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

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(Article begins on next page)

1 **Foundation species loss affects vegetation structure more than ecosystem function in a**

2 **northeastern USA forest**

3 **Abstract**

4 Loss of foundation tree species rapidly alters ecological processes in forested ecosystems.

5 *Tsuga canadensis*, an hypothesized foundation species of eastern North American forests, is

6 declining throughout much of its range due to infestation by the nonnative insect *Adelges*

7 *tsugae* and by removal through pre-emptive salvage logging*.* In replicate 0.81-ha plots, *T.*

8 *canadensis* was cut and removed, or killed in place by girdling to simulate adelgid damage.

9 Control plots included undisturbed hemlock and mid-successional hardwood stands that

10 represent expected forest composition in 50–100 years. Vegetation richness, understory

11 vegetation cover, soil carbon flux, and nitrogen cycling were measured for two years prior to,

12 and five years following, application of experimental treatments. Litterfall and coarse woody

13 debris (CWD), including stumps, snags, and fallen logs and branches, have been measured since

14 treatments were applied. Overstory basal area was reduced 60–70% in girdled and logged plots.

15 Mean understory cover and richness did not change in hardwood or hemlock control plots, but

16 increased rapidly in girdled and logged plots. Following logging, litterfall immediately decreased

17 then slowly increased, whereas in girdled plots, there was a short pulse of hemlock litterfall as

18 trees died. CWD volume remained relatively constant throughout, but was 3–4× higher in

19 logged plots. Logging and girdling resulted in small, short-term changes in ecosystem dynamics

20 due to rapid regrowth of vegetation but in general, interannual variability exceeded differences

21 among treatments. Soil carbon flux in girdled plots showed the strongest response: 35% lower

22 than controls after three years and slowly increasing thereafter. Ammonium availability

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 ≈10 000 km^2 and comprises ≈2 × 10^8 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

compares and contrasts the rates, magnitudes, and trajectories of changes in hemlock-

dominated stands to two mechanisms of foundation species loss: (1) death in place of eastern

hemlock by girdling, which mimics tree disintegration that follows infestation by the hemlock

woolly adelgid (Yorks, Leopold & Raynal 2003); or (2) loss and removal of hemlock following

commercial logging (Brooks 2001). Patterns, processes, and dynamics studied include: forest

vegetation structure, standing and downed dead wood, and three measures of ecosystem

function: litterfall (a substantial component of net primary productivity; *e.g.,* Zheng, Prince &

Hame 2004), soil carbon flux, and soil nitrogen dynamics.

In this paper, we report two years of pre-treatment data and the first five years of

changes in vegetation structure and ecosystem functions following our experimental

manipulations but prior to the infestation of our experimental plots by the adelgid. In

particular, we examine and test three predictions that, relative to both hemlock and hardwood

controls:

(1) Vegetation structure – species richness and cover of understory herbs, and density and

cover of tree seedlings and saplings – increases slowly following girdling but more

rapidly following hemlock removal and soil scarification from logging;

(2) Volume of standing dead wood and snags is highest in girdled plots, but downed coarse

woody debris is higher in logged plots;

(3) Core ecosystem functions – litterfall and soil carbon fluxes decline while rates of soil

nitrogen (as nitrate and ammonium) mineralization and soil nitrogen availability

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 & Mausel 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 ($42.47^o - 42.48^o$ N, $72.22^o - 72.21^o$ 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

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-m^2 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 m$^2 \cdot$ ha^{-1}) than in the hardwood control plots (29.7 – 35.6 m$^2 \cdot$ 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 m^2) 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   ^{o}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 m^2 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 CO_2 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 mL $\cdot$ L^{-1} CO_2 and 594 mL $\cdot$ L^{-1} 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 NH_4-N and NO_3-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   NH_4-N and NO_3-N, respectively. Net N mineralization was calculated as the difference in

339   concentration of inorganic N (NH_4-N + NO_3-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 ^{o}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), *Erichtites 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 $3.5 \times 10^5 \cdot ha^{-1}$ – in the girdled treatment

411   through time. Cover of tree seedlings was consistently lowest in hemlock control (< 1% cover)

412   and hardwood control (≈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 × 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 (≈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 & McClaugherty 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

Changes in standing and downed dead wood

Changes in coarse woody debris volume (Fig. 2f, 2g) were consistent with our second

prediction. By the end of 2009, most dead trees were still standing in the girdled treatment

plots. Once they fall, however, volume of fallen wood will more than double the levels currently

found in the logged plots. Ironically, although the hemlock canopy is lost, this large input of

CWD onto the soil surface will bring the dead wood structure of this treatment closer to that

seen in old-growth *T. canadensis* stand structure (D'Amato, Orwig & Foster 2008) than to the

volume of standing dead wood or CWD in young hardwood stands. These fallen boles likely will

provide safe sites for seedling establishment and cover for amphibians (Mathewson 2009) and,

as they decompose, also will slowly release nutrients into the soil.

565

Changes in ecosystem functions

Our third prediction was supported most clearly for changes in litterfall, an index of

aboveground primary productivity (Zheng, Prince & Hame 2004). In the girdled treatment plots,

there was a sharp pulse in litterfall followed by a gradual decline (Fig. 3a, 3b; see also Yorks,

Leopold & Raynal 2003; Nuckolls *et al.* 2009). This is a transient loss of standing biomass, which

then recovered to pretreatment levels as vegetation colonized or regrew in the experimental

plots. Total litterfall following girdling recovered within four years to levels observed in both

hemlock and hardwood controls as *Pinus strobus*, *Quercus* spp. and *Betula* spp. growth

increased. Very similar patterns and total amounts of litterfall were observed four years after

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 ^{14}C. 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 (Kizlinksi *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

Conclusions

619

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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920   **Table legends**:

921   **Table 1.** Changes in total average basal area (m^2 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 *response variable* = β_0 + β_1×*block* + β_2×*time* + β_3×*treatment* +

925   β_4×*time*×*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 *response variable* = β_0 + β_1×*block* + β_2×*time* + β_3×*treatment* +

933   β_4×*time*×*treatment*; if the response variable was *ln*-transformed prior to analysis, that is noted in the

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 (m^2 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 = β_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
Sources of variation							
Intercept	$F_{1,39} = 671.34$	$F_{1,47} = 132.35$	$F_{1,47} = 2967.94$	$F_{1,47} = 0.03$	$F_{1,15} = 148.05$	$F_{1,15} = 1135.32$	$F_{1,15} = 151.22$
	$P<0.0001$	$P<0.0001$	$P<0.0001$	$P=0.8615$	$P<0.0001$	$P<0.0001$	$P<0.0001$
Time	$F_{1,39} = 23.65$	$F_{1,47} = 21.82$	$F_{1,47} = 11.80$	$F_{1,47} = 82.57$	$F_{1,15} = 1.27$	$F_{1,15} = 10.85$	$F_{1,15} = 0.00$
	$P<0.0001$	$P<0.0001$	$P=0.0012$	$P<0.0001$	$P=0.2779$	$P=0.0049$	$P=0.9867$
Treatment	$F_{3,39} = 53.13$	$F_{3,47} = 80.34$	$F_{3,47} = 2.55$	$F_{3,47} = 32.84$	$F_{3,15} = 2.85$	$F_{3,15} = 14.53$	$F_{3,15} = 43.51$
	$P<0.0001$	$P<0.0001$	$P=0.0668$	$P<0.0001$	$P=0.0728$	$P=0.0001$	$P<0.0001$
Time x Treatment	$F_{3,39} = 4.29$	$F_{3,47} = 12.58$	$F_{3,47} = 4.16$	$F_{3,47} = 15.14$	$F_{3,15} = 0.49$	$F_{3,15} = 7.39$	$F_{3,15} = 0.90$
	$P=0.0104$	$P<0.0001$	$P=0.0108$	$P<0.0001$	$P=0.6929$	$P=0.0029$	$P=0.4634$
Parameter estimates							
Intercept (β_0)	*8.38 (1.57)*	0.78 (1.62)	*10.04 (0.34)*	*−1.98 (0.33)*	*3.42 (1.18)*	*3.22 (0.39)*	*25.42 (8.24)*

943

Table 3. Summary of ANCOVA analyses on ecosystem functional characteristics shown in Figure 3. The models fit were all of the form *response variable* = β_0 + β_1×*block* + β_2×*time* + β_3×*treatment* + β_4×*time*×*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*.

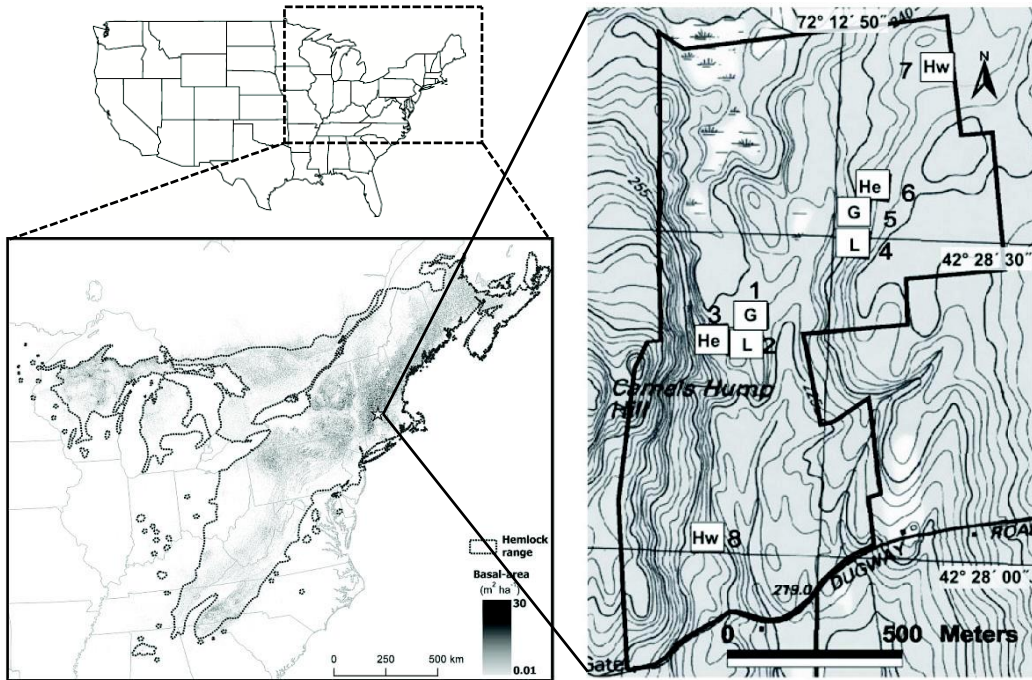|		ln(litterfall)	ln(hemlock litterfall)	Soil C flux	ln(NH$_4$)	NO$_3$	ln(N mineralization)
Sources of variation							
Intercept		$F_{1,23}$ = 10821.55	$F_{1,23}$ = 3.96	$F_{1,29}$ = 126.44	$F_{1,47}$ = 2347.54	$F_{1,47}$ = 8.35	$F_{1,47}$ = 397.38
		P<0.0001	P=0.0587	P<0.0001	P<0.0001	P=0.0058	P<0.0001
Time		$F_{1,23}$ = 0.14	$F_{1,23}$ = 6.46	$F_{1,29}$ = 0.84	$F_{1,47}$ = 2.53	$F_{1,47}$ <0.01	$F_{1,47}$ = 5.66
		P=0.7105	P=0.0182	P=0.3665	P=0.1183	P=0.9922	P=0.0214
Treatment		$F_{3,23}$ = 15.95	$F_{3,23}$ = 12.45	$F_{2,29}$ = 5.69	$F_{3,47}$ = 9.00	$F_{3,47}$ = 2.44	$F_{3,47}$ = 2.26
		P<0.0001	P<0.0001	P=0.0083	P<0.0001	P=0.0757	P=0.0933
Time x Treatment		$F_{3,23}$ = 3.26	$F_{3,23}$ = 5.53	$F_{2,29}$ = 2.05	$F_{3,47}$ = 2.14	$F_{3,47}$ = 0.91	$F_{3,47}$ = 2.39
		P=0.0399	P=0.0052	P=0.1475	P=0.1075	P=0.4435	P=0.0806
Parameter estimates							
Intercept (β_0)		*3.86 (0.20)*	*2.87 (1.16)*	*0.29 (0.03)*	*4.67 (0.25)*	62.80 (37.73)	*−1.04 (0.14)*

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945

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 km^2 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

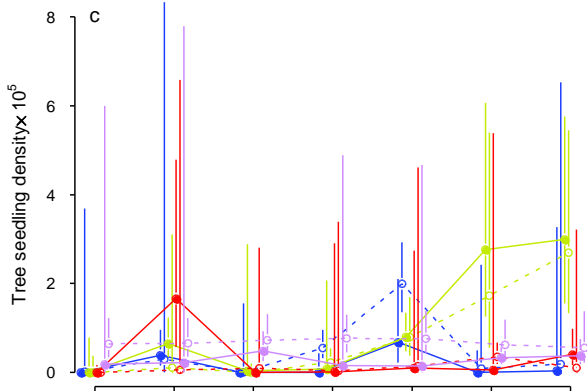956 controls; yellow – all hemlocks girdled; red – hemlocks logged; lavender – hardwood controls.
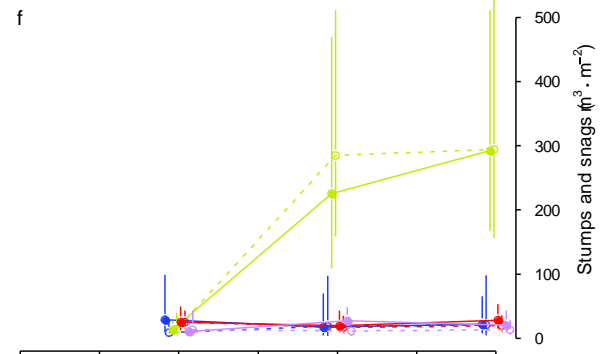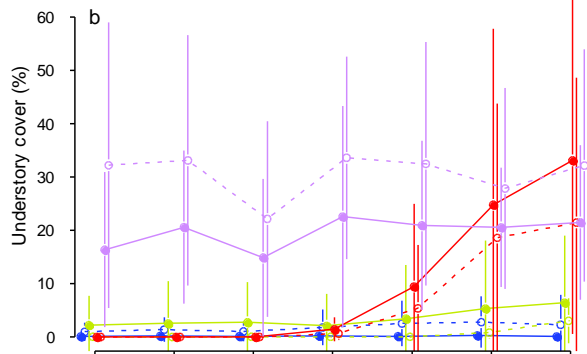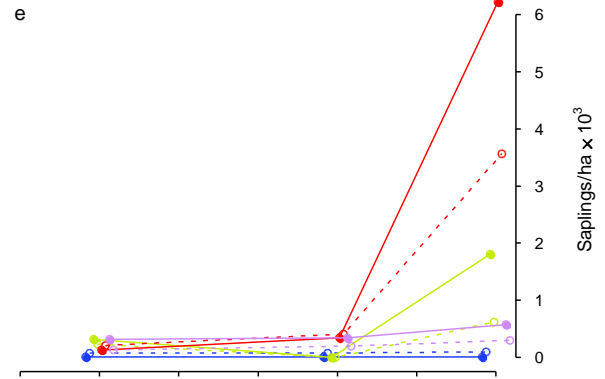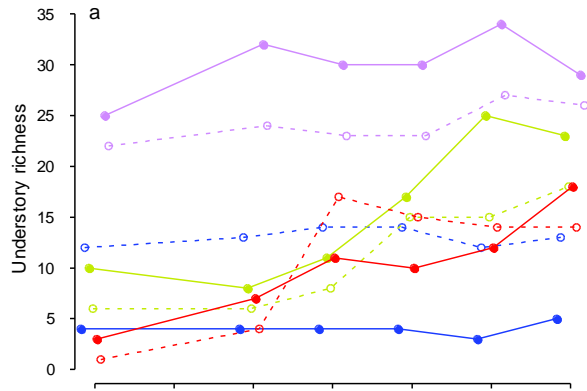
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958 **Fig. 3**. Temporal trajectories of ecosystem functional characteristics in the Harvard Forest Hemlock

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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