



Foundation species loss affects vegetation structure more than ecosystem function in a northeastern USA forest

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23 increased immediately after logging and two years after girdling, due to increased light and soil
24 temperatures and nutrient pulses from leaf-fall and reduced uptake following tree death. The
25 results from this study illuminate ecological processes underlying patterns observed
26 consistently in region-wide studies of adelgid-infested hemlock stands. Mechanisms of *T.*
27 *canadensis* loss determine rates, magnitudes, and trajectories of ecological changes in hemlock
28 forests. Logging causes abrupt, large changes in vegetation structure whereas girdling (and by
29 inference, *A. tsugae*) causes sustained, smaller changes. Ecosystem processes depend more on
30 vegetation cover *per se* than on species composition. We conclude that the loss of this late-
31 successional foundation species will have long-lasting impacts on forest structure but more
32 subtle impacts on ecosystem function.

33

34 **Introduction**

35 Changes in the distribution and abundance of canopy trees have system-wide impacts on
36 ecological processes in forests (Lovett *et al.* 2006; Wardle *et al.* 2011; Hicke *et al.* 2012).
37 Changes in species composition and associated ecological impacts also lead to changes in the
38 values – including economic, utilitarian, and aesthetic – that we place on forest ecosystems
39 (*e.g.*, Aukema *et al.* 2011; Cardinale *et al.* 2012). The vast majority of studies of the impacts of
40 species loss on ecological processes in forests and other ecosystems have examined how
41 changes in the absolute number (or percent) of species lost affects a wide range of ecosystem
42 services (recently reviewed by Wardle *et al.* 2011; Cardinale *et al.* 2012; Hooper *et al.* 2012;
43 Naeem, Duffy & Zavaleta 2012). However, species are not lost from ecosystems at random
44 (*e.g.*, Bunker *et al.* 2005) and it remains an open question whether particular species with
45 particular characteristics will disproportionately change how ecosystems function (Bunker *et al.*
46 2005; Suding *et al.* 2008; B. Baiser & A. M. Ellison unpublished data).

47 Foundation species (*sensu* Ellison *et al.* 2005a) define and structure many terrestrial,
48 aquatic, and marine ecosystems, yet because foundation species often are abundant and
49 widespread, their role in structuring ecosystems is often underappreciated or taken for
50 granted, and they are rarely of explicit conservation interest (Gaston 2010). Ellison *et al.*
51 (2005a) suggested that the loss of foundation species can cause strong, widespread, and long-
52 lasting changes to forest ecosystems because forest-wide biological diversity and ecosystem
53 processes such as primary productivity and fluxes of energy and nutrients are hypothesized to
54 depend more on foundation species than on any other species in the system.

55 Examples where loss of dominant, and possibly foundational, tree species have had
56 large impacts on forest ecology include: regional loss of associated fauna as white pines (*Pinus*
57 subgenus *strobus*) in western North America succumb to white pine blister rust (*Cronartium*
58 *ribicola* A. Dietr.); changes in canopy structure as a result of fire suppression, irruptions of
59 mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and climatic change (Kendall &
60 Keane 2001; Tomback & Achuff 2010); shifts in understory composition, recruitment, and
61 regeneration dynamics following loss of American beech (*Fagus grandifolia* Ehrh.), American
62 chestnut (*Castanea dentata* (Marsh.) Borkh.) or American elm (*Ulmus americana* L.) due to
63 beech-bark disease (*Nectria coccinea* (Pers. ex. Fr.) Fries var. *faginata* Lohman, Watson and
64 Ayers), chestnut blight (*Cryphonectria parasitica* (Murrill) Barr.), and Dutch elm disease
65 (*Ceratocystis ulmi* (Buism.) C. Moreau), respectively (McBride 1973; Houston 1975; Barnes
66 1976; Huenneke 1983; Twery & Patterson 1984; Myers, Walck & Blum 2004; Lovett *et al.* 2006);
67 changes in faunal (Wills 1993) and macrofungal diversity (Anderson *et al.* 2010), and functional
68 diversity of soil bacteria involved in carbon and nitrogen cycling (Cai *et al.* 2010) following loss
69 of *Eucalyptus* to *Phytophthora* outbreaks in Australia; bottom-up control by *Populus* spp. of
70 associated herbivorous arthropod populations, which in turn mediates how insectivorous birds
71 influence future tree growth in the southwestern United States (Bridgeland *et al.* 2010); and
72 the dependence of benthic biological diversity, productivity, and nutrient cycling on a handful
73 of species in mangrove forests (*e.g.*, Nagelkerken *et al.* 2008; Barbier *et al.* 2011).

74 *Tsuga canadensis* (L.) Carr. (eastern hemlock), an hypothesized foundation tree species
75 (Ellison *et al.* 2005a), covers $\approx 10\,000\text{ km}^2$ and comprises $\approx 2 \times 10^8\text{ m}^3$ of harvestable and
76 merchantable volume from the southern Appalachian Mountains north into southern Canada

77 and west across the upper Midwestern states in North America (Fig. 1; Smith *et al.* 2009). Like
78 other putative foundation tree species, *T. canadensis* can account locally for > 50% of the total
79 basal area, and its ecological traits create unique terrestrial and aquatic habitats. For example,
80 the deep shade cast by its dense evergreen foliage limits establishment of most understory
81 species (Rogers 1980; D'Amato, Orwig & Foster 2009). Its refractory leaf litter and the cool
82 temperatures at the soil surface beneath dark hemlock canopies result in low rates of
83 decomposition and nutrient cycling, rapid accumulation of organic matter (Aber & Melillo 1991;
84 Jenkins, Aber & Canham 1999), and nutrient-poor soils. The combination of nearly year-round
85 low photosynthetic and evapotranspiration rates of *T. canadensis* (Hadley *et al.* 2008) stabilizes
86 stream base-flows and decreases daily variation in stream temperatures (Ford & Vose 2007;
87 Nuckolls *et al.* 2009). The microhabitat created by eastern hemlock supports unique
88 assemblages of birds, arthropods, salamanders, and fish (Snyder *et al.* 2002; Tingley *et al.* 2002;
89 Ellison *et al.* 2005b; Dilling *et al.* 2007; Mathewson 2009; Rohr, Mahan & Kim 2009; Mallis &
90 Rieske, 2011; Sackett *et al.* 2011).

91 Despite its widespread distribution and high abundance, both locally and regionally, *T.*
92 *canadensis* is rapidly disappearing across an increasing extent of its range. The hemlock woolly
93 adelgid (*Adelges tsugae* Annand), an invasive insect from Japan that in North America feeds
94 exclusively on eastern hemlock and its southeastern (USA) endemic congener, Carolina hemlock
95 (*T. caroliniana* Engelmann), is moving rapidly both southward and northward (Fitzpatrick *et al.*
96 2012), killing >90% of hemlocks it encounters (Orwig *et al.* 2002; Eschtruth *et al.* 2006; Knoepp
97 *et al.* 2011). Hemlock has little resistance to the adelgid (Ingwell & Preisser 2011) and as yet has
98 shown no recovery from chronic infestations (McClure 1995; Orwig *et al.* 2012). In the absence

99 of successful biological control programs (Onken & Reardon 2011) and economically or
100 logistically feasible chemical control options (Ward *et al.* 2004; Cowles 2009), pre-emptive
101 cutting or salvage logging of hemlock has been a common management response to declining
102 and dead hemlock stands affected by the adelgid (Kizlinski *et al.* 2002; Orwig, Foster & Mausel
103 2002; Ward *et al.* 2004; Foster & Orwig 2006).

104 The combination of adelgid-induced morbidity and mortality, and pre-emptive salvage
105 logging of *T. canadensis* is radically changing the structure of eastern USA forests. Region-wide,
106 forest productivity and carbon sequestration are expected to decline by as much as 8-12%, but
107 establishment of mid-successional hardwoods (e.g., *Betula* and *Acer* species) is forecast to
108 result in forest carbon uptake recovering to, or even exceeding pre-adelgid conditions only
109 after 50 years or more (Albani *et al.* 2010; Knoepp *et al.* 2011). These model forecasts of the
110 impact of the adelgid have been made at coarse-grained scales (2.5° grid), but local impacts
111 may fall short of or dramatically exceed regional averages (P. C. Lemos & A. C. Finzi,
112 unpublished data). Fifteen years of observational studies of marked plots have illustrated high
113 variance in forest dynamics (e.g., Orwig, Foster & Mausel 2002; Orwig *et al.* 2008, 2012),
114 portions of which may be attributable to differences in climate, short- versus long-term impacts
115 of logging, and/or fine-scale effects of the adelgid itself (Stadler *et al.* 2005; Stadler, Müller &
116 Orwig 2006).

117 Only experimental studies can distinguish reliably among differences due to *in situ*
118 forest disintegration or logging, and so in 2003 we established a multi-hectare, long-term
119 manipulative study – the Harvard Forest Hemlock Removal Experiment (HF-HeRE; Ellison *et al.*
120 2010) – to study the various forest responses to the loss of hemlock. This ongoing experiment

121 compares and contrasts the rates, magnitudes, and trajectories of changes in hemlock-
122 dominated stands to two mechanisms of foundation species loss: (1) death in place of eastern
123 hemlock by girdling, which mimics tree disintegration that follows infestation by the hemlock
124 woolly adelgid (Yorks, Leopold & Raynal 2003); or (2) loss and removal of hemlock following
125 commercial logging (Brooks 2001). Patterns, processes, and dynamics studied include: forest
126 vegetation structure, standing and downed dead wood, and three measures of ecosystem
127 function: litterfall (a substantial component of net primary productivity; *e.g.*, Zheng, Prince &
128 Hame 2004), soil carbon flux, and soil nitrogen dynamics.

129 In this paper, we report two years of pre-treatment data and the first five years of
130 changes in vegetation structure and ecosystem functions following our experimental
131 manipulations but prior to the infestation of our experimental plots by the adelgid. In
132 particular, we examine and test three predictions that, relative to both hemlock and hardwood
133 controls:

134 (1) Vegetation structure – species richness and cover of understory herbs, and density and
135 cover of tree seedlings and saplings – increases slowly following girdling but more
136 rapidly following hemlock removal and soil scarification from logging;

137 (2) Volume of standing dead wood and snags is highest in girdled plots, but downed coarse
138 woody debris is higher in logged plots;

139 (3) Core ecosystem functions – litterfall and soil carbon fluxes decline while rates of soil
140 nitrogen (as nitrate and ammonium) mineralization and soil nitrogen availability
141 increase then decline slowly in girdled plots but rapidly in logged plots.

142 Other papers have described changes in the microenvironment (Lustenhouwer, Nicoll & Ellison
143 2012), species composition of the seed bank and understory vegetation (Sullivan & Ellison 2006;
144 Farnsworth, Barker Plotkin & Ellison 2012), diversity of ground-dwelling arthropods (Sackett *et*
145 *al.* 2011), and nitrogen leaching (Templer & McCann 2010) in the first decade following the
146 canopy manipulations in HF-HeRE. In total, our results lead us to hypothesize that vegetation
147 structure and ecosystem functions in the girdled and logged plots will converge through time,
148 and, at least on decadal scales, come to resemble the attributes of the hardwood control plots.

149 We note that we purposely sited HF-HeRE north of the northern limit (in 2003) of the
150 hemlock woolly adelgid so that we could first identify different effects on forest structure and
151 function caused by two different kinds of physical loss of *T. canadensis*. This experiment
152 complements a suite of studies in which we have examined landscape-level spread of the
153 adelgid (Orwig, Foster & Mauseel 2002; Fitzpatrick *et al.* 2012; Orwig *et al.* 2012), compositional
154 and structural changes in forest vegetation (Foster & Orwig 1998), and ecosystem functions in
155 forests infested by the adelgid (Cobb, Orwig & Currie 2006; Orwig *et al.* 2008) or that have been
156 salvage logged (Kizlinski *et al.* 2002, D. A. Orwig *et al.* unpublished data). Subsequent data
157 collected after the adelgid colonizes HF-HeRE (which occurred in 2010), will be used to further
158 distinguish effects on eastern North American forests of physical disintegration of *T. canadensis*
159 from additive, interactive, and/or nonlinear effects of the insect itself (*e.g.*, Stadler *et al.* 2005;
160 Stadler, Müller & Orwig 2006). The unique experimental design – with measurements made
161 pre-treatment; post-treatment but pre-adelgid; and post-treatment, post-adelgid –
162 distinguishes HF-HeRE from other studies, both observational and experimental, that have

163 examined the effects of foundation species loss but that cannot separate effects of physical loss
164 alone from those of the agent of loss itself.

165

166 **Materials and Methods**

167 ***Site Description***

168 HF-HeRE is located within the 121-ha Simes Tract (42.47° – 42.48° N, 72.22° – 72.21° W;
169 elevation 215 – 300 m a.s.l.) at the Harvard Forest Long Term Ecological Research Site in
170 Petersham, Massachusetts, USA (Ellison *et al.* 2010; Fig. 1). As in most New England forests, the
171 Simes Tract as was cleared for agriculture in the early and mid-1800s. Many of the trees that
172 had regenerated following agricultural abandonment in the mid- to late-1800s were blown
173 down in the 1938 Great Hurricane, and analysis of tree-cores from the tract show that the trees
174 in our experimental plots average 55 – 80 years old (Bettmann-Kerson 2007; A. M. Ellison, D. A.
175 Orwig & A. A. Barker Plotkin unpublished data), The soils are predominantly coarse-loamy,
176 mixed, active, mesic Typic Dystrudepts in the Charlton Series that are derived from glacial till
177 (USDA n.d.). Across the eight HF-HeRE study plots, the soil pH ranges from 3.0 – 3.4 in the
178 organic layer and from 3.5 – 4.0 in the mineral layer, and the soil C:N ratios range from 26 – 33.
179 Much of the central portion of the tract is poorly drained or swampy; elevated areas are better
180 drained. *Tsuga canadensis* and *Acer rubrum* L. (red maple) dominate the poorly drained soils,
181 whereas *T. canadensis*, along with *Quercus rubra* L. and *Q. alba* L. (red and white oaks), and
182 *Pinus strobus* L. (white pine) predominate on hills and slopes. *Betula lenta* L. (black birch), *Acer*
183 *saccharum* Marsh. (sugar maple), and other hardwoods grow at low frequency and density
184 throughout the tract (Ellison *et al.* 2010).

185

186 ***Experimental design and treatments***

187 The complete design of HF-HeRE is described by Ellison *et al.* (2010); only salient details are
188 repeated here. The eight 90 × 90 m (0.81 ha) plots comprising this experiment are grouped in
189 two blocks (Fig. 1), each consisting of three plots initially dominated by *T. canadensis* and one
190 plot of mixed hardwoods (Table 1). The “valley” block (plots 1–3 and 8) is in undulating terrain
191 bordered on its northern edge by a *Sphagnum*-dominated wetland (permission to work in this
192 wetland and in the adjacent bordering vegetation [“buffer zone”] was provided by the
193 Petersham, Massachusetts, Conservation Commission). The “ridge” block (plots 4–7) is on a
194 forested ridge. Plots were identified in 2003 and sampled for two growing seasons
195 (spring/summer in each of 2003 and 2004) prior to applying canopy manipulation treatments –
196 girdling, or harvesting of standing *T. canadensis* along with cutting of merchantable hardwoods
197 and *P. strobus* – to one plot in each block.

198 In the girdled treatment plots, the bark and cambium of all individual *T. canadensis*
199 trees, saplings, and seedlings were cut through using chain saws or hand knives over a 2-day
200 period in May 2005. Girdled trees died over a 2-year period but were left standing in place to
201 simulate the physical decline and mortality of hemlock resulting from infestation by the
202 hemlock woolly adelgid (Ellison *et al.* 2010). No other species were girdled and there was no
203 site disturbance other than walking between trees.

204 In the logged treatment plots, all *T. canadensis* trees > 20 cm diameter at breast height
205 (DBH, measured 1.3 m above ground) and 50% of the commercially valuable *Q. rubra* and *P.*
206 *strobus* were felled using a chainsaw and removed using a skidder between February and April

207 2005, when the ground was frozen. Because this logging operation mimicked the effects of an
208 intensive commercial hemlock salvage operation, trees of small size, poor quality, or little
209 economic value, such as *A. rubrum* and *B. lenta* were also removed to facilitate log removal or
210 to improve future stand quality, but some good-quality *Q. rubra* and *P. strobus* were retained.
211 We recognize that the removal of tree species other than *T. canadensis* can have some impacts
212 on changes forest dynamics in the otherwise hemlock-dominated stands. However, in the
213 logged plots, *T. canadensis* accounted initially for > 50% of the basal area, but made up > 80%
214 of both the number of felled trees and their basal area (Ellison et al. 2010). Thus, the effects of
215 hemlock loss were likely to dominate observed responses of the forest to this canopy
216 manipulation.

217 Two control plots in each block were not manipulated. In each block, one of each of
218 these control plots was dominated by hemlock, the other by mid-successional hardwoods of
219 the same general age of the remaining forest (55-80 years). The latter control plots represents
220 the most likely future forest conditions after hemlock has disappeared from the landscape
221 (Orwig & Foster 1998; Ellison *et al.* 2010).

222

223 **Measurements**

224 *Vegetation structure*

225 We measured species richness and cover of understory herbs, and density and cover of tree
226 seedlings and saplings to determine how these attributes of vegetation structure varied among
227 the two canopy manipulation treatments and the two different controls (Prediction 1). In 2003
228 (prior to canopy manipulations), we established two transects running through the central 30m

229 × 30m of each plot to quantify understory richness, cover, and density. Five 1-m² subplots were
230 spaced evenly along each transect and have been sampled annually since 2003. In each subplot,
231 tree seedlings (<1.3m tall) were counted and percent cover of tree seedlings, herbs, shrubs,
232 ferns and grasses was estimated to the nearest one percent. Grasses and sedges were
233 identified only to genus as most lacked flowers or fruits necessary for accurate species-level
234 identification. A species list has been compiled annually for the central 30 × 30-m core area of
235 each plot. Nomenclature follows Haines (2011). The number of sapling-sized trees (>1.3m tall
236 but <5cm DBH) was tallied by species in the 30 × 30-m core area of each plot in 2005, 2007 and
237 2009.

238 In 2003-2004, all trees ≥5 cm DBH in each plot were tagged with aluminum tags,
239 identified, measured (DBH) and mapped (x, y, z coordinates relative to a plot corner) using a
240 compass, auto-level, and stadia rods. Initial basal area was higher in the hemlock plots (45.6 –
241 53 m² · ha⁻¹) than in the hardwood control plots (29.7 – 35.6 m² · ha⁻¹) and basal area was
242 slightly higher in the ridge block than in the valley block (species composition data reported in
243 Table 1 of Ellison *et al.* 2010). Initial stem density ranged from 678 stems ha⁻¹ in the ridge
244 hemlock control plot to 1354 stems ha⁻¹ in the valley girdled plot. *Tsuga canadensis* comprised
245 50 – 69% of initial basal area and 55 – 70% of initial stem density in the six plots initially
246 dominated by this species (hemlock control, logged, and girdled plots). In the hardwood control
247 plots, *T. canadensis* comprised <10% of the initial basal area and 10-11% of the initial stem
248 density. Other species that comprised >10% initial basal area in any plot included *A. rubrum*,
249 and *A. saccharum* (hardwood valley plot only), *B. lenta*, *Q. rubra*, and *P. strobus*. Decline and
250 death of trees in the girdled plots was tracked following treatments; most *T. canadensis* had

251 died within 24 months (Ellison *et al.* 2010). In 2009, each tree was assessed for survival and
252 diameter growth (for living stems).

253

254 *Standing and downed dead wood*

255 Prediction 2 addresses changes in volume of coarse woody debris (CWD) – standing dead trees
256 (snags), stumps, and volume of fallen boles and branches >7.5cm in diameter – as a function of
257 canopy manipulation treatment. These variables have been surveyed biennially since 2005
258 (post-treatment only). In summer 2005, just after the girdling and logging were completed,
259 eight transects were established in each plot beginning from each cardinal and ordinal plot
260 corner/edge and extending 35-50 m towards the plot center. To measure standing dead wood,
261 snags and stumps were sampled along a 4-m wide strip plot that straddles the line transect.
262 Species (or species group) were recorded for each individual stump or snag; its lower diameter
263 was measured, and its top diameter and height either were measured directly or estimated if
264 the snag height exceeded the length of a stadia rod. From these measurements, snag volume
265 was calculated as the frustum of a cone (Harmon & Sexton 1996). Volume of downed wood was
266 estimated using the line-intercept method (Van Wagner 1968). The diameter, decay class (Rice
267 *et al.* 2004), and species (or species group) of each piece that intersected the line was recorded.
268

269 *Ecosystem function*

270 Prediction 3 is that primary productivity, soil carbon flux, and soil nutrient cycling and
271 availability should decline slowly in the girdled plots and rapidly in the logged plots. We used
272 litterfall as an index of annual aboveground productivity (e.g., Zheng, Prince & Hame 2004). Five

273 litterfall baskets (collection area 0.11 m²) were placed at random coordinates throughout each
274 90 × 90-m plot. Baskets were placed in the field at the beginning of September 2005 (after
275 canopy manipulations had been applied). Samples were collected quarterly: in early April, mid-
276 June, mid-September, and early December every year. Leaf litter was sorted to major species
277 groups (*Tsuga*, *Pinus*, *Quercus*, *Betula*, *Acer*, other deciduous trees), whereas twigs, bark, and
278 reproductive parts were pooled into one category. After sorting, samples were oven-dried at 70
279 °C for 48 hours prior to weighing. Annual litterfall is reported as the total of the June,
280 September and December collections, plus the subsequent year's April collection.

281 Measurements of soil carbon (C) flux ("soil respiration") were made using a vented,
282 flow-through, non-steady-state system (Livingston & Hutchinson 1995) at six randomly chosen
283 locations in the 30 × 30-m core area of each of the six hemlock (control, girdled, logged) plots
284 (2003 – 2009) and at two randomly chosen locations in the two hardwood control plots (2006 –
285 2007). At each location, soil respiration collars, each 25 cm in diameter (0.05 m² surface area)
286 and made from thin-walled polyvinylchloride (PVC) tubing cut into 10 cm lengths, were inserted
287 ≈5 cm into the ground. Soil respiration was measured manually every 2 weeks during the
288 growing season between 09:00 and 15:00 hours using a Li-Cor 6252 portable Infrared Gas
289 Analyzer (IRGA) (Li-Cor Inc., Lincoln, Nebraska, USA) mounted on a backpack frame. The IRGA
290 was connected to a vented white acrylonitrile-butadiene-styrene (ABS) chamber top (10 cm in
291 height) that was then placed over the soil respiration collar. A pump circulated the air at 0.5 L ·
292 min⁻¹ from the chamber top through the IRGA and back to the chamber top. The chamber top
293 was left on the collar for 5 min, and the change in CO₂ concentration within the chamber was
294 recorded using a Hewlett-Packard HP 200LX palmtop computer (Hewlett-Packard, Palo Alto,

295 California, USA). The calibration of the IRGA was checked each day that measurements were
296 made using both zero $\text{mL} \cdot \text{L}^{-1} \text{CO}_2$ and $594 \text{ mL} \cdot \text{L}^{-1} \text{CO}_2$ certified standards. A linear regression of
297 concentration of CO_2 versus time was used to determine the soil respiration rate, which was
298 then corrected for local atmospheric pressure and chamber air temperature. The response
299 variable used in subsequent analyses of treatment effects was soil respiration for the entire
300 sampling period (Day of Year [DOY] 191- 273) each year; this value was estimated by linearly
301 interpolating soil respiration measurements between sampling days for each collar and then
302 summing (integrating) all values over the 82-day sampling period.

303 Total soil respiration is the sum of two belowground components: heterotrophic
304 (microbial and microfaunal respiration) and autotrophic (root respiration). Measurements of
305 soil respiration in the control plots represent the sum of these belowground processes. Thus, to
306 a first approximation, differences in soil respiration between control and either logged or
307 girdled treatments reflect the contribution of eastern hemlock to autotrophic respiration.
308 Decreased soil respiration due to treatment effects were calculated by taking the pre-treatment
309 soil respiration over the sampling season and subtracting from it the post-treatment seasonal
310 soil respiration. These decreases represent a conservative estimate of autotrophic soil
311 respiration in treated plots. Potential limitations to this method include the loss of root
312 biomass, which could reduce heterotrophic respiration of soil organic matter via lack of
313 priming, and that the newly severed roots may temporarily increase carbon available for
314 heterotrophic respiration.

315 Because the majority of live tree roots in each plot were killed following logging or
316 girdling of hemlock, and because the percent cover of other vegetation in these treatments at

317 the beginning of this study was very low (< 2%), seasonal sums of soil respiration in these
318 canopy manipulation treatments can be used as estimates of heterotrophic soil respiration
319 (Hanson *et al.* 2000; Levy-Varon, Schuster & Griffin 2012).

320 Nitrogen (N) mineralization measurements were begun in August 2003, two growing
321 seasons prior to canopy manipulations, using a modified core method (Hart *et al.* 1994;
322 Robertson *et al.* 1999). In the central 30 × 30-m area of each canopy manipulation plot, closed-
323 topped cores were installed within four, 5 × 5-m, randomly located subplots each year at 7-
324 week intervals during the growing season (May – October), and for a 23-week overwinter
325 (October/November – April) incubation. At the beginning of each sampling period, soil was
326 extracted with sharpened PVC cores (25-cm long) and immediately separated into mineral and
327 organic layers. A second core was incubated in the field for 42 – 50 days and then removed and
328 separated by horizon. The bottom 2 cm of each core was removed to prevent root invasion
329 from below in incubated cores, and to standardize sample volume among the cores.

330 Soil samples were returned to the laboratory on ice and processed the next day. Organic
331 and mineral soils were passed through a 5.0-mm mesh screen, weighed for total mass, and
332 subsampled for gravimetric moisture and inorganic N. To determine soil NH₄-N and NO₃-N
333 concentration, ~10 g of organic and mineral soil were placed into 100 ml of 1M KCl for 48 hr
334 (Aber *et al.* 1993). Soil extracts were filtered through a coarse pore filter (0.45 – 0.6 μm) and
335 inorganic N concentrations were determined colorimetrically with a Lachat 8500 flow-injection
336 autoanalyzer (Lachat Instruments, Inc., Milwaukee, Wisconsin, USA), using the salicylate (Lachat
337 Instruments, Inc., 1990a) and cadmium reduction methods (Lachat Instruments, Inc., 1990b) for
338 NH₄-N and NO₃-N, respectively. Net N mineralization was calculated as the difference in

339 concentration of inorganic N ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) in incubated cores minus that in initial samples.

340 An additional assessment of forest floor N availability and mobility was determined at

341 each soil subplot using mixed-bed cation + anion resin bags (Binkley & Matson 1983).

342 Approximately 10 grams of resin was placed in nylon mesh bags and pretreated with 2M KCl

343 before deployment for 6-month intervals (growing season and overwinter). Resins were

344 deployed at the forest floor – mineral soil interface within 5 cm of where the N mineralization

345 incubations were located. Resins were returned to the laboratory on ice, dried at 105 °C for 24

346 h, and extracted in 2M KCl. Inorganic N was determined by the methods described above for

347 soil N extracts.

348

349 ***Statistical analysis and data availability***

350 The experimental design is a one-way blocked analysis of covariance (ANCOVA) (Ellison *et al.*

351 2010; Gotelli & Ellison 2012), and analyses reported here were executed using the lme function

352 in the nlme package in R version 2.9.2 (R Development Core Team 2009; Pinheiro *et al.* 2012).

353 In this design, the four canopy manipulations (hemlock control, hemlock girdled, logged,

354 hardwood control) were treated as “fixed” factors, the two blocks were treated as “random”

355 factors, and time entered the model as a covariate. Measures of vegetation structure and

356 ecosystem function parameters were log-transformed as needed to normalize data and

357 equalize variances; data are plotted back-transformed (Gotelli & Ellison 2012). Comparisons

358 among treatments were done using *a priori* contrasts. Although two blocks is the minimum

359 required to allow for estimates of variance within treatments, this small number of blocks

360 provided relatively low statistical power to detect true differences among treatments (i.e., the

361 probability of a Type II error – falsely accepting the null hypothesis – is high). Further, the
362 absence of replication of treatments within blocks precluded estimation of a block × treatment
363 interaction. Such trade-offs are inevitable in hectare-scale, decades-long experiments, however.

364 All data presented in this paper are publicly available through the Harvard Forest Data
365 Archive (<http://harvardforest.fas.harvard.edu/data-archive>), in a suite of datasets: HF106
366 (understory vegetation), HF126 (overstory vegetation), HF161 (litterfall), HF125 (coarse woody
367 debris), HF119 and HF130 (soil respiration), and HF179 (nitrogen pools and dynamics).

368

369 **Results**

370 ***Changes in vegetation structure***

371 *Overstory trees*

372 Following treatments, the girdled and logged treatments lost 67 – 72% of overstory basal area
373 and 61 – 71% of overstory stem density (Table 1). Only *T. canadensis* was affected in the girdled
374 treatment, but girdled individuals ranged from seedlings to canopy trees and they died within 2
375 years (data in Fig. 4 of Ellison *et al.* 2010). In contrast, basal area was immediately lost in the
376 logged treatment and included large-diameter *T. canadensis*, some large *Q. rubra* and *P.*
377 *strobus*, and many smaller *A. rubrum* and *B. lenta* (Table 1). By 2009, four years after
378 manipulations, growth of trees in the hemlock and hardwood control treatments resulted in
379 per-plot gains in basal area of 4% – 6%; concomitant background mortality led to a per-plot loss
380 of 6 – 12% of stems.

381

382 *Understory vegetation*

383 Understory species richness remained relatively constant in both hemlock control and
384 hardwood treatments over the course of the study, with hardwood treatment plots having the
385 highest herb and shrub richness (Fig. 2a, Table 2). Girdled treatment plots had < 10 understory
386 species prior to treatment. Species richness in this treatment increased gradually, resulting in a
387 doubling by 2009 (Fig. 2a, Table 2). Two nonnative species were first identified in the girdled
388 treatment at low abundance by 2007: *Berberis thunbergii* DC. (Japanese barberry) in the valley
389 girdled plot and *Celastrus orbiculatus* Thunb. (oriental bittersweet) in the ridge girdled plot. The
390 plots in the logged treatment similarly began with low species richness. In contrast to the
391 girdled treatment, understory species richness increased following logging, but then remained
392 approximately constant for the remainder of the study period (Fig. 2a, Table 2). No nonnative
393 species had recruited into the logged treatment plots by 2009.

394 Understory vegetation cover remained between 1 and 2% in the hemlock control and
395 from 16 to 32% in the hardwood control treatment throughout the sampling period (Fig. 2b,
396 Table 2). Percent cover of understory vegetation increased slowly in the girdled treatment and
397 exceeded cover in the hemlock control treatment by 2009. Understory cover increased more
398 rapidly in the logged treatment, especially after 2007 (Fig. 2b), significantly exceeding cover in
399 both the hemlock control and the girdled treatments, and equaling levels seen in the hardwood
400 control by 2009 (Fig. 2b). The main species driving the increase in understory cover were early
401 successional opportunists and species with long-lived seed banks, including *Aralia hispida* Vent.
402 (bristly sarsaparilla), *Erechtites hieracifolia* (L.) Raf. ex DC. (pilewort), *Rubus* spp. (raspberries and

403 blackberries), and to a lesser extent, *Lysimachia quadrifolia* L. (whorled loosestrife) and
404 *Dennstaedtia punctilobula* Michx. (T. Moore) (hay-scented fern).

405

406 *Tree regeneration*

407 Tree seedling density was low in the hemlock control and logged treatments both before and
408 after canopy manipulations (Fig. 2c); it was nearly 10-fold higher in the hardwood control and
409 this significant difference (Table 2) persisted from 2003 – 2009. Tree seedlings, especially of *B.*
410 *lenta* and *A. rubrum* increased significantly – to $3.5 \times 10^5 \cdot \text{ha}^{-1}$ – in the girdled treatment
411 through time. Cover of tree seedlings was consistently lowest in hemlock control (< 1% cover)
412 and hardwood control (\approx 5% cover) treatments, but increased slowly and significantly in both
413 girdled (to > 40% cover) and logged (to 15% cover) treatments (Fig. 2d; Table 2).

414 Prior to the manipulations, there were few saplings in any of the plots, and despite
415 some growth, we observed neither significant changes in sapling density through time nor
416 differences in sapling density among treatments (Fig. 2e). The few saplings in the hemlock
417 control treatment were eastern hemlock. Likewise, sapling density was low in the hardwood
418 control treatment throughout the study period; *A. rubrum* and *A. saccharum* were the most
419 common sapling species in the valley hardwood plot, whereas *A. rubrum* and *P. strobus* were
420 more common in the ridge hardwood plot. The girdling treatment removed all *T. canadensis*
421 saplings, and even by 2009, most tree regeneration in the girdled plots was still in the seedling
422 (< 1.3-m tall) size class and no stems had grown into the sapling size class until 2009. Most
423 saplings in the logged treatment were killed during logging, but stump sprouts of *A. rubrum*
424 were abundant by 2007 and a few *B. lenta* had grown from seedlings into saplings on the ridge.

425 By 2009, dense stands (3000 – 6000 saplings ha⁻¹) of *B. lenta* saplings covered the logged
426 treatment plots.

427

428 ***Standing and downed dead wood***

429 Volume of stumps and snags was very low in the hemlock and hardwood controls and in the
430 logged treatment plots (Fig. 2f). Volume of stumps and snags in the girdled treatment was
431 similar to both controls in 2003 but then rose significantly (Table 2), by two orders of
432 magnitude, as the girdled trees died (Fig. 2f). Volume of downed CWD in the logged treatment
433 was 2 – 3× greater than in any other treatment (Fig. 2g, Table 2). This trend persisted through
434 the five post-treatment years, although CWD volume declined from 2005 – 2009 as the wood
435 decayed.

436

437 ***Ecosystem function***

438 *Litterfall*

439 Litterfall in the hemlock and hardwood controls were not significantly different from one
440 another and remained relatively constant ($3 - 4 \times 10^3$ kg ha⁻¹) over the course of the study (Fig.
441 3a, Table 3). Total litterfall and hemlock litterfall amounts were significantly affected by
442 hemlock removal (Table 3), and the patterns of change in canopy structure were reflected
443 immediately in litterfall (Fig. 3a, 3b). A strong pulse of litter occurred in the girdled treatment in
444 Spring – Summer 2006, one year after *T. canadensis* were girdled (Fig. 3a). Hemlock litter
445 comprised >80% of the total litterfall collected in the girdled treatment during April –
446 September 2006 (Fig. 3b). Subsequently, total litterfall in this treatment increased to about the

447 same amount as in the hemlock and hardwood controls by 2009, but was composed mainly of
448 *Betula*, *Quercus* and *Pinus* litter (data not shown). Litterfall in the logged plots was significantly
449 reduced by logging, and slowly increased during the four years after logging to nearly 50% of
450 that observed in the controls (Fig. 3a).

451

452 *Soil respiration*

453 Average seasonal soil respiration dynamics showed some changes as a function of hemlock
454 canopy removal (Fig. 3c), but within-plot variation exceeded among-treatment variation in soil
455 respiration (Fig. 3c; Table 3). By differencing, hemlock roots accounted for approximately 35%
456 of the total soil respiration in intact hemlock stands.

457

458 *Nitrogen dynamics*

459 Hemlock removal led to transient increases in ammonium (NH_4^+) and nitrate (NO_3^-) availability
460 in soils (peaks in Fig. 3d, 3e). As with measures of soil respiration, within-treatment
461 heterogeneity exceeded among-treatment variation in NO_3^- availability, and neither treatment
462 significantly altered soil NO_3^- availability (Table 3). Nitrate mobility remained low following
463 cutting or girdling, except for a 2-year pulse beginning in 2008 in the girdled plot on the ridge
464 and beginning in 2007 in the logged plot on the ridge (Fig. 3e).

465 Across all treatments, net nitrogen mineralization declined significantly through time
466 (Table 3), but within-treatment variation exceeded among-treatment variation throughout the
467 study (Fig 3f). We observed a small ($\approx 5\%$), sustained increase in net nitrogen mineralization in

468 the girdled treatment from 2007 to 2009, and a similarly small, albeit transient, increase in net
469 nitrogen mineralization immediately following logging (Fig. 3f).

470

471 **Discussion**

472 Losses of individual species can have cascading effects on system-wide biological diversity and
473 ecosystem function, but whether *specific* species have different effects on ecosystem structure
474 function remains an open question that has been addressed much more in theory than in
475 practice (Bunker *et al.* 2005, Suding *et al.* 2008, Wardle *et al.* 2011). It is important to
476 distinguish between effects of loss of dominant (in terms of basal area or biomass) or abundant
477 species and effects of loss of foundation species. For example, American beech is declining
478 rapidly due to beech-bark disease (Houston 1975; Lovett *et al.* 2006), but because beech
479 resprouts readily, one consequence of beech-bark disease has been to change the size
480 structure of these forests. Large beech trees are now uncommon, but the number of saplings
481 (sprouts) and even the amount of beech's basal area in a stand may be much greater than
482 before the occurrence and spread of the disease (Houston 1975). Similarly, American elm, once
483 a co-dominant in many eastern North American forests, continued to recruit from small trees,
484 which can reproduce before they are killed by Dutch elm disease (Barnes 1976). Understory
485 composition changes rarely in beech stands infested by beech-bark disease (Twery and
486 Patterson 1984), and several authors have failed to find expected changes in invertebrate or
487 mammal abundance associated with widespread decline in beech nuts formerly produced by
488 large trees (Faison and Houston 2004, Garneau *et al.* 2012). Effects of beech decline on energy

489 and nutrient cycling varies with co-occurring hardwoods, rates of resprouting, and intensity of
490 infestation (Lovett *et al.* 2006).

491 In contrast, eastern hemlock has distinctive assemblages of understory plants and
492 animals (Snyder *et al.* 2002; Tingley *et al.* 2002; Ellison *et al.* 2005b; Dilling *et al.* 2007;
493 Mathewson 2009; Rohr, Mahan & Kim 2009; Mallis & Rieske, 2011; Sackett *et al.* 2011), and
494 affects carbon cycling and hydrological processes differently from both co-occurring hardwoods
495 and co-occurring conifers (Ford & Vose 2007, Hadley *et al.* 2008, Brantley, Ford & Vose *in*
496 *press*). Hemlock, unlike hardwoods, does not resprout, and the hemlock woolly adelgid feeds
497 on all ages and size-classes of hemlock. Thus, there is neither opportunity for rapid
498 regeneration through resprouting nor is there an opportunity for hemlock seedlings to reach
499 maturity and fruit before they are killed by the adelgid. Eastern hemlock, therefore, is a better
500 candidate for a foundation tree species than many other forest dominants. Its decline and
501 death have been hypothesized to lead to both short- and long-term changes in ecological
502 dynamics and ecosystem processes (Ellison *et al.* 2005a; Lovett *et al.* 2006).

503 The Harvard Forest Hemlock Removal Experiment (HF-HeRE) examines this hypothesis
504 by quantifying these changes and testing explicit predictions about how the magnitude and rate
505 of these changes are functions of the mechanism by which a foundation species is lost. In
506 general terms, we predicted that rates of change in biological diversity and ecosystem function
507 would parallel the rate of foundation species loss: slowly when hemlock was girdled (to mimic
508 decline due to infestation by the hemlock woolly adelgid; Yorks, Leopold & Raynal 2003) but
509 more rapidly when hemlock was cut and removed (to simulate a commercial logging operation;
510 Brooks 2001). We hypothesize that despite differences in initial rates, changes in vegetation

511 structure and ecosystem function caused by different mechanisms of hemlock loss will
512 converge and come to resemble those seen in the young hardwood stands that represent a
513 plausible scenario of our forests in the future, after hemlock has disappeared from the
514 landscape (Orwig & Foster 1998). Our results provide strong support for this hypotheses with
515 respect to most measures of vegetation structure, but for fewer measures of ecosystem
516 function.

517

518 ***Changes in vegetation structure***

519 Decline and loss of *T. canadensis* in the logged and girdled plots at HF-HeRE led to changes in
520 overstory densities and basal area (Table 1) that were similar to those seen in sites long
521 infested by the adelgid (Orwig & Foster 1998; Orwig, Foster & Mausel 2002) or that have been
522 salvage logged (Brooks 2001; Kizlinski *et al.* 2002). Light availability near ground-level increased
523 gradually over time following girdling but abruptly after logging, followed by a decline with
524 regrowth in the logged treatment (Lustenhouwer, Nicoll & Ellison 2012). Average daily soil and
525 air temperatures in logged and girdled plots were 2 – 4 °C warmer in summer and cooler in
526 winter relative to the hemlock or hardwood controls, and both diurnal and seasonal variances
527 in temperatures were highest in the logged treatment (Lustenhouwer, Nicoll & Ellison 2012).
528 Such changes in light and temperature can strongly impact both vegetation community
529 composition (D’Amato, Orwig & Foster 2009; Farnsworth, Barker Plotkin & Ellison 2012) and
530 associated ecosystem properties including decomposition (Berg & McLaugherty 2009), soil
531 respiration (Savage & Davidson 2001), and nutrient cycling (Kizlinski *et al.* 2002).

532 Removal of *T. canadensis* by girdling or logging resulted in a 2- to 3-fold increase in
533 species richness after either treatment. Consistent with our first prediction, understory cover in
534 the girdled treatment plots increased slowly (Fig. 2a, 2b) because overstory trees died slowly
535 and the majority of snags were still standing and providing partial shade 4 – 5 years after the
536 canopy manipulation treatment had been applied. We anticipate that understory vegetation in
537 this treatment will continue to increase in cover and species richness. In contrast, understory
538 vegetation cover in the logged treatment plots increased rapidly and matched total cover in the
539 hardwood control plots by 2009 (Fig. 2a, 2b). Shade intolerant species including *Rubus* spp.,
540 *Aralia hispida*, and *Carex* spp. initially were absent in all six *T. canadensis*-dominated plots, but
541 established from both the seed bank and the seed rain in soils scarified by logging (Farnsworth,
542 Barker Plotkin & Ellison 2012) and grew quickly in these scarified areas. Similar increases in
543 total richness and cover have been observed following girdling (Yorks *et al.* 2003; Ford *et al.*
544 2012) or salvage logging (Kizlinski *et al.* 2002; D. Orwig unpublished data) of *T. canadensis*
545 elsewhere. However, the heavy recruitment of birch (*Betula* spp.) into the sapling layer within
546 four years of girdling has not been observed in other girdling studies (Yorks, Leopold & Raynal
547 2003; Ford *et al.* 2012), perhaps due to lower deer browsing and lack of Rhododendron
548 (*Rhododendron maximum* L.) cover that limit rapid recruitment south of our study areas. These
549 results overall highlight the fact that healthy hemlock act as an ecological filter, limiting
550 seedling and understory plant establishment (Rogers 1980; D'Amato, Orwig & Foster 2009;
551 Orwig *et al.* 2012). Now that the adelgid has colonized the hemlock control plots, however, they
552 are also poised for change, and will provide important comparisons with responses observed
553 following girdling.

554

555 ***Changes in standing and downed dead wood***

556 Changes in coarse woody debris volume (Fig. 2f, 2g) were consistent with our second
557 prediction. By the end of 2009, most dead trees were still standing in the girdled treatment
558 plots. Once they fall, however, volume of fallen wood will more than double the levels currently
559 found in the logged plots. Ironically, although the hemlock canopy is lost, this large input of
560 CWD onto the soil surface will bring the dead wood structure of this treatment closer to that
561 seen in old-growth *T. canadensis* stand structure (D'Amato, Orwig & Foster 2008) than to the
562 volume of standing dead wood or CWD in young hardwood stands. These fallen boles likely will
563 provide safe sites for seedling establishment and cover for amphibians (Mathewson 2009) and,
564 as they decompose, also will slowly release nutrients into the soil.

565

566 ***Changes in ecosystem functions***

567 Our third prediction was supported most clearly for changes in litterfall, an index of
568 aboveground primary productivity (Zheng, Prince & Hame 2004). In the girdled treatment plots,
569 there was a sharp pulse in litterfall followed by a gradual decline (Fig. 3a, 3b; see also Yorks,
570 Leopold & Raynal 2003; Nuckolls *et al.* 2009). This is a transient loss of standing biomass, which
571 then recovered to pretreatment levels as vegetation colonized or regrew in the experimental
572 plots. Total litterfall following girdling recovered within four years to levels observed in both
573 hemlock and hardwood controls as *Pinus strobus*, *Quercus* spp. and *Betula* spp. growth
574 increased. Very similar patterns and total amounts of litterfall were observed four years after
575 girdling hemlock in southern Appalachian forests (Knoepp *et al.* 2011). In the logged treatment

576 plots, litterfall immediately decreased following logging then slowly increased. By 2009,
577 however, the amount of litterfall in the logged plots treatment was still lower than in the
578 girdled treatment or either of the two controls (Fig. 3a, 3b).

579 Contrary to our third prediction, variation in soil respiration, nitrogen availability, and
580 nitrogen cycling generally was higher within treatments and years than among treatments or
581 years, and any responses to treatments were modest and transient. Any initial differences
582 among treatments rapidly recovered to pre-treatment levels (Fig. 3c-f). Our approximate
583 autotrophic respiration rate estimates of 36 – 46% are similar to the 48% measured by
584 Gaudinski et al. (2000) at the Harvard Forest using isotopic analysis of respired ¹⁴C. We
585 measured 43% autotrophic respiration using the same isotopic analysis methodology as
586 Gaudinski et al. (2000) within the Simes girdled treatment plots (K. Savage & E. Davidson
587 unpublished data). Similar ranges attributed to autotrophs have been estimated in other
588 studies (Hansen *et al.* 2000; Levy-Varon, Schuster & Griffin 2012).

589 Despite the dramatic changes caused by girdling and logging in microenvironmental
590 conditions (Lustenhouwer, Nicoll & Ellison 2012), vegetation structure (Fig. 2; Table 2), and
591 productivity (Fig. 3a, 3b; Table 3) and the transient shifts in carbon dynamics (Fig. 3c; Table 3),
592 our experimental treatments resulted in only modest, short-term changes in nitrogen cycling
593 (Fig.3d-3f; Table 3). Ammonium availability in the girdled treatment plots did not increase until
594 two years after girdling and peaked one year later, a result expected because *T. canadensis*
595 trees did not die or drop their needles immediately. The short-lived duration of nutrient
596 capture on resins is likely related to the rapid regrowth of vegetation in the logging treatment
597 (see also Templer & McCann 2010). Short-lived increases in ammonium and nitrate availability

598 also have been observed in other logging and girdling studies (Kizlinski *et al.* 2002; Yorks,
599 Leopold & Raynal 2003; Nave *et al.* 2011), and in adelgid-infested forests (Jenkins, Aber &
600 Canham 1999; Orwig *et al.* 2008). Net nitrogen mineralization was not significantly affected by
601 logging or girdling, a result also seen other hemlock studies in girdled (Knoepp *et al.* 2011) and
602 logged stands (Kizlinski *et al.* 2002), and consistent with findings following a substantial physical
603 disturbance (simulated hurricane; Bowden *et al.* 1993). However, we also found no substantive
604 differences in nitrogen mineralization between hemlock and hardwood control plots. The lack
605 of major differences in soil pH or forest floor C:N is consistent with these findings, which are
606 also supported by recent meta-analyses (Mueller *et al.* 2012).

607 We caution, however, that it may take much longer than a decade or two for changes in
608 soil dynamics resulting from the loss of hemlock to be manifest (D. J. Lodge *personal*
609 *communication* 24 September 2004). One of the dominant drivers of soil dynamics –
610 decomposition of large fallen boles and other coarse woody debris – is very different in
611 hemlock (and other conifer-dominated) stands than in hardwood dominated stands. In the
612 former, brown-rot fungi dominate, and they primarily decompose cellulose. In the latter, white-
613 rot fungi dominate, and they primarily decompose lignin; in general, white-rot fungi are much
614 more efficient (and rapid) decomposers (Hatakka 2001; Floudas *et al.* 2012). We predict that
615 soil nutrient availability will decline significantly only once dead hemlock boles and smaller
616 coarse hemlock woody debris have decomposed and brown-rot fungi disappear, but this may
617 take one or two centuries.

618

619 **Conclusions**

620 Loss of the foundation tree species, *T. canadensis*, by either girdling or logging, leads to short-
621 and long-term changes in vegetation structure and ecosystem function. Rapid removal by
622 logging leads to abrupt, rapid changes, whereas girdling (and by inference, the adelgid itself)
623 causes slower but no less important responses of similar magnitude several years later.
624 Vegetation richness, cover, and density increase continuously following hemlock removal and
625 exert strong, potentially stabilizing, biotic control on the fluxes of nutrients. Thus, these
626 ecosystem processes exhibited short-term fluctuations following *T. canadensis* removal but
627 recovered to near pre-treatment levels within four years, highlighting the resilience – at least in
628 the short-term – of some forest ecosystem processes to disturbances (Bowden *et al.* 1993;
629 Foster *et al.* 1997). Results from HF-HeRE, together with results from observations and
630 experiments on other foundation species suggest that their continued losses, together with
631 human responses to ongoing environmental changes, may have profound impacts on the
632 structure and function of forested ecosystems for decades to come.

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646

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919

920 **Table legends:**

921 **Table 1.** Changes in total average basal area ($\text{m}^2 \text{ha}^{-1}$) and density (ha^{-1}) in the treatment plots of the
922 Harvard Forest Hemlock Removal Experiment.

923 **Table 2.** Summary of ANCOVA analyses on vegetation structural characteristics shown in Figure 2. The
924 models fit were all of the form $\text{response variable} = \beta_0 + \beta_1 \times \text{block} + \beta_2 \times \text{time} + \beta_3 \times \text{treatment} +$
925 $\beta_4 \times \text{time} \times \text{treatment}$; if the response variable was ln-transformed prior to analysis, that is noted in the
926 column heading. Values shown in the first four rows are F-statistics, associated degrees of freedom, and
927 P-values; parameter estimates (SE) for the four treatments – C (hemlock control); G (girdled), L (logged),
928 and H (hardwood control) – are given in the next three rows. Parameter estimates are not back-
929 transformed (for models fit to ln-transformed data). Parameter estimates that are significantly different
930 from 0 are shown in *italics*.

931 **Table 3.** Summary of ANCOVA analyses on ecosystem functional characteristics shown in Figure 3. The
932 models fit were all of the form $\text{response variable} = \beta_0 + \beta_1 \times \text{block} + \beta_2 \times \text{time} + \beta_3 \times \text{treatment} +$
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934 column heading. Values shown in the first four rows are F-statistics, associated degrees of freedom, and
935 P-values; parameter estimates (SE) for the four treatments – C (hemlock control); G (girdled), L (logged),
936 and H (hardwood control) – are given in the next three rows. Parameter estimates are not back-
937 transformed (for models fit to *ln*-transformed data). Parameter estimates that are significantly different
938 from 0 are shown in *italics*.

Table 1. Changes in total average basal area ($\text{m}^2 \text{ha}^{-1}$) and density (ha^{-1}) in the treatment plots of the Harvard Forest Hemlock Removal Experiment.

Canopy manipulation	Year	Basal area		Stem density	
		Valley plots	Ridge plots	Valley plots	Ridge plots
Hemlock control	2004	45.6	52.1	940	678
	2009	47.3	54.0	842	637
Girdled	2004	50.3	53.0	1354	1011
	2009	15.9	17.6	395	331
Logged	2004	47.9	49.5	1212	1089
	2009	15.4	13.8	469	373
Hardwood control	2004	29.7	35.6	1122	885
	2009	31.0	37.7	990	807

Table 2. Summary of ANCOVA analyses on vegetation structural characteristics shown in Figure 2. The models fit were all of the form $response\ variable = \beta_0 + \beta_1 \times block + \beta_2 \times time + \beta_3 \times treatment + \beta_4 \times time \times treatment$; if the response variable was ln-transformed prior to analysis, that is noted in the column heading. Values shown in the first four rows are F-statistics, associated degrees of freedom, and P-values; parameter estimates (SE) for the four treatments – C (hemlock control); G (girdled), L (logged), and H (hardwood control) – are given in the next three rows. Parameter estimates are not back-transformed (for models fit to ln-transformed data). Parameter estimates that are significantly different from 0 are shown in *italics*.

	Understory richness	Understory cover	ln(Tree seedling density)	ln(Tree seedling cover)	ln(Sapling density + 1)	ln(Snag and stump volume)	CWD volume
<i>Sources of variation</i>							
Intercept	F _{1,39} = 671.34	F _{1,47} = 132.35	F _{1,47} = 2967.94	F _{1,47} = 0.03	F _{1,15} = 148.05	F _{1,15} = 1135.32	F _{1,15} = 151.22
	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> =0.8615	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> <0.0001
Time	F _{1,39} = 23.65	F _{1,47} = 21.82	F _{1,47} = 11.80	F _{1,47} = 82.57	F _{1,15} = 1.27	F _{1,15} = 10.85	F _{1,15} = 0.00
	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> =0.0012	<i>P</i> <0.0001	<i>P</i> =0.2779	<i>P</i> =0.0049	<i>P</i> =0.9867
Treatment	F _{3,39} = 53.13	F _{3,47} = 80.34	F _{3,47} = 2.55	F _{3,47} = 32.84	F _{3,15} = 2.85	F _{3,15} = 14.53	F _{3,15} = 43.51
	<i>P</i> <0.0001	<i>P</i> <0.0001	<i>P</i> =0.0668	<i>P</i> <0.0001	<i>P</i> =0.0728	<i>P</i> =0.0001	<i>P</i> <0.0001
Time x Treatment	F _{3,39} = 4.29	F _{3,47} = 12.58	F _{3,47} = 4.16	F _{3,47} = 15.14	F _{3,15} = 0.49	F _{3,15} = 7.39	F _{3,15} = 0.90
	<i>P</i> =0.0104	<i>P</i> <0.0001	<i>P</i> =0.0108	<i>P</i> <0.0001	<i>P</i> =0.6929	<i>P</i> =0.0029	<i>P</i> =0.4634
<i>Parameter estimates</i>							
Intercept (β_0)	<i>8.38 (1.57)</i>	0.78 (1.62)	<i>10.04 (0.34)</i>	<i>-1.98 (0.33)</i>	<i>3.42 (1.18)</i>	<i>3.22 (0.39)</i>	<i>25.42 (8.24)</i>

Table 3. Summary of ANCOVA analyses on ecosystem functional characteristics shown in Figure 3. The models fit were all of the form $response\ variable = \beta_0 + \beta_1 \times block + \beta_2 \times time + \beta_3 \times treatment + \beta_4 \times time \times treatment$; if the response variable was *ln*-transformed prior to analysis, that is noted in the column heading. Values shown in the first four rows are F-statistics, associated degrees of freedom, and *P*-values; parameter estimates (SE) for the four treatments – C (hemlock control); G (girdled), L (logged), and H (hardwood control) – are given in the next three rows. Parameter estimates are not back-transformed (for models fit to *ln*-transformed data). Parameter estimates that are significantly different from 0 are shown in *italics*.

	ln(litterfall)	ln(hemlock litterfall)	Soil C flux	ln(NH₄)	NO₃	ln(N mineralization)
<i>Sources of variation</i>						
Intercept	F _{1,23} = 10821.55 P<0.0001	F _{1,23} = 3.96 P=0.0587	F _{1,29} = 126.44 P<0.0001	F _{1,47} = 2347.54 P<0.0001	F _{1,47} = 8.35 P=0.0058	F _{1,47} = 397.38 P<0.0001
Time	F _{1,23} = 0.14 P=0.7105	F _{1,23} = 6.46 P=0.0182	F _{1,29} = 0.84 P=0.3665	F _{1,47} = 2.53 P=0.1183	F _{1,47} <0.01 P=0.9922	F _{1,47} = 5.66 P=0.0214
Treatment	F _{3,23} = 15.95 P<0.0001	F _{3,23} = 12.45 P<0.0001	F _{2,29} = 5.69 P=0.0083	F _{3,47} = 9.00 P<0.0001	F _{3,47} = 2.44 P=0.0757	F _{3,47} = 2.26 P=0.0933
Time x Treatment	F _{3,23} = 3.26 P=0.0399	F _{3,23} = 5.53 P=0.0052	F _{2,29} = 2.05 P=0.1475	F _{3,47} = 2.14 P=0.1075	F _{3,47} = 0.91 P=0.4435	F _{3,47} = 2.39 P=0.0806
<i>Parameter estimates</i>						
Intercept (β₀)	<i>3.86 (0.20)</i>	<i>2.87 (1.16)</i>	<i>0.29 (0.03)</i>	<i>4.67 (0.25)</i>	62.80 (37.73)	<i>-1.04 (0.14)</i>

946 **Figure legends**

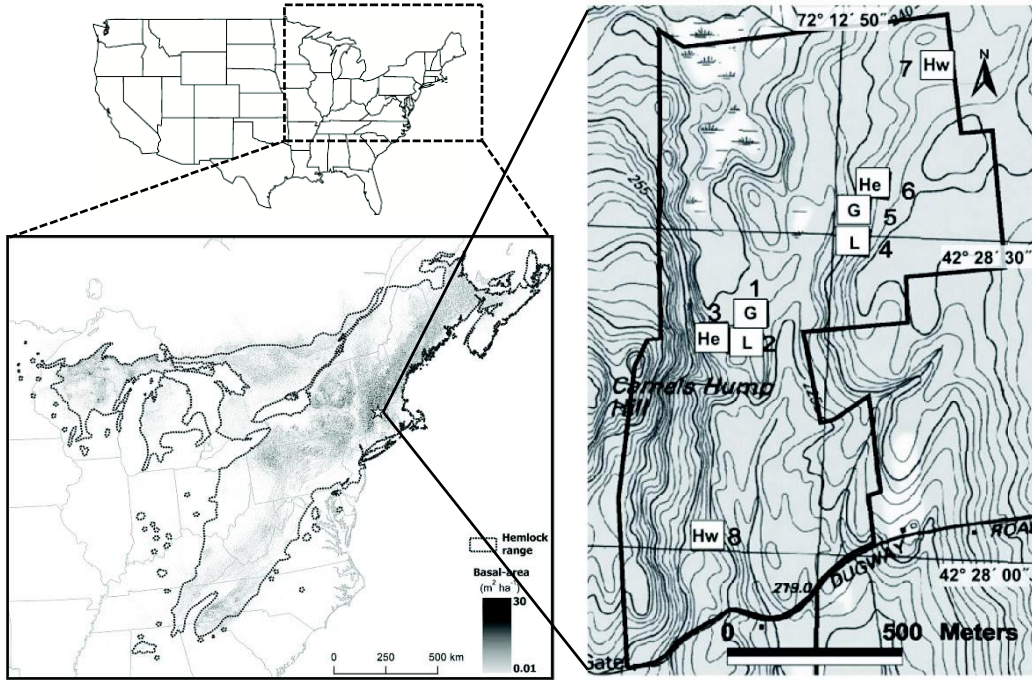
947 **Fig. 1.** Location of the Harvard Forest Hemlock Removal Experiment in Massachusetts, USA. The regional
948 map shows the basal area of eastern hemlock at a 1 km² resolution. The inset shows the location of the
949 experimental blocks and treatments. Plots 1, 2, 3, and 8 make up the valley block; plots 4 – 7 make up
950 the ridge block. Each canopy manipulation treatment – hemlock control (He), girdled (G), logged (L), and
951 hardwood control (Hw) – was applied to a 90 × 90 m plot within each block.

952 **Fig. 2.** Temporal trajectories of vegetation structural characteristics in the Harvard Forest Hemlock
953 Removal Experiment. Values shown are plot means and standard deviations (where multiple samples
954 were taken in each plot), back-transformed as necessary. Solid lines and symbols are plots in the valley;
955 dashed lines and open symbols are plots on the ridge. Colors indicate treatments: blue – hemlock
956 controls; yellow – all hemlocks girdled; red – hemlocks logged; lavender – hardwood controls.

957

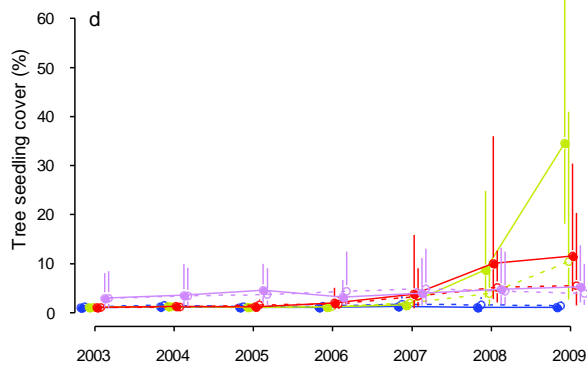
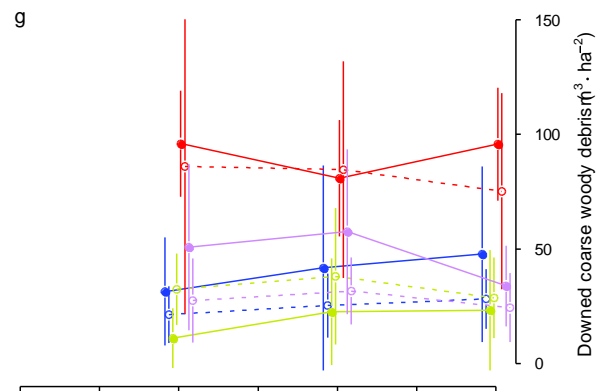
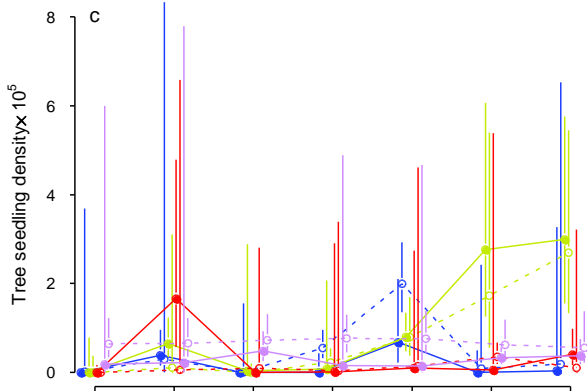
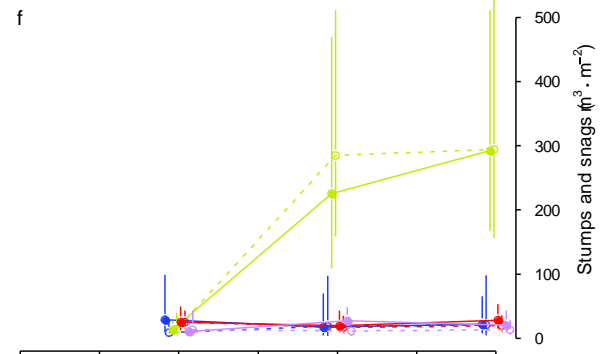
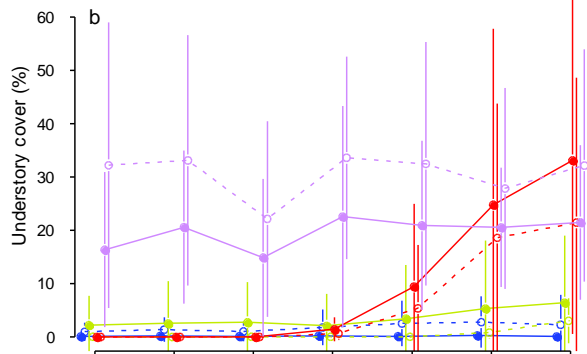
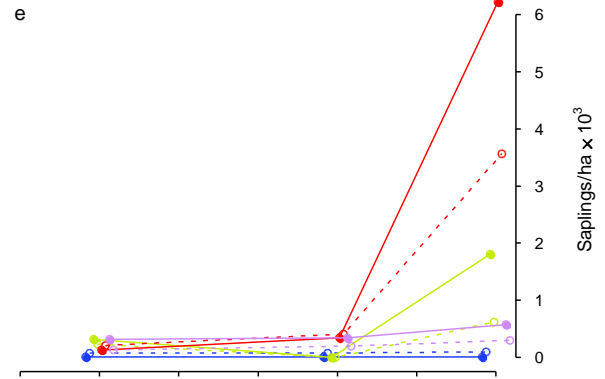
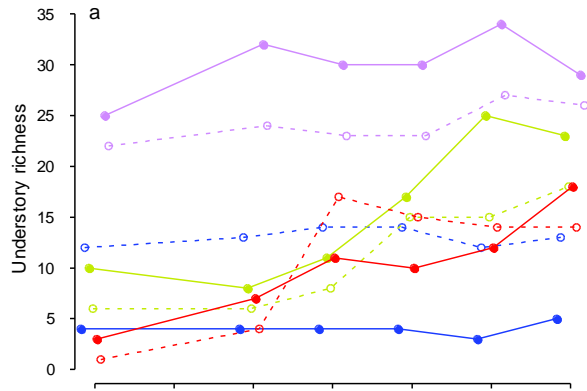
958 **Fig. 3.** Temporal trajectories of ecosystem functional characteristics in the Harvard Forest Hemlock
959 Removal Experiment. Values shown are plot means and standard deviations (where multiple samples
960 were taken in each plot), back-transformed as necessary. Solid lines and symbols are plots in the valley;
961 dashed lines and open symbols are plots on the ridge. Colors indicate treatments: blue – hemlock
962 controls; yellow – all hemlocks girdled; red – hemlocks logged; lavender – hardwood controls.

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