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Experimentally Testing the Role of Foundation Species in Forests: The Harvard Forest Hemlock Removal Experiment

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4 **Experimentally testing the role of foundation species in forests:**

5 **The Harvard Forest Hemlock Removal Experiment**

6

7 Aaron M. Ellison^{*}, Audrey A. Barker-Plotkin, David R. Foster, and David A. Orwig

8

9 *Harvard Forest, Harvard University, 324 North Main Street, Petersham, Massachusetts*

10

01366 USA

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

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14 Running head: *Foundation species experiments*

15 **Summary**

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

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

31 **3. Ongoing measurements and monitoring** – Ongoing long-term measurements to quantify the
32 magnitude and direction of forest ecosystem change as hemlock declines include: air and soil
33 temperature, light availability, leaf area and canopy closure; changes in species composition and
34 abundance of the soil seed bank, understory vegetation, and soil-dwelling invertebrates;
35 dynamics of coarse woody debris; soil nitrogen availability and net nitrogen mineralization; and
36 soil carbon flux. Short-term or one-time-only measurements include initial tree ages, hemlock-

37 decomposing fungi, wood-boring beetles, and throughfall chemistry. Additional within-plot,
38 replicated experiments include effects of ants and litter-dwelling microarthropods on ecosystem
39 functioning, and responses of salamanders to canopy change.

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

45

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

48 **Introduction**

49 Foundation species (*sensu* Dayton 1972) are taxa that are locally abundant and regionally
50 common, whose structural or functional characteristics create habitat for a large number of
51 associated species, and which modulate core ecosystem processes such as energy and nutrient
52 fluxes or water balance (reviewed by Ellison *et al.* 2005a). Because foundation species are
53 common and abundant, in most cases they are not in immediate threat of extinction and thus are
54 rarely of conservation concern (Gaston & Fuller 2008). Nonetheless, in terrestrial ecosystems
55 worldwide, a number of foundation tree species are declining as a result of introductions and
56 outbreaks of non-indigenous pests and pathogens, irruptions of native pests, and over-harvesting
57 or high-intensity logging (see review in Ellison *et al.* 2005a for detailed case-studies).

58 Paleocological studies have shown that foundation tree species such as eastern hemlock (*Tsuga*
59 *canadensis* (L.) Carr.) have declined in the past due to insects and climate change (Allison *et al.*
60 1986; Foster *et al.* 2006; Shuman *et al.* 2009). The occurrence and magnitude of these declines
61 are expected to increase with future climate change and an increase in extreme climatic events
62 (Gaston & Fuller 2007; Berggren *et al.* 2009). Such declines and the eventual local or regional
63 extinction of foundation species may result in cascades of evolutionary, ecological, and
64 environmental changes (*e.g.*, Smith & Knapp 2003; Whitham *et al.* 2008; Albani *et al.* 2010).

65 There are significant logistical and analytical challenges involved in experimentally
66 assessing the system-wide consequences of the loss of foundation species for individual
67 populations, multi-species assemblages, and ecosystem dynamics. The spatial scale of
68 manipulations must encompass at least substantial portions of entire ecosystems. The temporal
69 duration of monitoring following experimental manipulation must encompass lifespans of long-

70 lived organisms and capture slow turnover in plant- and soil-bound nutrients and carbon;
71 consequently, the time required to characterize effects fully requires at least decades, but can
72 exceed centuries (Harmon 1992). At the same time, the frequency of monitoring also must be
73 fast enough to identify the turnover and equilibrational dynamics of short-lived taxa and rapid
74 biogeochemical cycles, along with the transient dynamics of long-lived taxa and fast changes in
75 ecosystem processes (*e.g.*, Smith & Shugart 1993; Hastings 2001). Finally, the necessarily large
76 spatial grain, long duration, and intensity of instrumentation and measurements of these
77 experiments preclude the comparatively high replication common in small-scale ecological
78 studies (Witman & Roy 2009). Low replication and relatively short time-series (generally < 50
79 observations) present significant challenges for data analysis and strong inference.

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

91

92 The Hemlock – Hemlock Woolly Adelgid – Human System

93 Eastern hemlock (*Tsuga canadensis*; Coniferophyta: Pinaceae) is a long-lived, late-successional
94 conifer tree native to eastern North America, where it ranges from the southern Appalachian
95 Mountains northward to southern Canada and westward to the central Lake states (McWilliams
96 & Schmidt 2000; Fig. 1). In the northern part of its range, where HF-HeRE is sited, hemlock
97 stands are characterized by > 50% basal area of this single species, and the understory is species-
98 poor and open (Foster & Zebryk 1993; McLachlan *et al.* 2000). In these hemlock-dominated
99 stands, the combination of deep shade and acidic, slowly decomposing litter results in a cool,
100 damp microclimate, slow rates of nitrogen cycling, and nutrient-poor soils (Jenkins *et al.* 1999;
101 Orwig *et al.* 2008). Hemlock intercepts more snow and has a higher leaf area index and lower
102 transpiration rates per unit leaf area than do co-occurring deciduous tree species (Catovsky *et al.*
103 2002). Although hemlock continues to photosynthesize and store carbon in the spring and fall
104 when deciduous trees are leafless, during the summer hemlock stands overall fix less carbon and
105 transpire about 50% of the total water released by deciduous trees (Hadley 2000; Hadley &
106 Schedlbauer 2002; Daley *et al.* 2007). As a result of all of these characteristics, eastern hemlock
107 mediates soil moisture levels, stabilizes stream base-flows, and decreases diel variation in stream
108 temperatures (Ford & Vose 2007; Nuckolls *et al.* 2009). The environment created by this
109 foundation tree species provides critical habitat for unique assemblages of associated animals,
110 including birds, insects, salamanders, and fish (Snyder *et al.* 2002; Tingley *et al.* 2002; Ellison *et*
111 *al.* 2005b; Dilling *et al.* 2007; Mathewson 2009).

112 The hemlock woolly adelgid (*Adelges tsugae*; Hemiptera: Adelgidae) is a small (< 1-mm
113 long adult) flightless insect that was introduced to the United States from Japan in the early

114 1950s (Havill *et al.* 2006; Havill & Footit 2007). Since the early 1980s, it has been spreading
115 rapidly through both eastern hemlock and Carolina hemlock (*Tsuga caroliniana* Engelm.) stands
116 in the eastern United States (Fig. 1). The adelgid attacks trees of all size classes and ages, from
117 small seedlings and saplings to mature trees, eventually killing the tree within 5-15 years in
118 hemlock's northern range and 1-3 years in its southern range

119 The life-cycle of the adelgid includes two parthenogenic generations (the sexual
120 generation is absent in North America [Havill & Footit 2007]) that are tied to the annual
121 production of new hemlock needles (McClure 1987). The spring generation of adelgids
122 ('progreiens') develops from March to June, whilst the fall/over-wintering generation ('sistens')
123 develops from June through March. As the sistens hatch, they crawl and disperse onto newly
124 produced hemlock needles, where they settle and estivate (summer diapause). In early fall,
125 sistens emerge from estivation and begin to feed on ray parenchyma cells at the base of the
126 needle (Young *et al.* 1995). The sistens feed throughout the winter and produce progrediens in
127 early spring the following year. The progrediens continue to feed on the same branchlets and
128 needles as their parent sistens; these needles are mature but generally are less than 14 months old
129 (Young *et al.* 1995, Lagalante *et al.* 2006). Needles live 2-4 years (Powell 1991), and as adelgid
130 populations build, new needle production declines. In response, adelgid populations also may
131 decline, but they rebound when new needle production again increases (McClure 1991).

132 As the adelgid has spread and hemlock declines throughout its range, landowners,
133 including individuals and public agencies, have responded with a range of management
134 strategies. Chemical control of the adelgid is expensive and is usually limited to specimen trees
135 and small stands (Doccola *et al.* 2003). Systemic insecticides must be applied broadly because

136 the adelgid feeds on all age and size classes of hemlock, but these chemicals may have
137 significant non-target effects on soil fauna and nearby streams and other aquatic habitats (Cowles
138 2009). Biological control by the derodontid beetles *Laricobius nigrinus* Fender and *Laricobius*
139 *rubidus* Le Conte (introduced from western North America) and the coccinellids *Scymnus*
140 *sinuanodulus* Yu & Yao, *Scymnus ningshanensis* Yu & Yao, and *Sasajiscymnus tsugae* (Sasaji &
141 McClure) introduced from Asia have not yet controlled this pest in forested settings (Cheah &
142 McClure 2002; Mausel *et al.* 2008). To date, individuals or genetic lines of hemlock resistant to
143 the adelgid have not been described although screening programs are underway at Cornell
144 University¹ and the University of Rhode Island² (Ingwell *et al.* 2009).

145 One of the most common management responses is to harvest hemlock stands before
146 adelgid infestation kills the trees and decreases their generally modest economic value (Orwig *et*
147 *al.* 2002; Foster & Orwig 2006). In most of these commercial timber harvests, all of the
148 merchantable hemlocks are removed along with many of the more valuable hardwoods.
149 Associated species such as white pine (*Pinus strobus* L.) are also removed to increase revenue
150 from the logging operations (Kizlinski *et al.* 2002). In the northern parts of hemlock's range, both
151 preemptive salvage logging and post-infestation clear-felling are removing hemlock from the
152 landscape more rapidly than is the adelgid. As hemlock is removed, it is replaced by various
153 early-successional and fast-growing hardwood species, including black birch (*Betula lenta* L.)
154 and red maple (*Acer rubrum* L.). These processes result in a progressive homogenization of the
155 New England forested landscape (Foster & Orwig 2006; Albani *et al.* 2010), in which the extent

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

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

156 of young and even-aged deciduous forests is increasing as older multi-aged and structurally
157 diverse mixed evergreen and deciduous forest decline.

158

159 **Conceptual framework and hypotheses**

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

- 161 1. What are the processes by which forested ecosystems reorganize following loss of
162 hemlock, and how is this reorganization related to the biology of hemlock and the
163 adelgid?
- 164 2. Will the system reach new equilibria following this reorganization?
- 165 3. How does logging *versus* the adelgid alter these transitions and equilibria?

166 We hypothesize that the reorganization of this forested ecosystem will occur at several levels of
167 organization. First, we expect dramatic changes in both the mean and variance of seasonal light
168 availability, air and soil temperature, soil moisture and other microclimatic variables as hemlock,
169 which casts deep shade and has acidic needles that are slow to decompose, is replaced by
170 deciduous species. These environmental changes should lead to development of new soil
171 microbial communities and concomitant changes in rates of soil nitrogen and carbon cycling, and
172 soil formation. For example, in adelgid-infested stands, throughfall is enriched in nitrogen,
173 causing transient increases in nutrient and energy cycling under declining hemlock canopies
174 (Stadler *et al.* 2005, 2006). Soil respiration should decline dramatically when hemlock roots die,
175 and there should be a short-term pulse of nutrients into the soil as needles are shed (Kizlinski *et*
176 *al.* 2002, Orwig *et al.* 2008). Over decadal time-scales, models predict that rates of carbon uptake
177 should decline regionally as hemlock disappears (Albani *et al.* 2010). But these models also

178 forecast that over longer time scales, carbon uptake by the reassembled early- and mid-
179 successional hardwood stands may equal or even exceed that of the lost hemlock stands (Albani
180 *et al.* 2010).

181 Second, species that are dependent on hemlock or the habitat that it creates will disappear.
182 As a new forest develops, other species, both native and exotic, will colonize and interact (Rohr
183 *et al.* 2009). Because black birch-dominated forests are not a common feature of the eastern U.S.
184 landscape, the trajectory of this community re-assembly process is not easy to forecast. One
185 already evident change is an increase in local diversity of ants as omnivores and decomposers in
186 the genus *Formica*, normally absent from hemlock stands, colonize early-successional hardwood
187 stands (Ellison *et al.* 2005b). Ants are known to have broad effects on soil ecosystem dynamics
188 (Folgarait 1998). Disentangling the direct effects of hemlock loss on ecosystem processes from
189 indirect effects caused by changes in biological diversity associated with hemlock loss is a key
190 component of HF-HeRE (Fig. 2).

191 We hypothesize that the rate at which these reorganizations occur and the new equilibria
192 that they reach will depend on the dynamics of adelgid populations and on how hemlock stands
193 are managed. For example, pre-emptive salvage logging (Foster & Orwig 2006) changes canopy
194 composition much more abruptly than does the adelgid, and logging machinery compacts soil,
195 altering patterns of regeneration from the seed-bank. Nutrient pulses from slash piles should be
196 larger and more rapid than pulses of nutrient-enriched throughfall associated with the adelgid
197 (Stadler *et al.* 2005, 2006). All of these changes are likely to be mediated, even amplified, by
198 changes in microclimate associated with hemlock loss. These and other differences between

199 logged stands and stands that succumb slowly and more heterogeneously will feed back on and
200 interact with changes caused by biotic responses to hemlock loss.

201

202

203 **Site description**

204 The HF-HeRE is located within the 121-ha Simes Tract (42.47° – 42.48° N, 72.22° – 72.21° W;
205 elevation 215 – 300 m a.s.l.) at the Harvard Forest Long-Term Ecological Research Site in
206 Petersham, Massachusetts, USA (Fig. 3). This tract lies within the Chicopee River watershed and
207 extends up a valley in southern Petersham. A gentle slope (<10%) rises up the eastern side of the
208 tract, and a moderate to steep slope (~30%) runs along the western edge of the tract where the
209 tract abuts the 30,000-ha Quabbin Reservoir Reservation. Typical of hemlock forests throughout
210 this region, much of the central portion of the tract is poorly drained or swampy; elevated areas
211 have small hills and better drainage. The soils are predominantly coarse-loamy, mixed, active,
212 mesic Typic Dystrudepts in the Charlton Series that are derived from glacial till (USDA n.d.).
213 Eastern hemlock and red maple dominate the poorly drained soils, whereas red and white oaks
214 (*Quercus rubra* L. and *Q. alba* L.), white pine, and eastern hemlock dominate the hills and
215 slopes. Black birch and other hardwoods are common associates. Sugar maple (*Acer saccharum*
216 Marsh.) grows in the southern part of the tract. Much of the tract was cleared for agricultural use
217 or harvested for timber in the early and mid-1800s. The forest has been regenerating since the
218 late 1800s and early 1900s (Kernan 1980). Tree-core samples have revealed that the trees in the
219 experimental plots are 50-75 years old (Bettmann-Kerson 2007).

220

221 **Experimental design and treatments**

222 CANOPY MANIPULATION

223 The primary canopy-level manipulation – girdling or harvesting of standing hemlock – was done
224 in large ($90 \times 90 \text{ m} = 0.81 \text{ ha}$) plots using a replicated, blocked design with measurements
225 collected both before and after treatments (analogous to an *experimental* Before-After-Control-
226 Impact (BACI) design). Plots were identified in 2003 and sampled for two growing seasons
227 (spring/summer in each of 2003 and 2004) prior to canopy manipulations. The eight plots
228 comprising this experiment are grouped in two blocks (Fig. 3), each consisting of three plots
229 initially dominated by hemlock and one plot of mixed northern hardwoods (Table 1). The
230 “Valley” block (plots 1–3 and 8 in Fig. 3) is in undulating terrain bordered on its northern edge
231 by a *Sphagnum*-dominated wetland. The “Ridge” block (plots 4–7 in Fig. 3) is on a forested
232 ridge. The four treatments in each block include:

- 233 • **Girdling** to simulate the physical decline and mortality of hemlock resulting from its
234 death by the hemlock woolly adelgid. Over a 2-day period in May 2005, the bark and
235 cambium of all individual hemlocks were girdled using chain saws (on large trees) or
236 hand knives (on small saplings and seedlings). No other species were girdled and there
237 was no site disturbance. Girdling immediately reduced sap-flow by 50% (Fig. 4 – inset),
238 and girdled trees died within 2 years (Fig. 4). Thus, an important characteristic of
239 hemlock woolly adelgid infestation that is missing from this treatment is the very lengthy
240 period of decline (especially in northern regions) during which the plant is undergoing
241 physiological stress and metabolic imbalance that may induce biogeochemical and
242 microbial changes on the site (cf. Stadler *et al.* 2006). These additional (additive and/or

243 interactive) impacts of the adelgid over and above (or with) the physical decline of trees
244 can be assessed in the **hemlock control** treatment (see below).

245 • **Logging** to mimic the effects of a typical commercial hemlock salvage operation. All
246 hemlock individuals > 20 cm diameter at breast height (DBH) and other commercially
247 valuable trees, including larger hardwoods (primarily red oak) and white pine, were
248 removed for saw logs. Other hardwoods (red maple, black birch) and smaller stems that a
249 commercial logger might remove to improve future stand quality, facilitate log removal
250 and general operation, or initiate a new cohort of sprouts were also cut. Between 60 and
251 70% of the stand basal area was cut in these two plots (Fig. 4), using hand-felling by
252 chainsaw. Logs were removed by dragging them with a rubber-tired skidder. Slash (small
253 branches and damaged or rotted boles accumulating to ≤ 1.3 -m high) was left on site as
254 permitted by Massachusetts forest management laws. The intent was to harvest the stands
255 following the approach of a commercial harvest. To minimize soil damage and following
256 standard “best management” harvesting procedures (Kittredge & Parker 1999), logging
257 was done between February and April 2005, when the soil was frozen. Nonetheless, there
258 was scarification as well as damage to small remaining stems.

259 • **Hemlock control** plots are hemlock-dominated and received no manipulation. At the
260 start of this experiment, no adelgid was present at the Simes Tract. When we established
261 this experiment in 2003, we anticipated that the hemlock control plots would eventually
262 become infested by the adelgid. The adelgid was first observed at low densities in these
263 control plots in 2008 and was widespread in the plots, but still at low densities, in 2009.
264 Using data collected prior to 2010, contrasts of the hemlock control plots with the logged

265 or girdled plots will reveal effects of hemlock that was physically deteriorating or
266 removed. From 2010 onwards, the now adelgid-infested hemlock control plots will serve
267 as hemlock + adelgid plots that will be contrasted with the girdled plots to disentangle
268 effects of the adelgid from effects of physical loss of hemlock alone. These contrasts will
269 test our hypotheses about differences between logged and adelgid-infested stands in rates
270 and trajectories of the reorganization of these forested ecosystems.

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

274 In 2003 and 2004, all trees in each plot were tagged with permanent aluminum tags,
275 mapped (relative x , y , z coordinates) using a compass, autolevel, and stadia rod, and measured
276 (diameter at 1.3 m [DBH]) prior to treatment applications. Tags labeling logged trees were
277 relocated from boles to stumps as trees were cut in the logged plots. Plot boundaries were located
278 with a GPS device (Trimble Navigation Limited, Sunnyvale, CA, USA) and permanently staked
279 (etched, painted PVC posts or iron rods) at 30-m intervals. The interior of the plot was gridded
280 with etched, painted PVC posts at 15-m intervals. The center point of each plot was located with
281 GPS and permanently staked with an iron rod.

282

283 MONITORING, MEASUREMENTS, AND SUBPLOT EXPERIMENTS

284 To test our hypotheses about the directions and rates of reorganization of these forests, we make
285 a broad spectrum of measurements to quantify short- and long-term processes associated with the
286 decline of hemlock and its eventual replacement. We focus our intensive measurements and

287 sampling in the center 30×30 m “core” area of each 90×90 m experimental plot. Sampling
288 sites in the core area are located randomly within a grid of 5×5 -m squares (Fig. 5). The 30-m
289 wide, square “buffer” area surrounding the core is approximately equal in width to one tree
290 height (overstory tree heights range from ~25-35m). We site additional short-term, subplot-scale
291 experiments in this buffer area to provide additional mechanistic detail that we cannot obtain
292 through long-term observations and monitoring alone. These experiments are sited in the buffer
293 area because the small disturbances they create could compromise the integrity of the
294 observational data collected in the core area. The spatial scales and temporal frequency of these
295 measurements and experiments are detailed in the following subsections.

296

297 *Trajectories of reorganization*

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

309 support our hypothesis of increases in mean and temporal variance of temperatures (Fig. 6).
310 Light availability and leaf area index are measured throughout the entire 90 × 90 m plot on a 15-
311 m grid (25 points per plot) every April and September, when deciduous trees are leafless and
312 leafed-out, respectively. Hemispherical canopy photographs are taken with a Nikon 8-mm
313 “fisheye” lens and a Nikon F-3 film camera (prior to 2008) or (since 2008) D-3 digital camera in
314 full-frame (“FX”) mode. The camera is placed on a self-leveling mount atop a tripod and
315 positioned 1-2 m above ground. Hemispherical photographs are analyzed for canopy openness
316 and diffuse radiation (“direct site factor” and “indirect site factor”, respectively; Rich 1989, Rich
317 *et al.* 1993) and leaf area index using HemiView software version 2.1 (Delta-T Devices,
318 Cambridge, UK). As the ecological functioning of a forest stand is often related to the spatial
319 organization of the canopy, we have also used portable canopy laser detection and ranging
320 (LiDAR: Parker *et al.* 2004) to measure volumetric canopy structure the season after the girdling
321 and logging treatments were completed. LiDAR measures will be repeated at 5- and 15-year
322 intervals to develop an understanding of early structural dynamics and micrometeorological
323 consequences associated with the canopy removal treatments.

324 Forecast changes in nitrogen availability and changes in rates of nutrient fluxes are
325 assessed with resin bags and soil incubations (Robertson *et al.* 1999). Changes in carbon efflux
326 (soil respiration) are measured manually every two weeks during the growing season between
327 0900 and 1500 hrs in permanently embedded 30-cm diameter plastic (PVC) collars using a
328 portable infrared gas analyzer (Savage & Davidson 2003). Collars were installed in 2003 and are
329 embedded 10-cm into the soil. Soil moisture within the collars is measured with permanently
330 installed time-domain reflectometry (TDR) probes at the same time that soil respiration is

331 measured. Net primary productivity (both as litterfall into five randomly located litter baskets
332 and as diameter growth, in-growth, and mortality of all trees) and decomposition and turnover of
333 coarse woody debris are assessed throughout the entire 90 × 90-m plot using the line-intercept
334 method of Harmon & Sexton (1986).

335 Reorganization of biotic assemblages is measured as annual changes in species
336 composition and abundance of understory vegetation and key arthropod groups (ants, carabid
337 beetles, and spiders). Understory vegetation is sampled in five 1-m² quadrats spaced evenly
338 along each of two transects running north-south or east-west through the core of each plot (Fig.
339 5). We estimate percent cover of herbs, shrubs, and tree seedlings (individuals < 1.3 m tall) to the
340 nearest one percent and count the number of seedlings of each tree species. Arthropods are
341 sampled using grids of 25 pitfall traps in the core area of each plot (full methods in Ellison *et al.*
342 2005b). The seed bank in the core area was assessed prior to treatment (Sullivan & Ellison 2006)
343 and will be re-assessed at 5-10 year intervals to determine regeneration potential and turnover of
344 seeds in the soil. The seed bank data are complemented by collections of cones, seeds, and fruits
345 in litter baskets.

346

347 *Subplot experiments*

348 We use subplot experiments to separate direct and indirect effects of hemlock loss. For example,
349 Ellison *et al.* (2005b) documented increases in ant species richness with declines in hemlock
350 canopy cover. We have observed similar changes in our logged and girdled plots (A.M. Ellison,
351 *unpublished data*). Because assessment of the effects of these biotic changes on soil ecosystem
352 properties are confounded by the canopy-scale manipulation, determining main and interactive

353 effects of canopy structure and ant diversity requires additional manipulations of ant diversity
354 within canopy treatments. Thus, we have established subplot experiments in which we
355 manipulate species composition and abundance of ants in each of the canopy manipulation plots
356 (Fig. 5). Similar experiments measuring changes in forest carbon stocks and in the diversity and
357 abundance of litter microarthropods and amphibians, and the impacts of these changes on
358 ecosystem dynamics, have also been installed in the buffer zones of the large canopy
359 manipulation plots (Fig. 5).

360

361 **Statistical framework and analytical challenges**

362 Design and implementation of large-scale, long-term experiments involve tradeoffs between
363 realism and replication (*e.g.*, Carpenter 1990, 1998). In the HF-HeRE, our focus on realistic,
364 hectare-scale manipulations to uncover the responses of North American forested ecosystems to
365 loss of a long-lived foundation tree species limited, but did not completely eliminate, our ability
366 to replicate treatments. Although eastern hemlock is common and abundant in our forests, the
367 process of actually locating many hectare-sized plots, each of which had >50% basal area of
368 hemlock, had similar size and age structure, and were in locations that could be manipulated
369 without lengthy regulatory review (state laws regulate activities within 30-60 m of wetlands,
370 lakes, and streams) was surprisingly difficult. Even two replicates, however, allows us to
371 estimate treatment variances, and two years of pre-treatment monitoring for most response
372 variables have provided a useful baseline from which to compare responses to the canopy
373 manipulations.

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

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

395 investigator rarely has any say on where the impact sites are located and siting “controls” can be
396 similarly constrained.

397 In contrast, HF-HeRE is a designed, manipulative experiment, which provides
398 opportunities for additional, more powerful analysis. The experimental design (Fig. 2, 5) can be
399 treated as a standard one-way blocked analysis of variance (ANOVA), with any additional
400 experiments established in subplots within the large plots analyzed using split-plot ANOVA
401 (Gotelli & Ellison 2004). Unlike a strict BACI analysis, ANOVA permits estimation of effect
402 sizes and associated uncertainty, *a priori* contrasts among specified treatments or treatment
403 groups, and formal hypothesis tests. The primary factors are the four canopy manipulations
404 (hemlock control, hemlock girdled, logged, hardwood control) and the two blocks.

405 Manipulations are treated as fixed factors, and blocks are treated as random factors. The absence
406 of replication of treatments within blocks precludes estimation of a block \times treatment interaction.

407 Time (or sample date) enters the model as a continuous covariate, so when time series are
408 short (*e.g.*, seven years of annual data), we can use analysis of covariance (ANCOVA) to assess
409 temporal changes in response variables without resorting to time-series modeling for which we
410 lack sufficient data (Ellison & Gotelli *in preparation*). This is important, as degrees of freedom
411 are small because subsamples taken within a given plot (*e.g.*, multiple N mineralization cores)
412 must be pooled prior to analysis to avoid pseudoreplication (*sensu* Hurlbert 1984). The
413 subsamples do, however, provide a more accurate assessment of the within-plot response (Blume
414 & Royall 2003). Alternatively, the data could be analyzed with a repeated-measures ANOVA, in
415 which time enters the model as a fixed factor, but it is rare that the key assumption of repeated-
416 measures ANOVA – that the variance of the difference of observations between any pair of times

417 is equal ('circularity') – can be met (Gotelli & Ellison 2004). Because we are more interested in
418 the effect size – the slope of the line of the response variable as a function of time – than the *P*-
419 value (because we expect that all variables will change through time), an ANCOVA is a more
420 efficient and informative method to analyze these data (Gotelli & Ellison 2004, Ellison & Gotelli
421 *in preparation*).

422 The additional smaller-scale subplot experiments established in the buffer areas have
423 multiple replicates within each canopy manipulation plot. These include, for example, two
424 transects and 10 coverboards/transect for amphibians and 2-4 replicates each of four levels of ant
425 manipulations in the ants and ecosystem function experiment – unmanipulated, ant removal,
426 disturbance control, and ant addition (Fig. 5). Data from these experiments can be analyzed using
427 hierarchical ANOVA (Qian & Shen 2007) to assess treatment effects (*e.g.*, coverboard type or ant
428 manipulations) within canopy manipulations and blocks, and *a priori* contrasts to tease apart the
429 effects of individual treatments on ecosystem processes (Fig. 2). We use a hierarchical ANOVA
430 because it more clearly delineates effect sizes than does a mixed-model ANOVA (Qian & Shen
431 2007).

432 We illustrate the statistical partitioning of effects of whole-plot canopy manipulation and
433 subplot treatments by describing the method of analysis for the experiment in which we are
434 examining the direct effects of hemlock and direct vs. indirect effects of ants on soil ecosystem
435 processes (Fig. 2). One possible *a priori* contrast would be to distinguish “hemlock effects” as
436 the difference between plots with and without living hemlock. Other *a priori* contrasts could
437 include hemlock *versus* hardwood or type of mortality: girdled hemlock *versus* logged hemlock.
438 For the “hemlock effects” contrast, short-term canopy effects would be measured as

439 UNMANIPULATED HEMLOCK CANOPY (HE) – (mean of GIRDLED CANOPY (G) and LOGGED CANOPY
440 (L)), because this comparison will reveal ecosystem effects shortly after hemlock are removed
441 from the system. Then, short-term direct effects of ant activity at the subplot level can be
442 calculated as UNMANIPULATED HEMLOCK CANOPY (HE) – ANT REMOVAL (X). Thus:

443 Large-scale “hemlock effect” = HE – (mean G AND L)

444 Direct effect of ants within hemlock stands = HE – X

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

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

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

456 Finally, the two controls will yield valuable comparisons and baselines. Over time, the
457 girdled and logged plots should converge to the hardwood control plots in structure and function.
458 Now that the hemlock control plots have been infested by the adelgid (see next section), their
459 decline and reassembly will be contrasted first with trajectories of the girdled and logged plots
460 and subsequently with the hardwood control plots. These are neither space-for-time substitutions

461 nor exact temporal matches, but the plots will nonetheless provide important novel insights into
462 successional dynamics as well as ecosystem disassembly and reassembly.

463

464 **Future directions and challenges**

465 THE ADELGID COMETH

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

479

480 LONG-TERM MAINTENANCE OF THE EXPERIMENT AND THE DATA

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

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

499

500 AN INVITATION FOR COLLABORATION AND PARALLEL STUDIES

501 Finally, we highlight two important aspects of HF-HeRE. First, the Harvard Forest and its NSF-
502 supported LTER program has invested and continues to commit significant funds and personnel
503 time to the establishment and maintenance of HF-HeRE. This is not only a single experiment that
504 we designed to explore a set of fundamental ecological processes. It also should be considered as

505 scientific infrastructure that is available to colleagues and collaborators world-wide who are
506 interested in exploring complementary questions, and we encourage and invite such
507 collaborations. Studies of plant ecophysiology, vertebrates (birds, small mammals, browsing
508 ungulates), food web dynamics, biogeochemistry of elements other than C and N, and subsurface
509 hydrology are currently absent from HF-HeRE. The absence of these and other relevant studies
510 reflects only a lack of local expertise or resources, not a lack of opportunity.

511 HF-HeRE is also part of an evolving network of experimental sites focused on identifying
512 and understanding the role of single foundation species on population-, community-, and
513 ecosystem-level dynamics. Comparable studies include a hemlock removal experiment at the
514 Coweeta LTER site in North Carolina (Nuckolls *et al.* 2009) and an oak removal experiment at
515 the Black Rock Experimental Forest in New York (Ellison *et al.* 2007). Both of these
516 experiments removed canopy trees by girdling, and are similar to HF-HeRE in design and
517 analytical protocols. All these experiments complement long-term observational studies on
518 hemlock decline in eastern North America (Orwig & Foster 1998; Orwig *et al.* 2002, 2008),
519 sudden oak death in California and its arrival in New England (Rizzo & Garbelotto 2003;
520 Meetenmeyer *et al.* 2004; Douglas 2005), and recent mortality of several oak populations
521 resulting from drought and defoliation by native and exotics insects in coastal Massachusetts (D.
522 R. Foster *et al. unpublished data*). We look forward to new directions in ecology arising from
523 syntheses of all of these observations and experiments.

524

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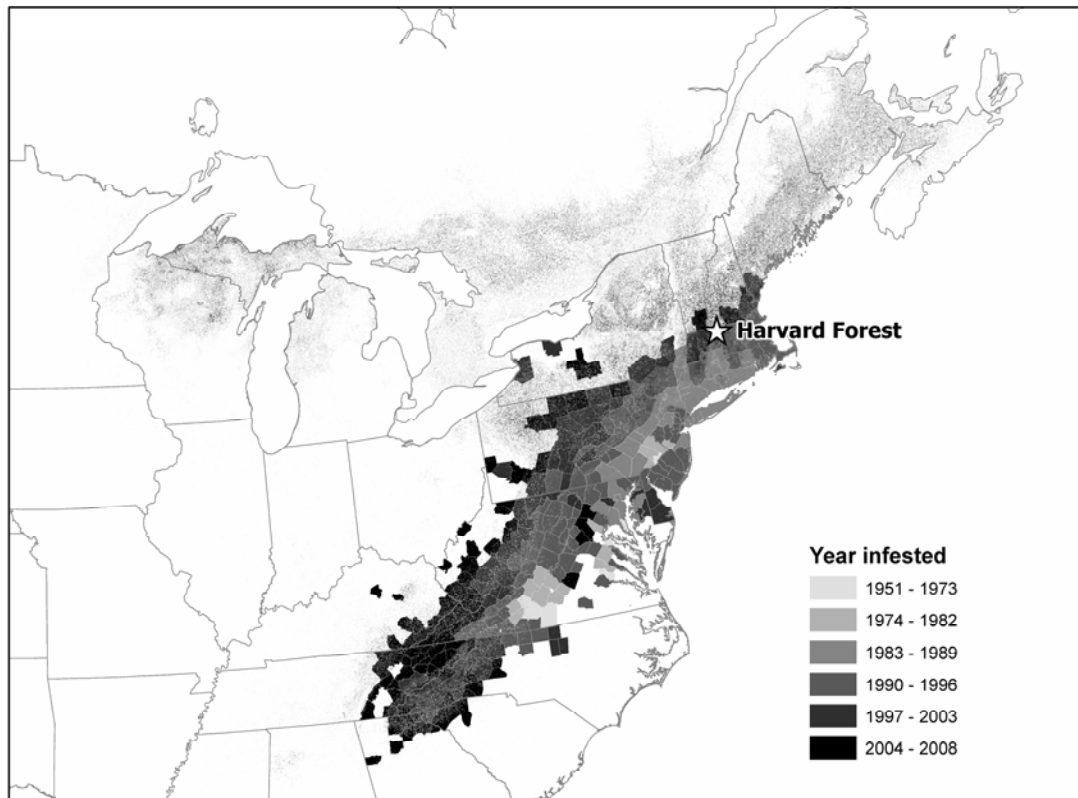
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- 752

753 **Table 1.** Initial (pre-treatment) overstory composition (percent basal area of each species) of the
 754 eight plots of the Harvard Forest Hemlock Removal Experiment. The diameters of all trees in
 755 each plot were measured, so these data are a complete inventory, not a statistical sample.
 756 “Other” species include *Betula alleghaniensis* Britt., *Betula papyrifera* Marsh., *Betula*
 757 *populifolia* Marsh, *Carpinus caroliniana* Walt., *Carya glabra* (Mill.) Sweet, *Carya ovata* (Mill.)
 758 K. Koch, *Castanea dentata* (Marsh) Borkh., *Fagus grandifolia* Ehrh., *Fraxinus americana* L.,
 759 *Fraxinus nigra* Marsh., *Hamamelis virginiana* L., *Ostrya virginiana* (Miller) K. Koch., *Prunus*
 760 *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 (m² 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

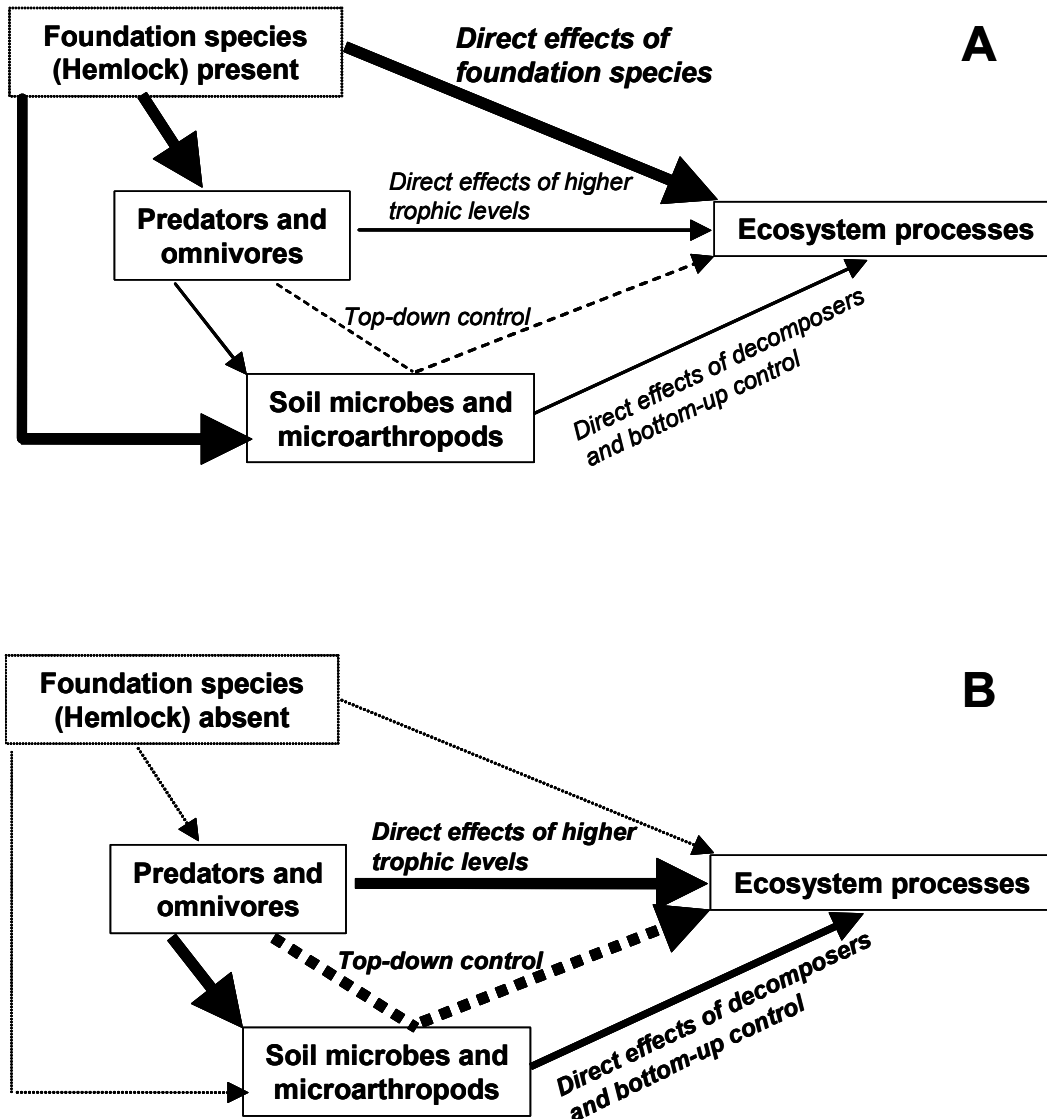
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762 **Figure 1.** Distribution of eastern hemlock (*Tsuga canadensis*) in eastern North America, based
763 on U.S. Forest Service Forest Inventory Analysis plots (gray shading) and spread of the hemlock
764 woolly adelgid (*Adelges tsugae*) since its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

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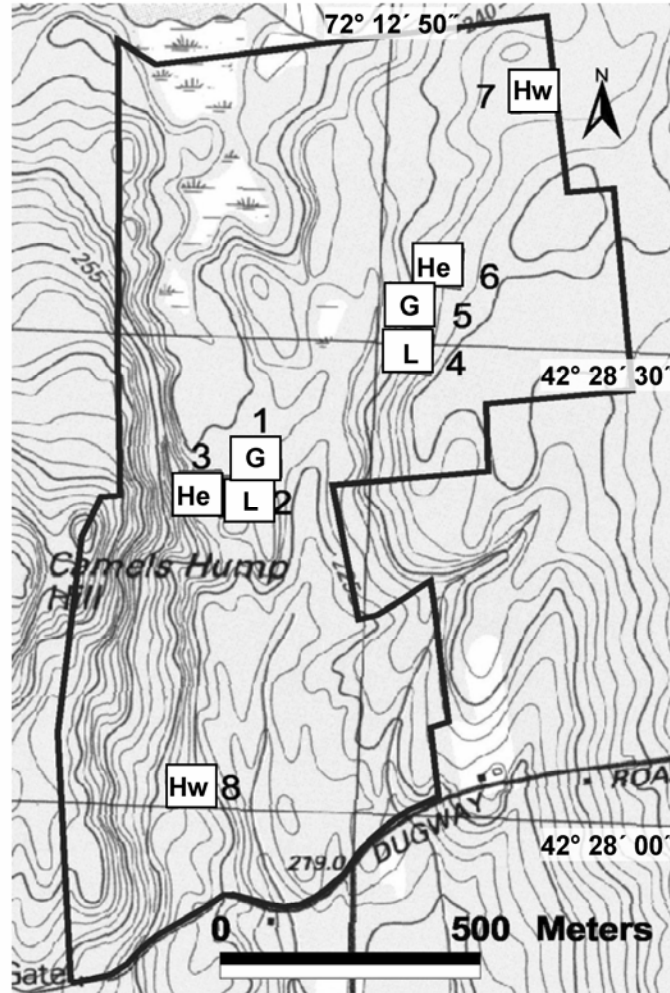
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769 **Figure 2.** Conceptual model for disentangling the direct effects on ecosystem processes of
 770 foundation species from indirect effects caused by changes in biological diversity associated with
 771 foundation species. **A** - in intact hemlock stands, this single foundation species is the dominant
 772 controller on both the composition and abundance of associated species and on core ecosystem
 773 processes (strength of influence indicated by width of arrows). **B** - when hemlock is lost, other
 774 taxa predominantly affect core ecosystem processes. For clarity, neither effects of hemlock on

775 microclimate nor other primary producers, including understory species, are shown. Hemlock
776 creates a uniquely cool and dark microclimate in which decomposition proceeds slowly and soil
777 organic matter accumulates relatively rapidly. As hemlock is replaced by hardwoods, there is less
778 of a role for particular species in mediating microclimate. These deciduous species are also
779 leafless for ~ 6 months in New England during which time microclimate is controlled more by
780 regional weather systems than by local biota. The understory is very sparse in the hemlock
781 forests of New England, but the denser understory vegetation of deciduous forests can alter rates
782 of nutrient fluxes prior to spring bud-burst (Zak *et al.* 1990).

783



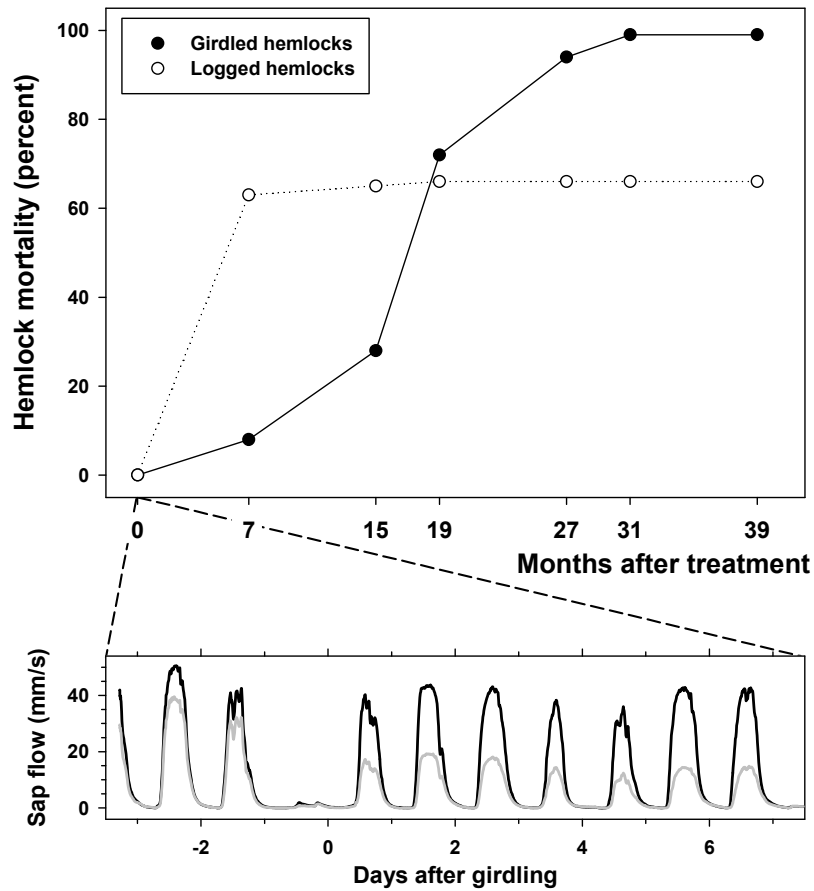
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785 **Figure 3.** Location of the blocks and treatments within the Simes Tract at the Harvard Forest.

786 This Before-After-Control-Impact replicated block design has two blocks (plots 1, 2, 3, and 8 are
 787 the “Valley” block, and plots 4-7 are the “Ridge” block). Each of the four treatments – Girdled
 788 (G), Logged (L), Hemlock control (He), and Hardwood control (Hw) – were applied in 90 × 90
 789 m plots within each block.

790

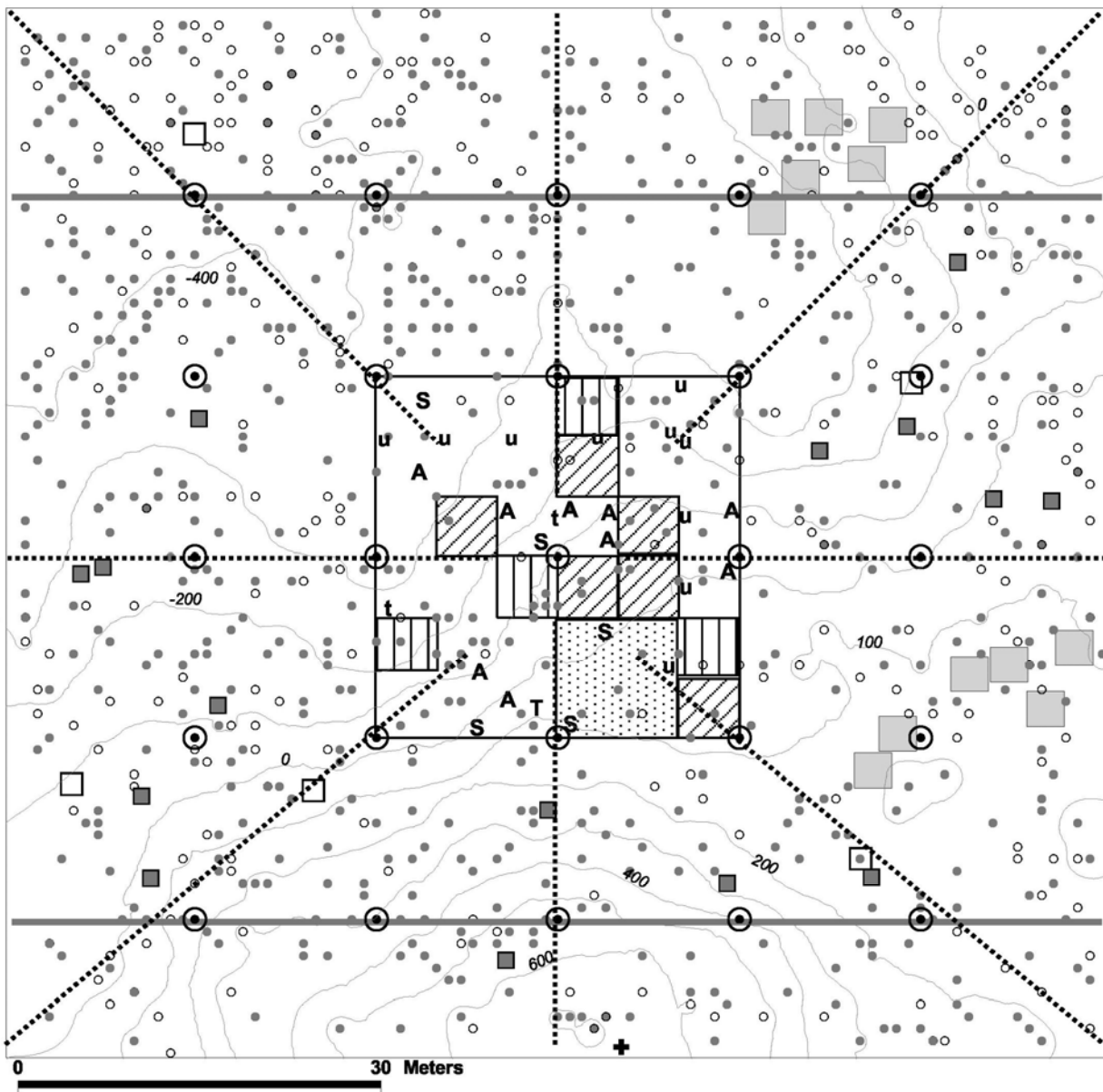
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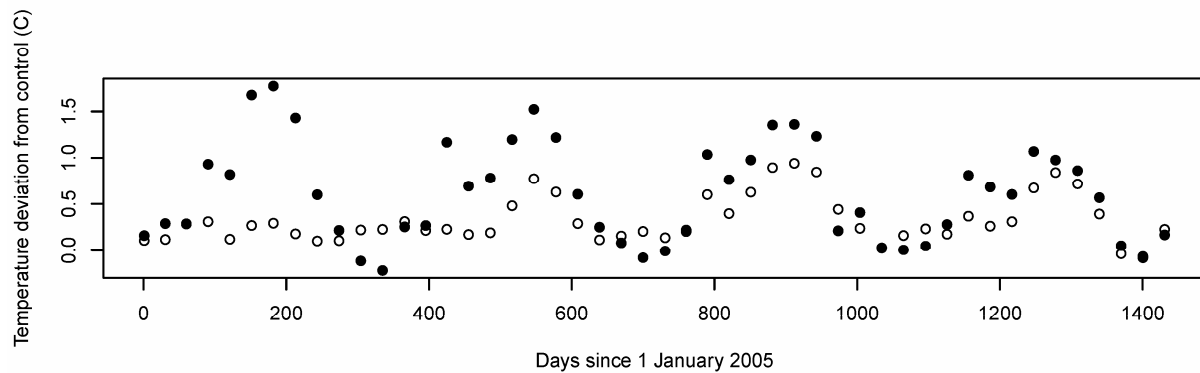
793 **Figure 4.** Mortality rate of eastern hemlock (*Tsuga canadensis*) in the core 30 × 30-m sampling
 794 areas in the girdled (●) and logged (○) plots following treatment application in April-May 2005.

795 **Inset** at bottom shows the average change in the rate of sap flow in three girdled (gray lines) and
 796 three reference (non-girdled) hemlock trees (black lines) before and after girdling (girdling
 797 occurred at Day = 0). A single 20-mm-long Granier sapflow probe was installed at 1.4 m above
 798 ground in each of the 6 trees. The day before trees were girdled, the site received 32mm of rain
 799 (data from Harvard Forest weather station: [http://harvardforest.fas.harvard.edu:8080/exist/
 800 xquery/data.xq?id=hf001](http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id=hf001)), and measured sap flow velocity was near zero.



801 **Figure 5.** Example of the layout and zoning of a plot in the Harvard Forest Hemlock Removal
 802 Experiment. Individual trees (gray circles: hemlock; white circles: other tree species) were
 803 mapped together with elevations in cm relative to a 0-cm baseline near the plot center (gray
 804 contours). The center 30 × 30-m area is used for intensive measurements and different research
 805 groups are assigned random areas (boxes: vertical striped – nitrogen mineralization; diagonal

806 striped – soil respiration; dotted – ant species diversity and abundance) for their specific studies.
807 Also illustrated are locations of litter baskets (white squares) and litter samples for arthropods
808 (**A**), understory vegetation quadrats (**u**), seed bank samples (**S**), throughfall samples (**t**),
809 thermocouple sensors for air and soil temperatures (**T**), fixed points for hemispherical
810 photographs (dotted circles) and panoramic photographs (**+**), and transects for sampling
811 salamanders (thick gray lines) and coarse woody debris (thick dotted lines). Locations in the
812 buffer area of two of the subplot experiments are illustrated with large light gray squares (ant
813 removals, additions, controls) and small dark gray squares (litter arthropods).



814

815 **Figure 6.** Temperature deviations in the logged (black circles) and girdled (white circles) plots
816 relative to the hemlock control plots. The summer after logging, logged plots were $> 1.5^{\circ}\text{C}$
817 warmer than control plots, but girdled plots were not different from control plots. As trees died in
818 the girdled plots over the next two summers, these plots warmed up relative to the control plots.
819 Over the same time interval in the logged plots, hardwood stumps sprouted and seedlings
820 emerged. This increase in understory cover reduced the difference in air temperature between
821 logged and control plots.

822