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

Aaron M. Ellison[*], Audrey A. Barker-Plotkin, David R. Foster, and David A. Orwig

Harvard Forest, Harvard University, 324 North Main Street, Petersham, Massachusetts 01366 USA

*Author for correspondence: aellison@fas.harvard.edu

Running head: *Foundation species experiments*

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, understory 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 microarthoropods 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 modeling 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 concern (Gaston & Fuller 2008). Nonetheless, in terrestrial ecosystems worldwide, 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 *et al.* 1986; Foster *et al.* 2006; Shuman *et al.* 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 lifespans 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 equilibrial 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 (*Tsuga 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 *et al.* 2002). We focus here on the experimental setting, design, and layout of HF-HeRE, describe a statistical framework that can be used to analyze 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 (*Tsuga 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 understory is species-poor and open (Foster & Zebryk 1993; McLachlan *et al.* 2000). In these hemlock-dominated stands, the combination of deep shade and acidic, slowly decomposing litter results in a cool, damp microclimate, slow rates of nitrogen cycling, and nutrient-poor soils (Jenkins *et al*. 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 *et al*. 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 & Footit 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 parthenogentic generations (the sexual generation is absent in North America [Havill & Footit 2007]) that are tied to the annual production of new hemlock needles (McClure 1987). The spring generation of adelgids (‘progrediens’) develops from March to June, whilst the fall/over-wintering generation (‘sistens’) develops from June through 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 *et al.* 1995). The sistens feed throughout the winter and produce progrediens in early spring the following year. The progrediens continue to feed on the same branchlets and needles as their parent sistens; these needles are mature but generally are less than 14 months old (Young *et al.* 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 have 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 programs are underway at Cornell University[1] and the University of Rhode Island[2] (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 *et al.* 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 preemptive 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

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[1] http://www.reeis.usda.gov/web/crisprojectpages/208986.html

[2] http://cels.uri.edu/preisserlab/research/resistance.html

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 reorganize following loss of hemlock, and how is this reorganization related to the biology of hemlock and the adelgid?
2. Will the system reach new equilibria following this reorganization?
3. How does logging *versus* the adelgid alter these transitions and equilibria?

We hypothesize that the reorganization 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 development of new soil microbial communities and concomitant changes in rates of soil nitrogen and carbon cycling, and soil formation. For example, in adelgid-infested stands, throughfall is enriched in nitrogen, causing transient increases in nutrient and energy cycling under declining hemlock canopies (Stadler *et al.* 2005, 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 reassembled early- and mid-successional hardwood stands may equal or even exceed that of the lost hemlock stands (Albani *et al.* 2010).

Second, 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 *et al.* 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 reorganizations 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, 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.

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, Massachusetts, 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 (~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 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:

- **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 *et al*. 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).

- **Logging** to mimic the effects of a typical commercial hemlock salvage operation. All hemlock individuals > 20 cm diameter at breast height (DBH) 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 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.
- **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 + 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 reorganization of these forested ecosystems.

- **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 aluminum tags, mapped (relative *x, y, z* coordinates) using a compass, autolevel, and stadia rod, and measured (diameter at 1.3 m [DBH]) prior to treatment applications. Tags labeling 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 PVC posts or iron rods) at 30-m intervals. The interior of the plot was gridded with etched, painted PVC posts at 15-m intervals. The center 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 reorganization 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 center 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-m squares (Fig. 5). The 30-m wide, square “buffer” area surrounding the core is approximately equal in width to one tree height (overstory tree heights range from ~25-35m). 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 reorganization

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 center 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). 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 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 "fisheye" lens and a Nikon F-3 film camera (prior to 2008) or (since 2008) D-3 digital camera in full-frame ("FX") mode. The camera is placed on a self-leveling mount atop a tripod and positioned 1-2 m above ground. Hemispherical photographs are analyzed 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 *et al.* 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 (Robertson *et al.* 1999). Changes in carbon efflux (soil respiration) are measured manually every two weeks during the growing season between 0900 and 1500 hrs in permanently embedded 30-cm diameter plastic (PVC) collars using a portable infrared gas analyzer (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 (1986).

Reorganization of biotic assemblages is measured as annual changes in species composition and abundance of understory vegetation and key arthropod groups (ants, carabid beetles, and spiders). Understory vegetation is sampled in five 1-m^2 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 one percent 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 5-10 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 tradeoffs 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 two years of pre-treatment monitoring for most response variables have provided a useful baseline from which to compare responses to 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 hour 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 five-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 datasets are based on samples and measurements collected quarterly, semi-annually, annually (*e.g.,* soil carbon flux, soil nitrogen dynamics, understory 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* before-after-control-impact (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 (Fig. 2, 5) can be treated as a standard one-way blocked analysis of variance (ANOVA), with any additional experiments established in subplots within the large plots analyzed 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 × treatment interaction.

Time (or sample date) enters the model as a continuous covariate, so when time series are short (*e.g.,* seven years of annual data), we can use analysis of covariance (ANCOVA) to assess temporal changes in response variables without resorting to time-series modeling for which we lack sufficient data (Ellison & Gotelli *in preparation*). 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 analyzed 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 analyze these data (Gotelli & Ellison 2004, Ellison & Gotelli *in preparation*).

The additional smaller-scale subplot experiments established in the buffer areas have multiple replicates within each canopy manipulation plot. These include, for example, two 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 analyzed 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 *versus* hardwood or type of mortality: girdled hemlock *versus* 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:

Indirect effects of ants = (HE – (mean G AND L)) – (HE – X) = X – (mean G AND L).

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 reassembly 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 reassembly.

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 six 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) program, so there are ongoing, albeit modest, funds (< U.S. $10,000/year) that provide for a fraction of the labor 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 two years of collection; most data are posted more rapidly, however. Harvard Forest is committed to long-term storage and migration of electronic datasets, but there are costs associated with these activities that must be factored in to 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 program has 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 reflects 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 *et al.* 2002, 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 *et al*. *unpubublished data*). We look forward to new directions in ecology arising from syntheses of all of these observations and experiments.

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

	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								
Tsuga canadensis (L.) Carr.	73	50	66	3	69	59	53	9
Pinus strobus L.	14	19	6	3	2	2	18	35
Acer rubrum L.	6	3	6	13	6	7	12	17
Quercus rubra L.	0	0	0	11	0	0	0	0
Quercus alba L.	2	22	7	36	8	12	3	15
Betula lenta L.	1	3	8	24	11	15	3	15
Other	5	4	7	10	4	5	11	9

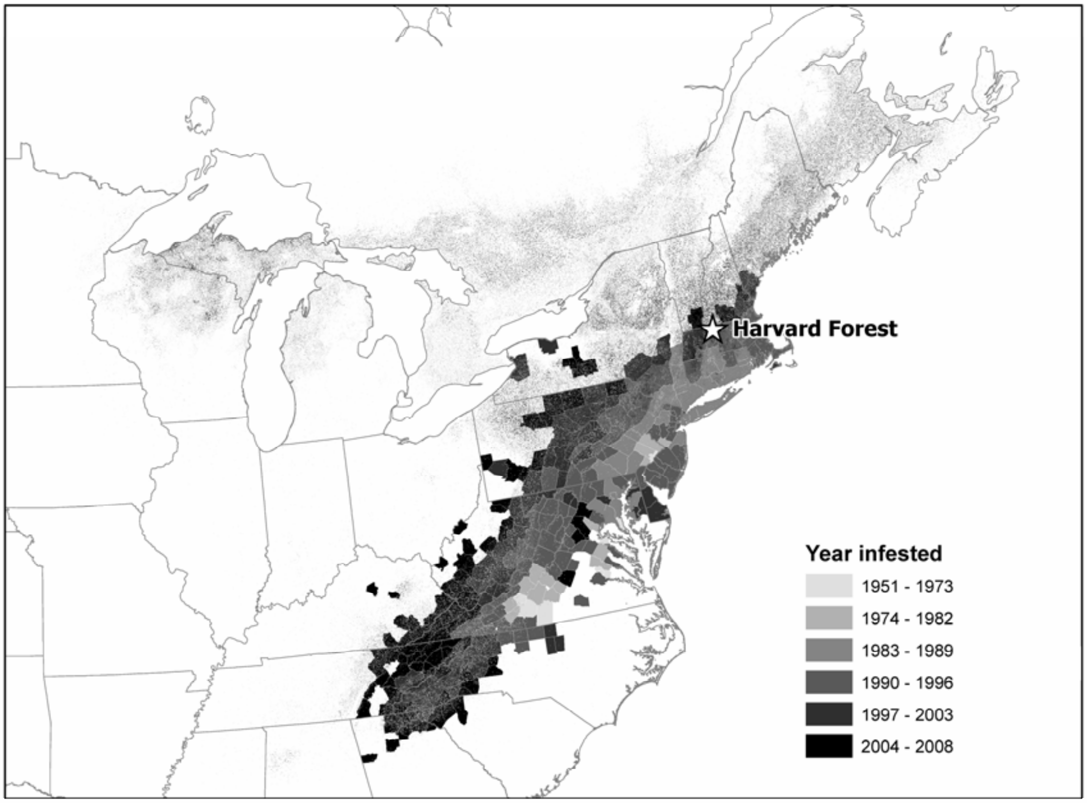

Figure 1. Distribution of eastern hemlock (*Tsuga canadensis*) in eastern North America, based on U.S. Forest Service Forest Inventory Analysis plots (gray shading) and spread of the hemlock woolly adelgid (*Adelges tsugae*) since its initial introduction into Virginia in 1951 (polygons), based on data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

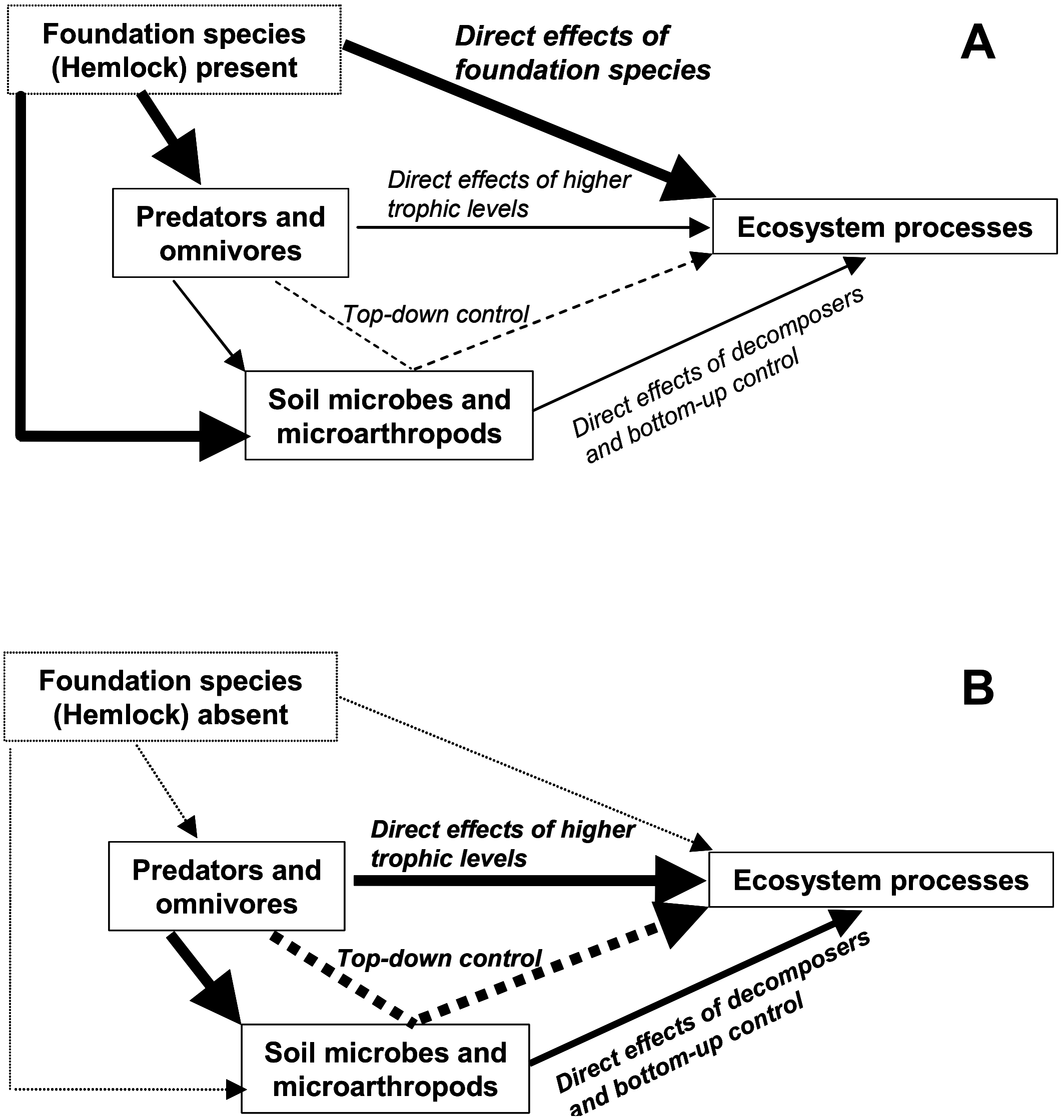

Figure 2. Conceptual model for disentangling the direct effects on ecosystem processes of foundation species from indirect effects caused by changes in biological diversity associated with foundation species. **A** - in intact hemlock stands, this single foundation species is the dominant controller 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 understory 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 ~ 6 months in New England during which time microclimate is controlled more by regional weather systems than by local biota. The understory is very sparse in the hemlock forests of New England, but the denser understory vegetation of deciduous forests can alter rates of nutrient fluxes prior to spring bud-burst (Zak *et al.* 1990).

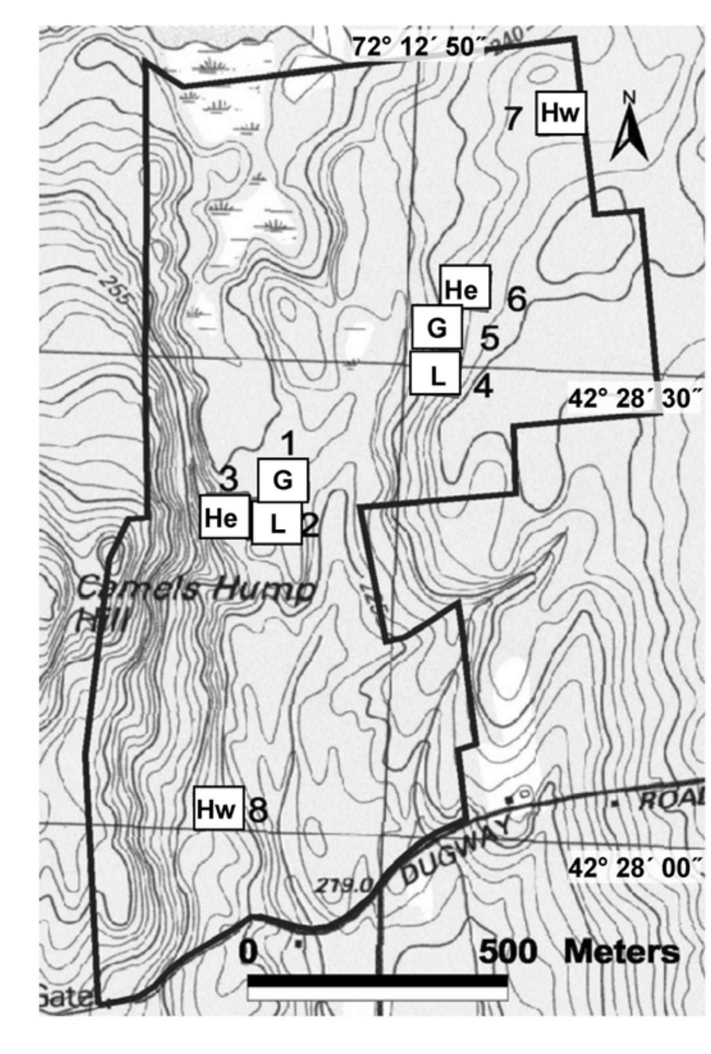

Figure 3. Location of the blocks and treatments within the Simes Tract at the Harvard Forest. This Before-After-Control-Impact replicated block design has two blocks (plots 1, 2, 3, and 8 are the "Valley" block, and plots 4-7 are the "Ridge" block). Each of the four treatments – Girdled (G), Logged (L),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

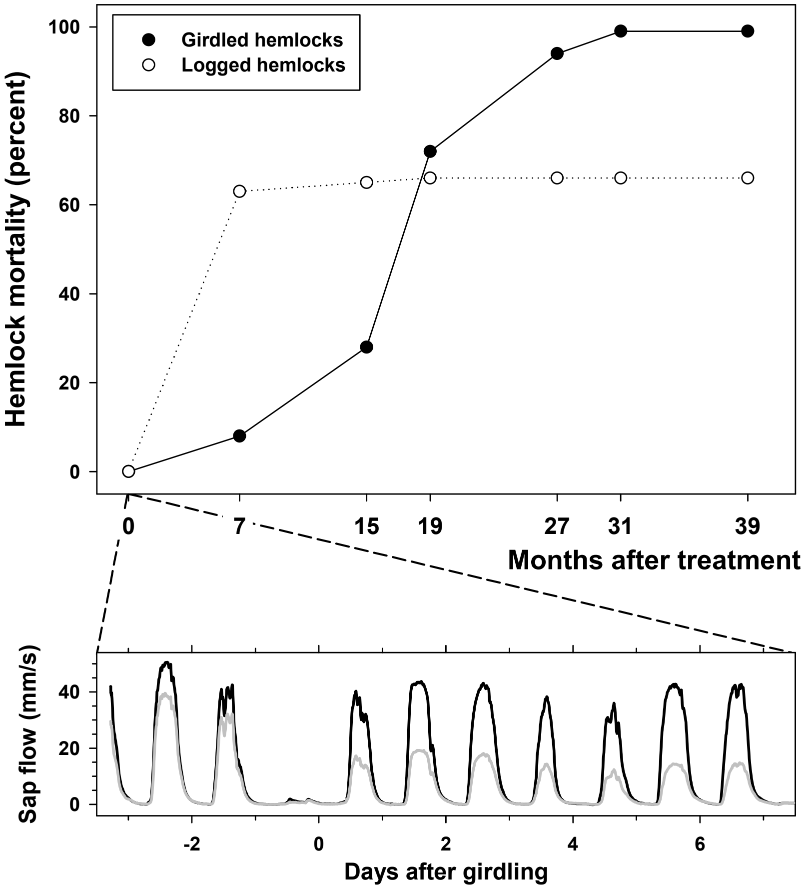

Figure 4. Mortality rate of eastern hemlock (*Tsuga canadensis*) in the core 30 × 30-m sampling areas in the girdled (●) and logged (○) plots following treatment application in April-May 2005. **Inset** at bottom shows the average change in the rate of sap flow in three girdled (gray lines) and three 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 6 trees. The day before trees were girdled, the site received 32mm 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 zero.

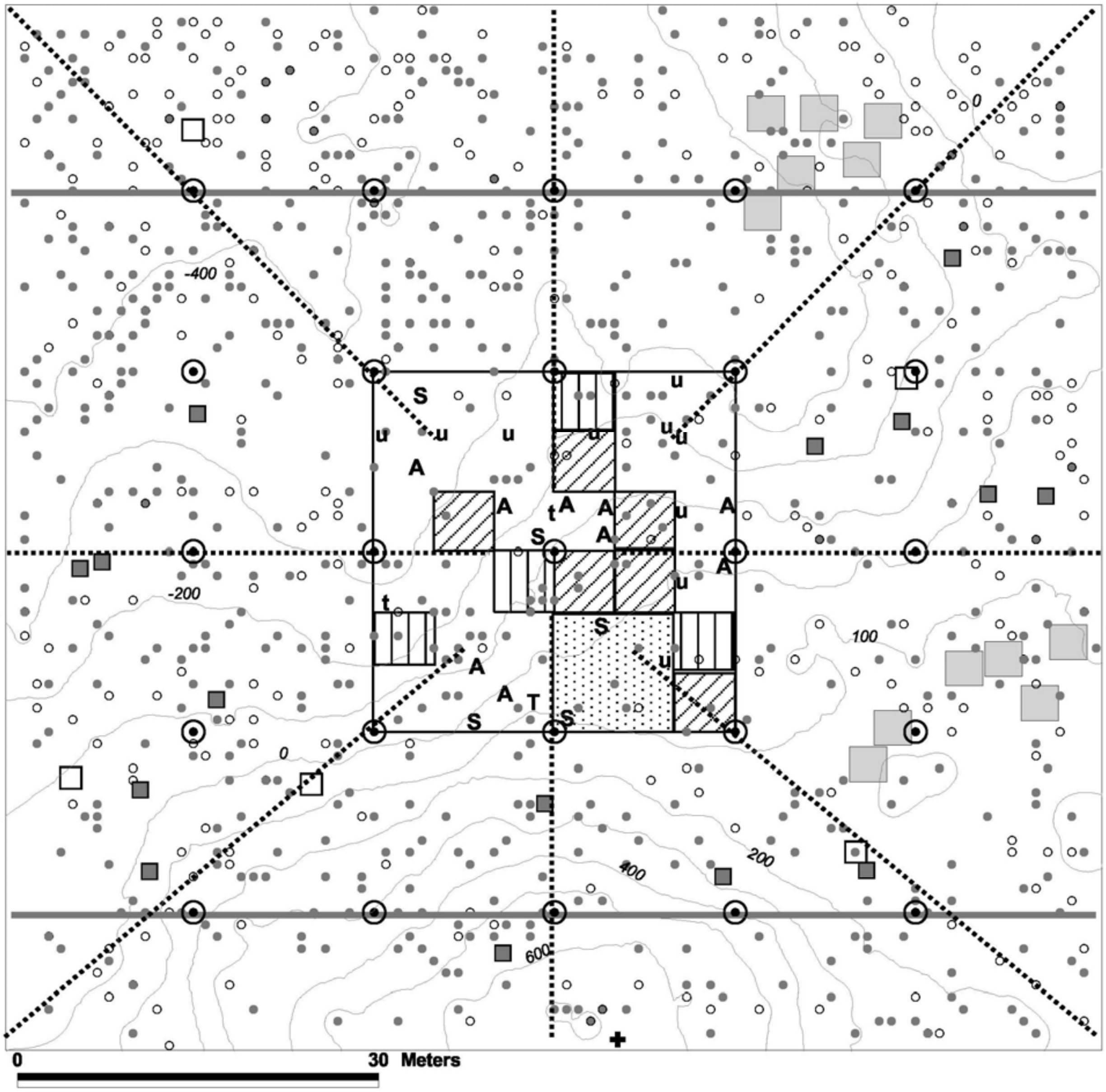

Figure 5. Example of the layout and zoning of a plot in the Harvard Forest Hemlock Removal Experiment. Individual trees (gray circles: hemlock; white circles: other tree species) were mapped together with elevations in cm relative to a 0-cm baseline near the plot center (gray contours). The center 30 × 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 gray lines) and coarse woody debris (thick dotted lines). Locations in the buffer area of two of the subplot experiments are illustrated with large light gray squares (ant removals, additions, controls) and small dark gray squares (litter arthropods).

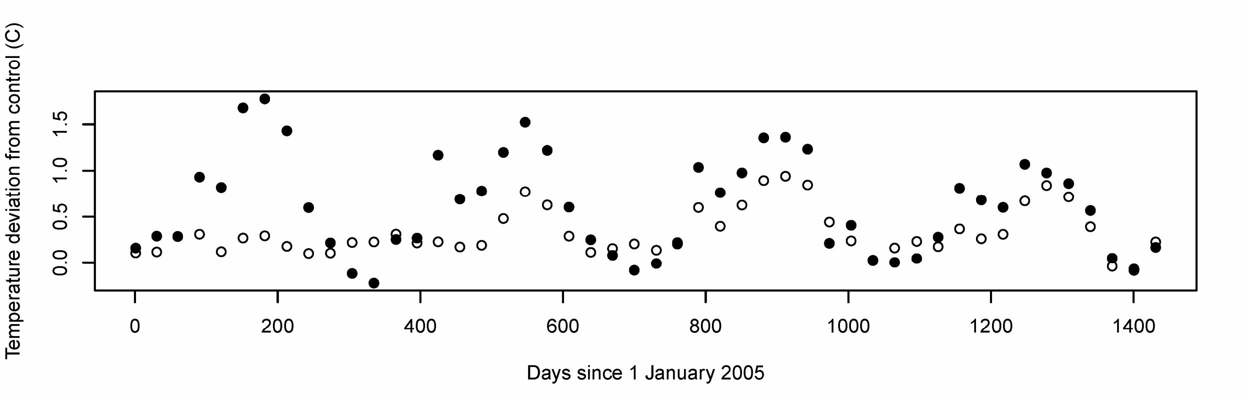

Figure 6. Temperature deviations in the logged (black circles) and girdled (white circles) plots relative to the hemlock control plots. The summer after logging, logged plots were > 1.5 °C warmer than control plots, but girdled plots were not different from control plots. As trees died in the girdled 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 understory cover reduced the difference in air temperature between logged and control plots.