now adelgid-infested hemlock control plots will serve as hemlock plus adelgid plots that will be contrasted with the girdled plots to disentangle effects of the adelgid from effects of physical loss of hemlock alone. These contrasts will test our hypotheses about differences between logged and adelgid-infested stands in rates and trajectories of the re-organization of these forested ecosystems.

4. Hardwood control plots represent the most likely future forest conditions after hemlock has disappeared from the landscape (Orwig & Foster 2000; Albani *et al.* 2010). These plots received no manipulation.

In 2003 and 2004, all trees in each plot were tagged with permanent aluminium tags, mapped (relative *x*, *y*, *z* coordinates) using a compass, autolevel and stadia rod, and measured (at 1.3 m d.b.h.) prior to treatment applications. Tags labelling logged trees were relocated from boles to stumps as trees were cut in the logged plots. Plot boundaries were located with a GPS device (Trimble Navigation Limited, Sunnyvale, CA, USA) and permanently staked [etched, painted poly-vinyl chloride (PVC) posts or iron rods] at 30 m intervals. The interior of the plot was gridded with etched, painted PVC posts at 10 m intervals. The centre point of each plot was located with GPS and permanently staked with an iron rod.

MONITORING, MEASUREMENTS AND SUBPLOT EXPERIMENTS

To test our hypotheses about the directions and rates of re-organization of these forests, we make a broad spectrum of measurements to quantify short- and long-term processes associated with the decline of hemlock and its eventual replacement. We focus our intensive measurements and sampling in the centre 30×30 m 'core' area of each 90×90 m experimental plot. Sampling sites in the core area are located randomly within a grid of 5×5 m² (Fig. 5). The 30-m wide, square 'buffer' area surrounding the core is approximately equal in width to one tree height (overstorey tree heights range from *c.* 25 to 35 m). We site additional short-term, subplot-scale experiments in this buffer area to provide additional mechanistic detail that we cannot obtain through long-term observations and monitoring alone. These experiments are sited in the buffer area because the small disturbances they create could compromise the integrity of the observational data collected in the core area. The spatial scales and temporal frequency of these measurements and experiments are detailed in the following subsections.

Trajectories of re-organization

We hypothesize that loss of the hemlock canopy should cause increases in the mean and variance of the measured microclimatic variables – air and soil temperature, light availability, and soil moisture. The much greater temporal variability of canopy cover in deciduous stands relative to hemlock stands and interactions between the surrounding forest and the diurnal track of the sun result in increased variance in temperature and light as hemlock declines. Although soil moisture might be expected to decline in the warmer and brighter logged and girdled plots, this is only true at the ground surface. Below the surface, soil moisture in open plots is generally higher than in forested plots because the reduction in transpiration more than offsets evaporation at the soil surface. In the centre of each plot, air temperature 1 m above-ground and soil temperatures in the organic and mineral layers are measured every minute with thermocouples. Data are averaged each hour and stored in Campbell dataloggers (Campbell Scientific, Logan, UT, USA). Initial data support our hypothesis of increases in mean and temporal variance of temperatures (Fig. 6). Light availability and leaf area index are measured throughout the entire

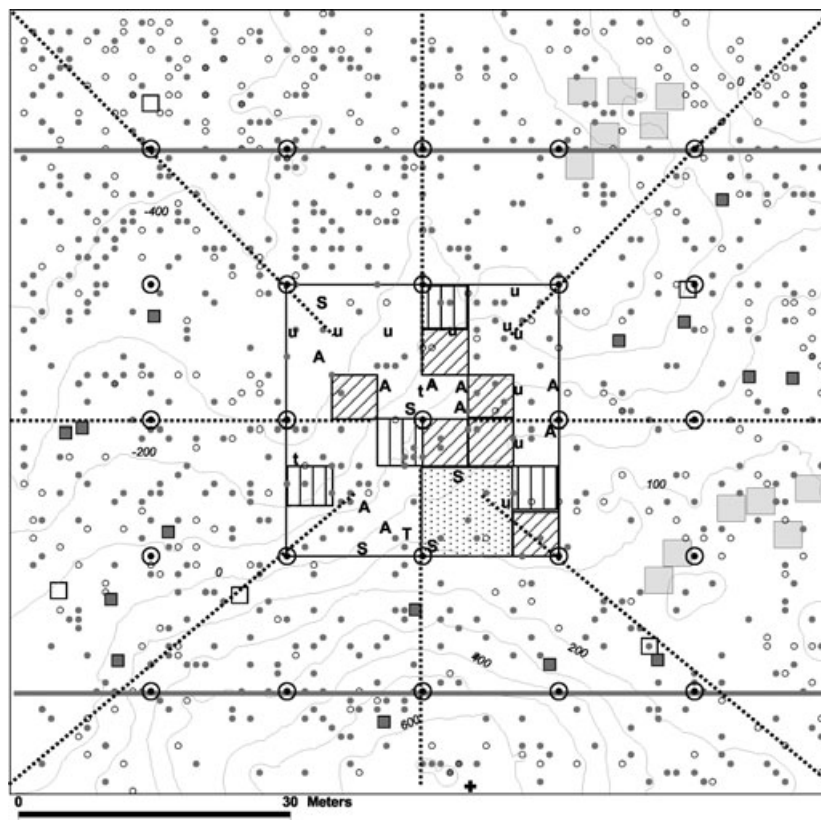


Fig. 5. Example of the layout and zoning of a plot in the Harvard Forest Hemlock Removal Experiment. Individual trees (grey circles: hemlock; white circles: other tree species) were mapped together with elevations in cm relative to a 0-cm baseline near the plot centre (grey contours). The centre 30×30 -m area is used for intensive measurements and different research groups are assigned random areas (boxes: vertical striped – nitrogen mineralization; diagonal striped – soil respiration; dotted – ant species diversity and abundance) for their specific studies. Also illustrated are locations of litter baskets (white squares) and litter samples for arthropods (A), understory vegetation quadrats (u), seed bank samples (S), throughfall samples (t), thermocouple sensors for air and soil temperatures (T), fixed points for hemispherical photographs (dotted circles) and panoramic photographs (+), and transects for sampling salamanders (thick grey lines) and coarse woody debris (thick dotted lines). Locations in the buffer area of two of the subplot experiments are illustrated with large light grey squares (ant removals, additions, controls) and small dark grey squares (litter arthropods).

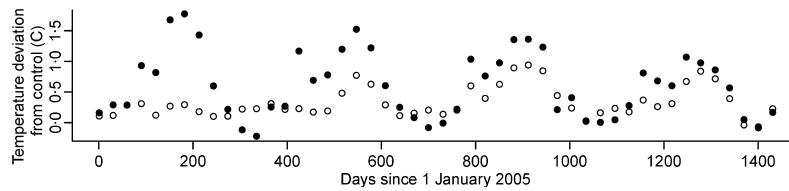


Fig. 6. Temperature deviations in the logged (black circles) and girdled (white circles) plots relative to the hemlock control plots. The summer after logging, logged plots were > 1.5 °C warmer than control plots, but girdled plots were not different from control plots. As trees died in the girdled plots over the next two summers, these plots warmed up relative to the control plots. Over the same time interval in the logged plots, hardwood stumps sprouted and seedlings emerged. This increase in understorey cover reduced the difference in air temperature between logged and control plots.

90 × 90 m plot on a 15-m grid (25 points per plot) every April and September, when deciduous trees are leafless and leafed-out, respectively. Hemispherical canopy photographs are taken with a Nikon 8-mm ‘fish-eye’ lens and a Nikon F-3 film camera (prior to 2008) or (since 2008) D-3 digital camera in full-frame (FX) mode (Nikon Inc., Melville, NY, USA). The camera is placed on a self-leveling mount atop a tripod and positioned 1–2 m above-ground. Hemispherical photographs are analysed for canopy openness and diffuse radiation (‘direct site factor’ and ‘indirect site factor’, respectively; Rich 1989; Rich *et al.* 1993) and leaf area index using HemiView software version 2.1 (Delta-T Devices, Cambridge, UK). As the ecological functioning of a forest stand is often related to the spatial organization of the canopy, we have also used portable canopy laser detection and ranging (LiDAR; Parker, Harding, & Berger 2004) to measure volumetric canopy structure the season after the girdling and logging treatments were completed. LiDAR measures will be repeated at 5- and 15-year intervals to develop an understanding of early structural dynamics and micrometeorological consequences associated with the canopy removal treatments.

Forecast changes in nitrogen availability and changes in rates of nutrient fluxes are assessed with resin bags and soil incubations (Roberston *et al.* 1999). Changes in carbon efflux (soil respiration) are measured manually every 2 weeks during the growing season between 09:00 and 15:00 hours in permanently embedded 30-cm diameter plastic (PVC) collars using a portable infrared gas analyser (Savage & Davidson 2003). Collars were installed in 2003 and are embedded 10 cm into the soil. Soil moisture within the collars is measured with permanently installed time-domain reflectometry (TDR) probes, at the same time that soil respiration is measured. Net primary productivity (both as litterfall into five randomly located litter baskets and as diameter growth, in-growth and mortality of all trees) and decomposition and turnover of coarse woody debris are assessed throughout the entire 90 × 90-m plot using the line-intercept method of Harmon & Sexton (1996).

Re-organization of biotic assemblages is measured as annual changes in species composition and abundance of understorey vegetation and key arthropod groups (ants, carabid beetles and spiders). Understorey vegetation is sampled in five 1-m² quadrats spaced evenly along each of two transects running north-south or east-west through the core of each plot (Fig. 5). We estimate percent cover of herbs, shrubs and tree seedlings (individuals < 1.3 m tall) to the nearest 1% and count the

number of seedlings of each tree species. Arthropods are sampled using grids of 25 pitfall traps in the core area of each plot (full methods in Ellison *et al.* 2005b). The seed bank in the core area was assessed prior to treatment (Sullivan & Ellison 2006) and will be re-assessed at 5- to 10-year intervals to determine regeneration potential and turnover of seeds in the soil. The seed bank data are complemented by collections of cones, seeds and fruits in litter baskets.

Subplot experiments

We use subplot experiments to separate direct and indirect effects of hemlock loss. For example, Ellison *et al.* (2005b) documented increases in ant species richness with declines in hemlock canopy cover. We have observed similar changes in our logged and girdled plots (A. M. Ellison, unpublished data). Because assessment of the effects of these biotic changes on soil ecosystem properties are confounded by the canopy-scale manipulation, determining main and interactive effects of canopy structure and ant diversity requires additional manipulations of ant diversity within canopy treatments. Thus, we have established subplot experiments in which we manipulate species composition and abundance of ants in each of the canopy manipulation plots (Fig. 5). Similar experiments measuring changes in forest carbon stocks and in the diversity and abundance of litter microarthropods and amphibians, and the impacts of these changes on ecosystem dynamics, have also been installed in the buffer zones of the large canopy manipulation plots (Fig. 5).

Statistical framework and analytical challenges

Design and implementation of large-scale, long-term experiments involve trade-offs between realism and replication (e.g. Carpenter 1990, 1998). In the HF-HeRE, our focus on realistic, hectare-scale manipulations to uncover the responses of North American forested ecosystems to loss of a long-lived foundation tree species limited, but did not completely eliminate, our ability to replicate treatments. Although eastern hemlock is common and abundant in our forests, the process of actually locating many hectare-sized plots, each of which had $> 50\%$ basal area of hemlock, had similar size and age structure, and were in locations that could be manipulated without lengthy regulatory review (state laws regulate activities within 30–60 m of wetlands, lakes and streams) was surprisingly

difficult. Even two replicates, however, allows us to estimate treatment variances, and 2 years of pre-treatment monitoring for most response variables have provided a useful baseline from which to compare responses with the canopy manipulations.

The overall experiment yields data at a variety of temporal and spatial scales. At one extreme, air and soil temperature data are recorded continuously and logged at 1 h intervals (hourly means, minima and maxima) and robust time-series analysis (Shumway & Stoffer 2006) of these data is already possible (Fig. 6). At the other extreme, LiDAR and tree diameter growth measurements are made at 5-year intervals and it will be decades before we accumulate sufficient data to provide more than descriptions of qualitative patterns. However, the bulk of the data sets are based on samples and measurements collected quarterly, semi-annually, annually (e.g. soil carbon flux, soil nitrogen dynamics, understorey vegetation composition) or biennially (coarse woody debris). Although there is no 'one size fits all' method of analysis for the different data sets, there are several features of the design of which we can take full advantage.

There are both impacted (logged or girdled) plots and control plots, and for the majority of variables of interest, measurements and observations were made both before and after the imposition of treatments. Although a standard set of statistical tools has been developed for *observational* BACI studies (Stewart-Oaten & Bence 2001), the goal of standard BACI analysis is normally a determination of whether or not the impacted site(s) have changed following environmental impacts. In a classic BACI analysis, the 'control' is used as a covariate, inferences are model-based (as opposed to design-based), and it is unwise to extrapolate conclusions to a broader scale (i.e. unsampled sites or populations). The standard design-based alternative to BACI is 'impact vs. reference sites' (Underwood 1992; 'IVRS' in the lexicon of Stewart-Oaten & Bence 2001), which requires multiple, randomly selected unimpacted sites to serve as controls. But both BACI and IVRS studies are 'observational' – the investigator rarely has any say on where the impact sites are located and siting 'controls' can be similarly constrained.

In contrast, HF-HeRE is a designed, manipulative experiment, which provides opportunities for additional, more powerful analysis. The experimental design (Figs 2, 5) can be treated as a standard one-way blocked ANOVA, with any additional experiments established in subplots within the large plots analysed using split-plot ANOVA (Gotelli & Ellison 2004). Unlike a strict BACI analysis, ANOVA permits estimation of effect sizes and associated uncertainty, *a priori* contrasts among specified treatments or treatment groups, and formal hypothesis tests. The primary factors are the four canopy manipulations (hemlock control, hemlock girdled, logged, hardwood control) and the two blocks. Manipulations are treated as fixed factors, and blocks are treated as random factors. The absence of replication of treatments within blocks precludes estimation of a block \times treatment interaction.

Time (or sample date) enters the model as a continuous covariate, so when time series are short (e.g. 7 years of annual

data), we can use ANCOVA to assess temporal changes in response variables without resorting to time-series modelling for which we lack sufficient data (A. M. Ellison & N. J. Gotelli, unpublished data). This is important, as degrees of freedom are small because subsamples taken within a given plot (e.g. multiple N mineralization cores) must be pooled prior to analysis to avoid pseudoreplication (*sensu* Hurlbert 1984). The subsamples do, however, provide a more accurate assessment of the within-plot response (Blume & Royall 2003). Alternatively, the data could be analysed with a repeated-measures ANOVA, in which time enters the model as a fixed factor, but it is rare that the key assumption of repeated-measures ANOVA – that the variance of the difference of observations between any pair of times is equal (circularity) – can be met (Gotelli & Ellison 2004). Because we are more interested in the effect size – the slope of the line of the response variable as a function of time – than the *P*-value (because we expect that all variables will change through time), an ANCOVA is a more efficient and informative method to analyse these data (Gotelli & Ellison 2004; A. M. Ellison & N. J. Gotelli, unpublished data).

The additional smaller-scale subplot experiments established in the buffer areas have multiple replicates within each canopy manipulation plot. These include, for example, 2 transects and 10 coverboards/transect for amphibians and 2–4 replicates each of four levels of ant manipulations in the ants and ecosystem function experiment – unmanipulated, ant removal, disturbance control and ant addition (Fig. 5). Data from these experiments can be analysed using hierarchical ANOVA (Qian & Shen 2007) to assess treatment effects (e.g. coverboard type or ant manipulations) within canopy manipulations and blocks, and *a priori* contrasts to tease apart the effects of individual treatments on ecosystem processes (Fig. 2). We use a hierarchical ANOVA because it more clearly delineates effect sizes than does a mixed-model ANOVA (Qian & Shen 2007).

We illustrate the statistical partitioning of effects of whole-plot canopy manipulation and subplot treatments by describing the method of analysis for the experiment in which we are examining the direct effects of hemlock and direct vs. indirect effects of ants on soil ecosystem processes (Fig. 2). One possible *a priori* contrast would be to distinguish 'hemlock effects' as the difference between plots with and without living hemlock. Other *a priori* contrasts could include hemlock vs. hardwood or type of mortality: girdled hemlock vs. logged hemlock. For the 'hemlock effects' contrast, short-term canopy effects would be measured as Unmanipulated hemlock canopy (He) – (mean of Girdled canopy (G) and Logged canopy (L)), because this comparison will reveal ecosystem effects shortly after hemlock are removed from the system. Then, short-term direct effects of ant activity at the subplot level can be calculated as Unmanipulated hemlock canopy (He) – Ant removal (X). Thus:

Large-scale hemlock effect = He – (mean G and L),

Direct effect of ants within hemlock stands = He – X.

Finally, the indirect effects of ants, possibly mediated by microbial activity, (as measured by soil respiration) can be measured as the difference between net effects and direct effects:

$$\begin{aligned} \text{Indirect effects of ants} &= (\text{He} - (\text{mean G and L})) - (\text{He} - \text{X}) \\ &= \text{X} - (\text{mean G and L}). \end{aligned}$$

Long-term canopy effects could be measured as Unmanipulated hemlock canopy (He) – Unmanipulated hardwood canopy (Hw), because this comparison would reveal ecosystem effects after hemlock has been replaced by hardwoods through succession. We note that this interpretation must be made cautiously. We assume that these hardwood stands are a good representation of the hardwood stands that we have seen replace adelgid-infested hemlock stands throughout New England (Orwig & Foster 1998). This interpretation will have to be revisited if these hardwood stands reflect only local environmental conditions and turn out to be distinct in structure from the stands that eventually replace hemlock on our sites.

Finally, the two controls will yield valuable comparisons and baselines. Over time, the girdled and logged plots should converge to the hardwood control plots in structure and function. Now that the hemlock control plots have been infested by the adelgid (see next section), their decline and re-assembly will be contrasted first with trajectories of the girdled and logged plots and subsequently with the hardwood control plots. These are neither space-for-time substitutions nor exact temporal matches, but the plots will nonetheless provide important novel insights into successional dynamics as well as ecosystem disassembly and re-assembly.

Future directions and challenges

THE ADELGID COMETH

A central component of the design of HF-HeRE was that the adelgid was not present at the site when the experiment was established, but we expected that it would eventually arrive in our area and infest our sites. We first observed the adelgid at the Simes Tract in hemlock trees adjacent to plot 2 in 2006, but it was not until 2008 that we found it in the experimental plots themselves. A thorough survey in summer 2009 revealed that the adelgid was present on 44% of the hemlock saplings and trees in the hemlock control plots and 42% of the hemlock saplings and trees in the hardwood control plots. Thus, our hemlock ‘controls’ have now been transformed into adelgid plots, and the first 6 years of this experiment will provide the only data on uninfested stands at this site. That is, these plots can no longer be used to distinguish the impact of our canopy manipulations from environmental variation. Going forward, these ‘new’ adelgid plots will serve as a Before-After set of plots for impact of the adelgid and as a way for us to separate effects of physical death of hemlock alone from additive and/or interactive effects of the adelgid on ecosystem processes.

LONG-TERM MAINTENANCE OF THE EXPERIMENT AND THE DATA

Additional challenges associated with long-term experiments are maintaining the experimental infrastructure itself and curating and publishing the data. The HF-HeRE is now a core

experiment of the Harvard Forest Long Term Ecological Research (LTER) programme, so there are ongoing, albeit modest, funds (< US \$10 000 year⁻¹) that provide for a fraction of the labour needed to make regular measurements and the basic maintenance and upkeep of the plots, such as installation of more permanent plot and subplot markers and recalibration and repair of dataloggers, batteries and solar panels used to collect meteorological data. Detailed descriptions of plots and the associated experimental design are stored on paper in the climate-controlled Harvard Forest Archives. Panoramic and hemispherical canopy photographs were taken with film cameras through mid-2008, and the slides and negatives are similarly stored in the Harvard Forest Archives. Our shift to digital photography in late 2008 means that these and subsequent photographs will be handled as electronic data in the same way as other electronic data files in the Harvard Forest data archive (<http://harvardforest.fas.harvard.edu/data/archive.html>). Because HF-HeRE is a core LTER project, all data collected must be posted and publicly available within 2 years of collection; most data are posted more rapidly, however. Harvard Forest is committed to long-term storage and migration of electronic data sets, but there are costs associated with these activities that must be factored into annual budgets and long-term financial projections.

AN INVITATION FOR COLLABORATION AND PARALLEL STUDIES

Finally, we highlight two important aspects of HF-HeRE. First, the Harvard Forest and its NSF-supported LTER programme have invested and continues to commit significant funds and personnel time to the establishment and maintenance of HF-HeRE. This is not only a single experiment that we designed to explore a set of fundamental ecological processes. It also should be considered as scientific infrastructure that is available to colleagues and collaborators world-wide who are interested in exploring complementary questions, and we encourage and invite such collaborations. Studies of plant ecophysiology, vertebrates (birds, small mammals, browsing ungulates), food web dynamics, biogeochemistry of elements other than C and N, and subsurface hydrology are currently absent from HF-HeRE. The absence of these and other relevant studies reflect only a lack of local expertise or resources, not a lack of opportunity.

HF-HeRE is also part of an evolving network of experimental sites focused on identifying and understanding the role of single foundation species on population-, community-, and ecosystem-level dynamics. Comparable studies include a hemlock removal experiment at the Coweeta LTER site in North Carolina (Nuckolls *et al.* 2009) and an oak removal experiment at the Black Rock Experimental Forest in New York (Ellison *et al.* 2007). Both of these experiments removed canopy trees by girdling, and are similar to HF-HeRE in design and analytical protocols. All these experiments complement long-term observational studies on hemlock decline in eastern North America (Orwig & Foster 1998; Orwig, Foster, & Mausel 2002; Orwig *et al.* 2008), sudden oak death in California

and its arrival in New England (Rizzo & Garbelotto 2003; Meetenmeyer *et al.* 2004; Douglas 2005), and recent mortality of several oak populations resulting from drought and defoliation by native and exotics insects in coastal Massachusetts (D. R. Foster unpublished data). We look forward to new directions in ecology arising from syntheses of all of these observations and experiments.

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