



# Assessing the impacts of the decline of *Tsuga canadensis* stands on two amphibian species in a New England forest

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1 **Assessing the impacts of the decline of *Tsuga canadensis* stands on two amphibian species**  
2 **in a New England forest**

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21 **Abstract**

22 Disturbances such as outbreaks of herbivorous insects and pathogens can devastate unique  
23 habitats and directly reduce biodiversity. The foundation tree species *Tsuga canadensis* (eastern  
24 hemlock) is declining due to infestation by the nonnative insect *Adelges tsugae* (hemlock woolly  
25 adelgid). The decline and expected elimination of hemlock from northeastern US forests is  
26 changing forest structure, function, and assemblages of associated species. We assessed 10 years  
27 of changes in occupancy, detection probability, and relative abundance of two species of  
28 terrestrial salamanders, *Plethodon cinereus* (eastern red-back salamander) and *Notopthalmus*  
29 *viridescens viridescens* (eastern red-spotted newt), to the experimental removal in 2005 of *T.*  
30 *canadensis* at Harvard Forest. Salamanders were sampled under cover boards and using visual  
31 encounter surveys before (2004) and after (2005, 2013, 2014) canopy manipulations in replicate  
32 0.81-ha plots. In 2004, occupancy of *P. cinereus* was 35% lower in stands dominated by *T.*  
33 *canadensis* than in associated mixed-hardwood control stands, whereas detection probability and  
34 estimated abundance of *P. cinereus* were, respectively, 60% and 100% greater in *T. canadensis*  
35 stands. Estimated abundance of *N. v. viridescens* in 2004 was 50% higher in *T. canadensis*  
36 stands. Removal of the *T. canadensis* canopy increased occupancy of *P. cinereus* but  
37 significantly reduced its estimated detection probability and abundance. Estimated abundance of  
38 *N. v. viridescens* also declined dramatically after canopy manipulations. Our results suggest that  
39 ten years after *T. canadensis* loss due to either the adelgid or pre-emptive salvage logging, and  
40 50-70 years later when these forests have become mid-successional mixed deciduous stands, that  
41 the abundance of these salamanders likely will be < 50% of their abundance in current, intact *T.*  
42 *canadensis* stands. This study adds to our understanding of how forest disturbance, directly and  
43 indirectly caused by invasive species, can contribute to declines in the relative abundance of  
44 amphibians.

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46 **Keywords:** abundance, *Adelges tsugae*, detection probability, Harvard Forest, indicator species,  
47 monitoring, *Notophthalmus viridescens*, occupancy, *Plethodon cinereus*, *Tsuga canadensis*

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## Introduction

49           Recent reports have indicated that increases in utilization of natural resources and  
50 frequency of natural disturbances will lead to changes in ecological patterns and processes. The  
51 loss of foundation species because of exploitation, habitat fragmentation, or other disturbances  
52 may have particularly large consequences for the diversity of associated species and for  
53 ecological dynamics. Foundation species are species that control the distribution and abundance  
54 of associated species and modulate important ecosystem processes (Dayton 1972, Ellison et al.  
55 2005a). In terrestrial environments, foundation species tend to be large, abundant, occupy basal  
56 positions in local food webs, and control ecosystem processes and dynamics principally through  
57 non-trophic interactions (Baiser et al. 2013).

58           *Tsuga canadensis* (L.) Carrière (eastern hemlock) is a foundation tree species in  
59 northeastern North American forests (Ellison et al. 2005a, 2014, Orwig et al. 2013). Throughout  
60 its range, stands dominated by *T. canadensis* are different, both structurally and functionally,  
61 from surrounding mixed deciduous stands (Orwig et al. 2002, Ellison et al. 2005a). Hemlock-  
62 dominated stands are dark, cool, and moist (Rogers 1980, Benzinger 1994, D'Amato et al. 2009,  
63 Lustenhouwer et al. 2012); have acidic, nutrient-poor soils with slow rates of nutrient cycling  
64 (e.g., Orwig and Foster 1998, Orwig et al. 2013), and are populated by generally species-poor  
65 assemblages of associated plants and animals (e.g., Ellison et al. 2005b, Rohr et al. 2009, Orwig  
66 et al. 2013, Ellison et al. 2016).

67           *Tsuga canadensis* also is declining throughout its range. The nonnative insect *Adelges*  
68 *tsugae* Annand (hemlock woolly adelgid), introduced to the US from Japan in the early 1950s, is  
69 killing hemlock seedlings, saplings, and mature trees (Ellison et al. 2010). In addition, many  
70 landowners and land managers have been logging *T. canadensis* prior to the arrival of the adelgid  
71 (Orwig et al. 2002, Foster and Orwig 2006). In New England, as *T. canadensis* declines or is

72 logged out, it has been replaced by deciduous species including *Acer rubrum* L. (red maple)  
73 *Betula lenta* L. (black birch), and *Quercus rubra* L. (northern red oak) (Orwig and Foster 1998,  
74 Orwig 2002, Brooks 2004).

75 The faunal assemblages of *T. canadensis* stands generally have fewer species than nearby  
76 mixed hardwood stands (Sackett et al. 2011, Ellison et al. 2016), but the former provide habitat  
77 for a number of associated arthropods (Ellison et al. 2005b, Rohr et al. 2009), birds (Tingley et  
78 al. 2002), and salamanders (Mathewson 2009, 2014). Although the loss of *T. canadensis* from  
79 eastern North American forests is predicted to result in a cascade of associated faunal changes  
80 (Ellison et al. 2010, Ellison 2014), less is known about how specific animals will respond to the  
81 different ways in which *T. canadensis* is lost from stands that it currently dominates.

82 Terrestrial salamanders such as *Plethodon cinereus* (Green) (eastern red-backed  
83 salamander; henceforth “red-backs”) and the juvenile phase of *Notopthalmus viridescens*  
84 *viridescens* Rafinesque (eastern red-spotted newt; henceforth “red efts”) are abundant and  
85 centrally located in food webs of northeast forest ecosystems (Burton and Likens 1975, Welsh  
86 and Droege 2001). For example, at the Hubbard Brook Experimental Forest, terrestrial  
87 salamanders accounted for as much biomass as small mammals and twice the biomass of  
88 breeding birds (Burton and Likens 1975). As predators of soil invertebrates, salamanders also  
89 have important effects on soil decomposition rates (e.g., Hairston 1987, Wyman 1998, Best and  
90 Welsh 2014; but see Hocking and Babbitt 2014). Red-backs also are prey for snakes (Uhler et al.  
91 1939, Arnold 1982) and birds (Coker 1931, Eaton 1992). In contrast, the toxins in the skin of red  
92 efts make them unpalatable to most potential predators (Hurlbert 1970, Uhler et al. 1939). Their  
93 abundance, site fidelity, and ecological importance suggest that terrestrial salamanders are ideal  
94 indicators of ecological changes in many systems, including forests (Welsh and Droege 2001,  
95 Best and Welsh 2014).

96 Here, we ask how experimental removal of *T. canadensis* through either logging or  
97 simulated infestation by the adelgid (Ellison et al. 2010) affects the relative abundance  
98 occupancy, and detectability of red-backs and red efts over a ten-year period. We also examine  
99 plausible cause-and-effect relationships between hemlock decline and associated changes in  
100 habitat characteristics on salamander abundance. Our results provide additional insights into the  
101 use of salamanders as indicator species for ecological changes in eastern North American forests.

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## Materials and Methods

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### *Study site and experimental design*

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We studied red-backs and red efts within the Harvard Forest Hemlock Removal Experiment (HF-HeRE), located at the Harvard Forest Long Term Ecological Research (LTER) site in Petersham, Massachusetts, USA (42.47°–42.48° N, 72.22°–72.21° W; elevation 215–300 m a.s.l.). HF-HeRE was designed to assess long-term, large scale effects of the decline and loss of *T. canadensis* on forest dynamics and biodiversity (Ellison et al. 2010, Ellison 2014). A full description of the design of HF-HeRE, together with standard methods for statistical analysis of data from this experiment, are given in Ellison et al. (2010); key details are repeated here.

HF-HeRE is a replicated block design with two blocks and four treatments within each block. Both blocks are located within the ≈150-ha Simes Tract of the Harvard Forest (Ellison et al. 2014); The northern “ridge” block and the southern “valley” block are separated from each other by ≈500 m. Each block contains four ≈90 × 90-m (≈0.81) ha-plots. Three of the plots in each block initially were dominated (> 65% basal area) by *T. canadensis*, whereas the fourth was dominated by young (< 50-year-old) mixed hardwoods. Plot locations were identified in 2003; in 2005, canopy manipulations were applied to two of the *T. canadensis*-dominated plots in each block. One of the plots in each block was “girdled”: the cambium of all *T. canadensis*

120 individuals, from seedlings to mature trees was cut through with chainsaws or knives to kill the  
121 trees slowly but leave them standing in place, as would happened following adelgid infestation  
122 (see also Yorks et al. 2003). The other manipulated plot was “logged” in a simulation of a  
123 commercial pre-emptive salvage cut: all *T. canadensis* trees > 20 cm diameter at 1.3 m above  
124 ground (DBH), along with merchantable *Pinus strobus* L. (white pine) and hardwoods (primarily  
125 *Q. rubra*), were logged and removed. The remaining *T. canadensis*-dominated plot in each block  
126 was left as a control to await adelgid infestation (which occurred in 2009-2010: Kendrick et al.  
127 2015), whereas the plot dominated by mixed-hardwoods represented the expected future  
128 condition of the forest after *T. canadensis* has been lost from the landscape.

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#### *Study species*

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Red-backed salamanders (*Plethodon cinereus*) belong to the Plethodontidae, the family  
of “lungless” salamanders that includes about 240 species in the United States and Canada  
(Petranka 1998). Red-backs are completely terrestrial and have no aquatic larval stage; embryos  
undergo direct development (Wake and Hanken 1996). The home range of red-backs is relatively  
small: 13 m<sup>2</sup> for males and juveniles and 24 m<sup>2</sup> for females (Kleeberger and Werner 1982).  
There are no data on the life span of red-backed salamanders in the wild. LeClair et al. (2006)  
estimated the longevity of *P. cinereus* individuals in Quebec using skeletochronology. Of 330  
specimens analyzed, he average age of adult females was 5.8 years (the oldest female was eight  
years old) and the average age of adult males was 5.2 years (the oldest male was nine years old).  
Other plethodontid salamanders can live as long as 32 years., and the majority of individuals in  
populations of the congener *Plethodon jordani* live at least ten years. (Hairston 1983). Red-  
backs spend their entire lifetime lives in forested areas, living in moist soils or on the surface of  
the forest floor under leaf litter, coarse woody debris, rocks, or other natural cover objects



144 (Burger 1935, Heatwole 1962). On average, red-backs normally move < 1 m/day but daily  
145 movement can exceed 1m on days when total rainfall exceeds 1 cm. (Kleeberger and Werner  
146 1982). This limited mobility suggests that red-backs should be an excellent indicator of changes  
147 to environmental conditions in the forested ecosystems in which they live (Welsh and Droege  
148 2001).

149         Similar to red-backs, red efts are very common and abundant in our study area  
150 (Mathewson 2014). As the juvenile terrestrial phase of the eastern red-spotted newt (family  
151 Salamandridae) red efts spend approximately 4-7 years in upland forests before returning to  
152 aquatic habitats to breed (Healy 1973, 1974). Red efts prey on a great diversity of invertebrates  
153 including land snails, mites and ticks, springtails, adult flies, and caterpillars (MacNamara 1977,  
154 Burton 1976). However, toxins in their skin make them less attractive prey than other terrestrial  
155 salamanders to predators such as birds and snakes (Uhler 1939, Hurlbert 1970). This toxicity  
156 makes it possible for red efts to forage on the surface of the forest floor during the day,  
157 especially within 24 hours of rain events (Mathewson 2014). The home range of red efts is  
158 estimated to be approximately 270 m<sup>2</sup> (Healy 1975).

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### *Sampling*

161         We counted red-backs under artificial cover objects (ACOs) on three (in 2004), five (in  
162 2005), two (in 2013), and five (in 2014) sampling dates from May through July in 2004 (before  
163 canopy treatments were applied) and 2005 (post-treatment but before the infestation of the plots  
164 by the adelgid), and again in June and July of 2013 and 2014 (post-treatment and during the now  
165 ongoing adelgid infestation). During the second and third weeks of September 2003, four 1 ×  
166 0.25 × 0.02-m rough-sawn *T. canadensis* boards (ACOs) were placed at randomly selected points  
167 along 75-m transects in each of the eight HF-HeRE plots. These ACOs were removed in 2006;

168 new ACOs were put in the plots in early May 2013 and sampled in mid-June and July of 2013  
169 and 2014. All ACOs were placed at least 15 m from the edge of the plots. In all years, we usually  
170 sampled all of the ACOs in all of the plots on the same day; if not, at least one plot of every  
171 treatment type was always sampled on the same day. The 1–2-week interval between sampling  
172 individual ACOs was sufficient to ensure that repeated sampling did not impact detection  
173 probability (Marsh and Goicocchea 2003).

174 Red efts were sampled using visual encounter surveys only in 2004 (pre-treatment) and  
175 2014, both concurrently with sampling ACOs for red-backs. The 2004 visual-encounter survey  
176 was done along two  $90 \times 1$  m transects randomly-positioned  $> 15$  m from edge of each plot  
177 (Mathewson 2014). The 2014 survey was done along two  $60 \times 1$ -m parallel transects separated  
178 by 30 m from one another.

179 All amphibian sampling methods were approved by Harvard University’s Institutional  
180 Animal Care and Use Committee (File 13-02-144; last updated June 02, 2014).

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### 182 *Habitat characteristics*

183 Habitat characteristics and local environmental conditions, including understory  
184 vegetation (i.e., seedling density and seedling percent cover) and relative humidity, were  
185 measured and used as covariates in the analysis. Seedling density and seedling percent cover has  
186 been measured annually in two sets of five  $1\text{-m}^2$  plots equally spaced along 30-m transects in  
187 each canopy manipulation plot (detailed methods and data in Orwig et al. 2013). Relative  
188 humidity data were acquired from the Fisher meteorological station at Harvard forest.

189

### 190 *Estimation of detection and occupancy probabilities and relative abundance*

191 Three variables – detection and occupancy probabilities and relative abundance – were  
192 selected to assess the response of red-backs and red efts to the experimental treatments in HF-  
193 HeRE. Occupancy probability is an estimate of the proportion of sites or areas occupied by a  
194 focal species out of the total sampling area, given that the species is known to be present in the  
195 area (McKenzie 2002). Occupancy is considered to be one of the most important variables used  
196 for long-term monitoring of the population status of amphibian species in US forests and it is an  
197 excellent metric for assessing population dynamics and conservation status (e.g. Amphibians  
198 Research and Monitoring Initiative - ARMI - <http://armi.usgs.gov/>). Estimation of occupancy  
199 relies on three assumptions: 1) During the time of the study and in the study area, the population  
200 is closed to immigration, emigration, births and deaths; 2) sampling sites within the study region  
201 are independent from one another; and 3) there is no unexplained heterogeneity in detection  
202 ability or habitat during the sampling period. Detection probability is the probability that a given  
203 species will be found in a particular location, given that it is known to be present in the area (i.e.,  
204 given occupancy = 1). Estimation of detection probability is based on occurrence information for  
205 the species from multiple sampling occasions in each site. Details about estimating both  
206 occupancy and detection probabilities are described in detail by Mackenzie et al. (2002).

207 Our estimate of abundance of red-backs was based on counts of individuals observed  
208 under ACOs. Our estimate of abundance of red efts was determined from counts of individuals  
209 observed within the area of each strip transect ( $1 \times 60$  or  $1 \times 90$  m). Raw counts of both red-  
210 backs (number individuals/ACO) and red efts (individuals/transect) were converted to density/m<sup>2</sup>  
211 as a measure of relative abundance. **Because our focus was on using abundance only as an index**  
212 **of population size, we did not adjust our estimates of abundance for detection probability.** We  
213 have shown elsewhere how to use detection probability to better estimate actual abundance of  
214 these species from ACO and searches of leaf litter along transects (Siddig et al. 2015).

215 We estimated both occupancy and detection probabilities of red-backs and red efts using  
216 single-species, single-season occupancy modeling (Mackenzie et al. 2002) as implemented in the  
217 *unmarked* package of R (Fiske and Chandler 2011) running within R version 3.1.2 (R Core Team  
218 2013). Site covariates in the occupancy and detection probability models included experimental  
219 block (ridge, valley) and relative humidity on the days when salamanders were sampled. The  
220 variables used to estimate detection and occupancy were chosen from the full model based on  
221 Akaike Information Criterion (AIC) values (Mackenzie 2006). Final estimates of occupancy and  
222 detection probabilities were based on best model which has the lowest AIC value (Table 2).  
223 Although we could estimate detection and occupancy for red-backs for all four sampling years,  
224 we could estimate these quantities for red efts only for 2014, as sample sizes for this species  
225 were inadequate in 2004 ( $N = 4$ ), and this species was not censused in 2005 or 2013.

226 Last, we examined potential relationships among decline of *T. canadensis*, other elements  
227 of habitat change, and abundance of salamanders using analysis of covariance (ANCOVA).  
228 Because habitat variables (understory vegetation – seedling density and seedlings percent cover)  
229 were strongly correlated, we first calculated a multivariate (principal component) score for them  
230 using the `prcomp()` function in R. We then used the ANCOVA model described in Ellison et al.  
231 (2010) and Orwig et al. (2013) to test for effects of canopy manipulation, habitat characteristics  
232 (principal axis scores – first axes, PC1), climate (relative humidity), and sample year (reflecting  
233 pre-treatment, post-treatment but pre-adelgid, and post-treatment and post-adelgid) on the  
234 abundance of red-backs. For red efts we used the same ANCOVA model except it only assessed  
235 the year and treatment effects, given the data deficit for other terms. The ANCOVA models were  
236 fit using the `lme()` function in the *nlme* library of R. In this model, block (ridge/valley) entered as  
237 a random effect, whereas all other terms entered as fixed effects (and canopy treatments were

238 nested within block). In reporting results, only the ANCOVA tables of the fixed effects are  
239 shown. Reported parameter estimates are adjusted for the random effects.

240

#### 241 *Data availability*

242 All raw data from this study are available from the Harvard Forest Data Archive  
243 (<http://harvardforest.fas.harvard.edu/data-archive>), datasets HF075 (2004, 2005 salamander  
244 data), HF270 (2013, 2014 salamander data), HF106 (understory vegetation) and HF001-10  
245 (relative humidity). A summary of data collected and analyses used in this study is given in  
246 Table 1.

247

#### 248 **Results**

249 Prior to applying the treatments, the occupancy probability of red-backs in the hemlock-  
250 dominated plots (what would become the logged, girdled, and hemlock control plots) was lower  
251 (mean = 76%, range = [0.65 – 0.82]) than in the hardwood plots (1.0) (Fig. 1A). In contrast,  
252 detectability of red-backs was twice as high in the hemlock-dominated plots (mean = 57 %,  
253 range = [0.55 – 0.63]) as in the hardwood plots (0.30) (Fig. 1B). The average relative abundance  
254 of red-backs in the hemlock-dominated plots was slightly higher than in the hardwood plots (2.0  
255 individuals/m<sup>2</sup> versus 1.2 individuals/m<sup>2</sup>, respectively; Fig. 1C).

256 One year after the canopy-manipulation treatments had been applied, the occupancy  
257 probability of red-backs had substantially increased to almost 100% in all plots (Fig. 1A). The  
258 associated standard errors of these occupancy estimates were 0.03 in hemlock-control plots and  
259 0.05 in the hardwood plots, but they were wider in the girdled and logged plots (0.13 and 0.29,  
260 respectively). In contrast, the detection probability of red-backs declined significantly in all plots  
261 following canopy manipulation, although the magnitude of change was lower in the hardwood

262 plots. The relative abundance of red-backs also decreased dramatically in all plots (including the  
263 hemlock control plots) after the manipulations: from 2.0 to 0.1 individuals/m<sup>2</sup> in the logged  
264 plots, from 2.4 to 0.6 individuals/m<sup>2</sup> in the girdled plots, from 1.6 to 0.2 individuals/m<sup>2</sup> in the  
265 hemlock-control plots, and from 1.2 to 0.2 individuals/m<sup>2</sup> in the hardwood control plots.

266 Ten years after the treatments, red-backs still occupied nearly 100% (standard error of the  
267 mean [SE] = 0.53) of the logged plots (Fig. 1A), 70% of the girdled and hardwood plots, and 62%  
268 of the hemlock-control plots. Detection probability was about the same in the logged plots ten  
269 years following canopy treatment as it was one year following canopy treatment. Over the same  
270 time, detection probability decreased three-fold in the girdling plots (12% to 4%) but increased  
271 almost nine-fold in the hemlock-control plots (from 7% to 62%) and five-fold in the hardwood  
272 plots (from 5% to 25%). Likewise, the relative abundance of red-backs increased slightly in the  
273 logged plots (0.1 individuals/m<sup>2</sup> to 0.2 individuals/m<sup>2</sup>), seven-fold in the hemlock-control plots  
274 (from 0.2 individuals/m<sup>2</sup> to 1.4 individuals/m<sup>2</sup>), and four-fold (from 0.2 individuals/m<sup>2</sup> to 0.8  
275 individuals/m<sup>2</sup>) in the hardwood plots. Overall, the current relative abundance of red-backs in  
276 hemlock-control plots was 1.6 individuals/m<sup>2</sup>, five times higher than in the girdled plots, seven  
277 times higher than in the logged plots, and about two times higher than in the hardwood plots.

278 Analysis of covariance revealed that there were no significant direct effects of canopy  
279 treatment, understory density, understory cover or relative humidity on the relative abundance of  
280 red-backs (Table 3). However, interaction between canopy treatments and relative humidity  
281 significantly affected the relative abundance of red-backs ( $F_{3,15} = 4.05$ ,  $P < 0.05$ ). Parameter  
282 estimates of the canopy treatment  $\times$  relative humidity interaction term (all relative to the hemlock  
283 controls and adjusted for random effects of the two blocks) equaled  $-0.27$  for the girdled plots,  $-$   
284  $0.07$  for the logged plots, and  $-0.19$  for the hardwood controls.

285 Similar to abundance pattern of red-backs, the relative density/m<sup>2</sup> of red efts before  
286 treatments was 0.07 individuals/m<sup>2</sup> (range = [0.05 – 0.08]) in the hemlock-dominated plots and  
287 0.04 individuals/m<sup>2</sup> in the hardwood plots (Fig. 2). However, the precision of the density  
288 estimates as indicated by the standard errors was higher in the hardwood plots (SE = 0.002) than  
289 in the hemlock plots (SE = 0.005).

290 Ten years after canopy manipulations, the relative density of red efts was significantly  
291 lower in the logged and girdled plots ( $F_{3,8} = 4.07$ ,  $P = 0.04$ ; Fig. 2). **However, red efts occupied**  
292 **equivalent areas in all plots and occupancy probability in all four plots was 100% (Fig. 2).**  
293 Detection probability in the hemlock-control plots was twice that of the logged and girdled plots  
294 and 1.5 times greater than in the hardwood plots (Fig. 2). Analysis of covariance revealed no  
295 significant direct effects of canopy treatments on the abundance of red efts ( $F_{3,8} = 1.62$ ,  $P > 0.05$ )  
296 or interactions between year and treatment ( $F_{3,8} = 3.83$ ,  $P > 0.05$ , but there was a significant  
297 direct effect of sample year on red eft abundance (estimate = -0.001;  $F_{1,8} = 28.89$ ,  $P < 0.01$ ;  
298 Table 3 and Fig. 2).

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## Discussion

302 This study provides a glimpse into three possible futures for populations of terrestrial  
303 salamanders in stands currently dominated by *T. canadensis* in central New England. The first  
304 two views are of what populations of salamanders may look like in ten years following two  
305 modes of *T. canadensis* loss – direct mortality caused by the adelgid and pre-emptive salvage  
306 logging. The third is a vision of what populations of salamanders will look like 50 – 70 years  
307 from now, when stands previously dominated by *T. canadensis* are succeeded by mixed

308 deciduous stands. Our results suggest that all three potential future forests will have fewer  
309 salamanders.

310 It appears that ten years following the loss of *T. canadensis* either by adelgid infestation  
311 or by pre-emptive salvage logging, the relative abundance of both red-backs and red efts will be  
312 significantly lower, and that the mode of *T. canadensis* loss will have little impact on the severity  
313 of the decline of either species (Figs. 1C and 2). The declines we observed in our experimental  
314 treatments were greater than any declines seen in a meta-analysis of twenty-four studies  
315 examining the effect of timber removal on the relative abundance of terrestrial salamanders  
316 (Tilghman et al. 2012). However, Hocking et al. (2013) observed declines similar to those that  
317 we observed (i.e.,  $\approx 85\%$ ), in group cuts, patch cuts, and clear-cuts. The decline in the relative  
318 abundance of red-backs was immediate and drastic in the logged plots. In contrast, a decline in  
319 the relative abundance of red-backs in the girdled plots was not seen in the first year following  
320 treatments, which was not especially surprising, as little foliar loss was seen in the first months  
321 following the girdling treatment (Orwig et al. 2013). Here we note that detection probability for  
322 red-backs also declined in the logged and girdled stands ten years after the treatments.

323 Our results also suggest that the relative abundance of red-backs will take at least 50  
324 years to recover to their relative abundance observed prior to logging if the 40% rate of increase  
325 observed between one-year post-treatment and ten years' post-treatment continues (Fig. 1C). The  
326 partial recovery of these populations observed in the logged plots could have been due to  
327 availability of dense understory vegetation in these plots (Orwig et al. 2013, Ellison et al. 2016),  
328 even though this variable did not have statistically significant effects on salamander abundance  
329 (Table 3). It is also possible that no recovery has occurred in the logged plots at all, as the  
330 relative abundance of red-backs in the logged plots was 40% lower than in the control plots in  
331 2005, but was 86% lower in 2014 (Fig. 1C). Further sampling in the girdled plots will be



332 required to determine whether red-backs are increasing or decreasing in these plots, since the  
333 treatment had just been applied in 2005, and we cannot yet determine whether relative  
334 abundance is still declining or whether it reached its lowest point somewhere between one and  
335 10 years after the experimental treatments were applied.

336 Finally, the hardwood control plots provide one scenario as to what the relative  
337 abundance of red-backs and red efts could be like 50-70 years after the loss of *T. canadensis*  
338 from these forests. Populations of these salamanders are unlikely to return to the levels seen in *T.*  
339 *canadensis*-dominated stands prior to adelgid infestation, and salamander population size may  
340 decline by as much as 50%. Given the significant contribution terrestrial salamanders make to  
341 the overall vertebrate biomass in forests (e.g., Burton and Likens 1975), decline in the relative  
342 abundance of terrestrial salamanders may impact populations of vertebrates that prey on them.

343 Declines in the relative abundance of both species of salamanders in both the hemlock-  
344 and hardwood-control plots between 2004 and 2014 also suggests that populations of both  
345 species may be experiencing declines caused by factors other than logging or simulated adelgid  
346 infestation. A far-ranging study assessing populations of plethodontid salamanders in 22 eastern  
347 North American states reported declines in the relative abundance of 180 out of 205 populations,  
348 but only 22 could be attributed to habitat destruction; soil acidification was one potential  
349 explanation for these declines (Highton 2005). Increases in temperatures or changes in  
350 precipitation are other potential causes. Another potential explanation, at least in our hemlock-  
351 control plots, is that adelgid infestation is causing changes in habitat that may have indirect  
352 negative effects on the relative abundance of each species. Finally, we note that sampling in  
353 control plots may not have been conducted far enough away from logged and girdled plots so as  
354 to eliminate edge effects; the abundance of salamanders in disturbed habitats can be impacted up  
355 to 34 m into the surrounding forest (Hocking et al. 2013). However, we carefully considered the

356 assumptions of modeling occupancy and detection probability in estimating these quantities, and  
357 subsequent estimates of abundance, from our data. Because each survey was done in a single  
358 season, we were unlikely to have violated the closure assumption. Surveys were done from late  
359 May – July, when adults are dispersing but red-backs juveniles have not yet emerged, reducing  
360 the influence of the latter in our estimates (Gotelli and Ellison 2012). Second, as our ACOs were  
361 more widely separated from one another (15 m apart) than the home range (~ 3×3m) of red-  
362 backs, it was reasonable to consider them as independent replicates. Due to the large home range  
363 of red efts we are not expecting this assumption to hold though. Finally, we accounted for habitat  
364 heterogeneity by including habitat characteristics in the statistical models.

365 Salamanders are sensitive to forest disturbances. Because of their position in the middle  
366 of food webs, where salamanders are both prey and predator, they are thought to be efficient and  
367 effective indicator species that can be used to monitor local environmental changes (Welsh and  
368 Droege 2001, Best and Welsh 2014). Consistent with this, both species showed significant  
369 responses to canopy manipulation treatments that simulated habitat disturbances. Long-term,  
370 systematic and integrated assessment of populations of red-backs and red efts, together with  
371 selected relevant habitat variables in focal research areas across New England (such as the  
372 Harvard Forest and Hubbard Brook LTER sites), may provide useful data with which to  
373 understand ongoing environmental changes in the region. However, for effective future  
374 monitoring, given the recent decline in relative abundance and detection probability, sampling  
375 these candidate indicators species may require increasing sample size and sampling occasions.

376 Overall, although this study experimentally assessed the response of hemlock decline on  
377 red backs and red efts at a small scale in Harvard Forest, we think that its findings have broader  
378 relevance. Declines in the relative abundance of salamanders in hemlock stands at Harvard  
379 Forest likely reflect similar declines in hemlock stands throughout the northeastern United

380 States. Along with relative abundance, occupancy probability, and detection probability, future  
381 investigations should examine other state variables, including age/stage structure, sex ratio, and  
382 body conditions so as to better describe the changes in these populations due to such habitat  
383 disturbances. Finally, our results add to the growing body of literature reporting on how the loss  
384 of foundation species such as *T. canadensis* impacts associated fauna.

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Table 1: Summary of the methodology of assessing the impacts of Hemlock decline on terrestrial amphibians in the Harvard Forest Hemlock Removal Experiment (HF-HeRE), including local climate conditions during summers of 2004, 2005, 2013 and 2014.

Species	Year / Period	Sampling method*	Sampling Occasions	Average relative humidity % during the sampling period	Variables assessed
<i>P. cinereus</i>	2004	CB	3	68	Abundance, occupancy and detectability
	May - July				
	2005	CB	5	69	Abundance, occupancy and detectability
	May - July				

Species	Year / Period	Sampling method*	Sampling Occasions	Average relative humidity % during the sampling period	Variables assessed
	2013 May - June	CB	2	84	Abundance, occupancy and detectability
	2014 May - July	CB	5	74	Abundance, occupancy and detectability
<i>N. viridescens</i>	2004 May - July	VES	3	68	Abundance

Species	Year / Period	Sampling method*	Sampling Occasions	Average relative humidity % during the sampling period	Variables assessed
	2014 May - July	VES	5	74	Abundance, occupancy and detectability

\*CB = hemlock Cover board 1× 0.25 ×0.02 m; VES = visual encounter surveys along 1× 60 m strip transects.

Table 2. Candidate models of occupancy and detection probabilities and their AIC values.

Parameter estimates (Est) and their standard errors (SE) are given for each model. The best-fit model (lowest AIC) is indicated with bold type.

1. Red-backed salamanders							
Year	Treatment	Model	Occupancy		Detectability		AIC
			Est	SE	Est	SE	
2004	Hardwood control	Intercept only	1	0.008	0.29	0.09	<b>32.98</b>
		Relative humidity	0.99	0.06			34.56
		Block only	1	0.007			36.77
		Block, Relative humidity	1	0.006			38.48
	Logged	Intercept only	0.82	0.18	0.55	0.14	<b>33.3</b>
		Relative humidity	0.76	0.16			33.84
		Block only	0.75	0.15			36.18
		Block, Relative humidity	0.75	0.15			37.45
	Girdled	Intercept only	0.82	0.18	0.55	0.14	<b>36.18</b>
		Relative humidity	0.81	0.17			37.61

		Block only	1	0.007			NA
		Block, Relative humidity	0.81	0.17			41.61
		<hr/>					
		Intercept only	0.65	0.18	0.63	0.14	<b>33.25</b>
		Relative humidity	0.66	0.18			35.14
	Hemlock control	Block only	0.74	0.21			35.18
		Block, Relative humidity	0.73	0.21			36.33
		<hr/>					
		Intercept only	0.99	0.05	0.05	0.03	<b>19.88</b>
		Relative humidity	0.85	0.56			21.91
	Hardwood control	Block only	0.99	0.07			23.88
		Block, Relative humidity	0.99	0.1			25.82
		<hr/>					
2005		Intercept only	0.99	0.29	0.03	0.03	<b>13.08</b>
		Relative humidity	0.97	0.63			14.78
	Logged	Block only	0.99	0.09			15.94
		Block, Relative humidity	0.99	0.07			17.72
		<hr/>					
		Intercept only	0.99	0.13	0.12	0.05	<b>34.14</b>
	Girdled	Relative humidity	0.99	0.04			34.87
		<hr/>					

		Block only	1	0.02			37.91
		Block, Relative humidity	0.99	0.07			38.79
		<hr/>					
		Intercept only	0.99	0.03	0.07	0.04	<b>25.31</b>
		Relative humidity	0.99	0.08			25.41
	Hemlock control	Block only	1	0.02			28.52
		Block, Relative humidity	1	0.021			28.94
		<hr/>					
		Intercept only	0.45	0.32	0.33	0.24	<b>37.4</b>
		Relative humidity	0.39	0.26			38
	Hardwood control	Block only	0.46	0.29			40.18
		Block, Relative humidity	0.41	0.23			41.07
		<hr/>					
2013		Intercept only	0.99	0.16	0.07	0.04	25.31
		Relative humidity	0.99	0.32			<b>23.04</b>
	Logged	Block only	0.99	0.09			28.94
		Block, Relative humidity	1	0.001			26.6
		<hr/>					
		Intercept only	0.99	0.28	0.05	0.03	<b>19.88</b>
	Girdled	Relative humidity	1	0.01			21
		<hr/>					



		Block only	0.99	0.26			21.88
		Block, Relative humidity	0.99	0.06			23.01
		Intercept only	0.42	0.11	0.76	0.13	45.66
		Relative humidity	0.41	0.11			<b>43.95</b>
	Hemlock control	Block only	0.42	0.12			49.66
		Block, Relative humidity	0.4	0.11			47.5
		Intercept only	0.99	0.03	0.16	0.03	<b>91.94</b>
		Relative humidity	0.99	0.03			93.91
	Hardwood control	Block only	0.99	0.02			93.93
		Block, Relative humidity	1	0.02			95.91
2014		Intercept only	0.98	0.78	0.01	0.01	<b>15.2</b>
		Relative humidity	0.98	0.78			15.8
	Logged	Block only	0.99	0.28			16.97
		Block, Relative humidity	0.99	0.47			17.57
		Intercept only	0.44	0.19	0.2	0.09	<b>62.01</b>
	Girdled	Relative humidity	0.42	0.18			62.32

	Block only	0.43	0.19			63.8
	Block, Relative humidity	0.42	0.18			64.1
	Intercept only	0.83	0.09	0.48	0.06	<b>130.8</b> 3
	Relative humidity	0.82	0.09			132.8 3
Hemlock control	Block only	0.83	0.09			133.8 1
	Block, Relative humidity	0.82	0.09			135.8 1
<hr/>						
Red efts						
<hr/>						
	Intercept only	1	0.01	0.26	0.04	96.11
	Relative humidity	0.99	0.02			<b>95.12</b>
	Block only	1	0.01			98.04
	Block, Relative humidity	0.99	0.03			97.05
2014	Intercept only	1	0.009	0.17	0.04	78.2
	Relative humidity	0.99	0.01			<b>72.87</b>
	Block only	1	0.008			80.19
	Block, Relative humidity	0.99	0.02			74.86

	Intercept only	0.86	0.36	0.16	0.07	67.94
Girdled	Relative humidity	0.85	0.36			69.94
	Block only	1	0.02			<b>67.34</b>
	Block, Relative humidity	0.99	0.05			69.35
	Intercept only	0.99	0.01	0.32	0.05	104.4 9
Hemlock control	Relative humidity	0.99	0.04			<b>101.8 2</b>
	Block only	1	0.004			105.9 8
	Block, Relative humidity	1	0.005			102.8 4
	Intercept only	0.99	0.01	0.32	0.05	104.4 9

Table 3: Results of the analysis of covariance (ANCOVA) testing direct effects of canopy treatments, local habitat characteristics changes, and their interaction terms on the abundances of *P. cinereus* and *N. viridescens* in the Harvard Forest Hemlock Removal Experiment.

<b>Model: <i>P. cinereus</i> ~ Treatment * (density + cover + RH) + year</b>					
	<b>DF</b>	<b>Sum Sq.</b>	<b>Mean Sq.</b>	<b>F-value</b>	<b>P-value</b>
Treatment	3	5.516	1.839	1.516	0.2510
Year	1	4.049	4.049	3.339	0.0876
Understory density	1	1.457	1.457	1.201	0.2904
Understory percent cover	1	4.242	4.242	3.498	0.0811
Relative humidity	1	0.157	0.157	0.129	0.7244
Treatment : Understory density	3	2.780	0.927	0.764	0.5317
Treatment : Understory % cover	3	2.790	0.930	0.767	0.5302
Treatment : relative humidity	3	14.766	4.922	4.059	0.0269 *
Residuals	15	18.191	1.213		
<b>Model: <i>N. viridescens</i> ~ Treatment * year</b>					
	<b>DF</b>	<b>Sum Sq.</b>	<b>Mean Sq.</b>	<b>F-value</b>	<b>P-value</b>
Year	1	0.0025	0.0025	28.890	0.0007 ***

Treatment	3	0.0004	0.0001	1.621	0.2597
Treatments: year	3	0.0010	0.0003	3.832	0.0571
Residuals	8	0.0007	0.0001		

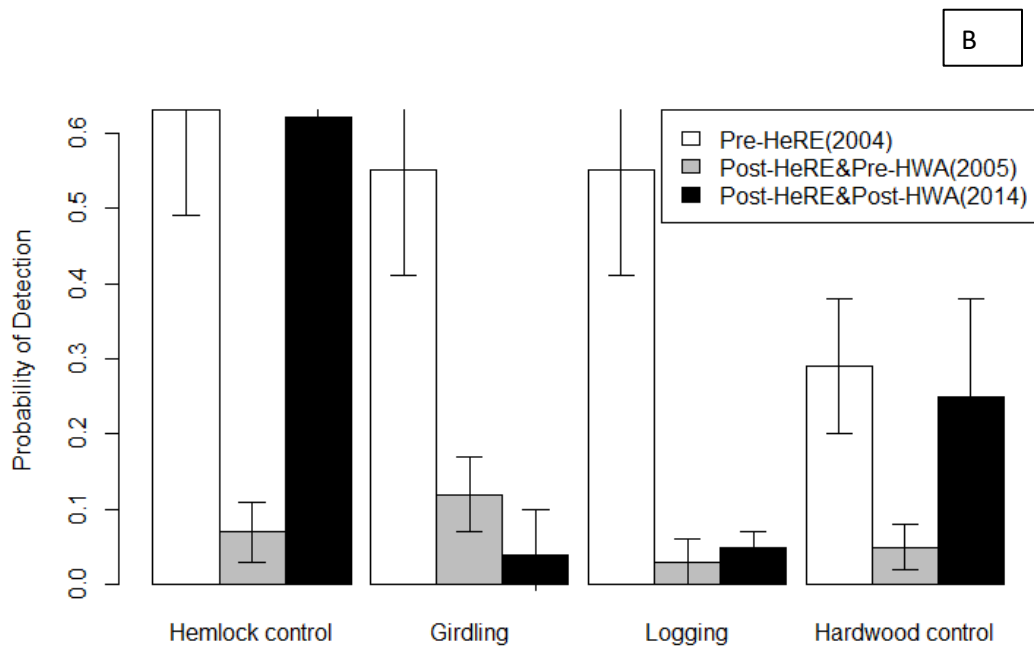
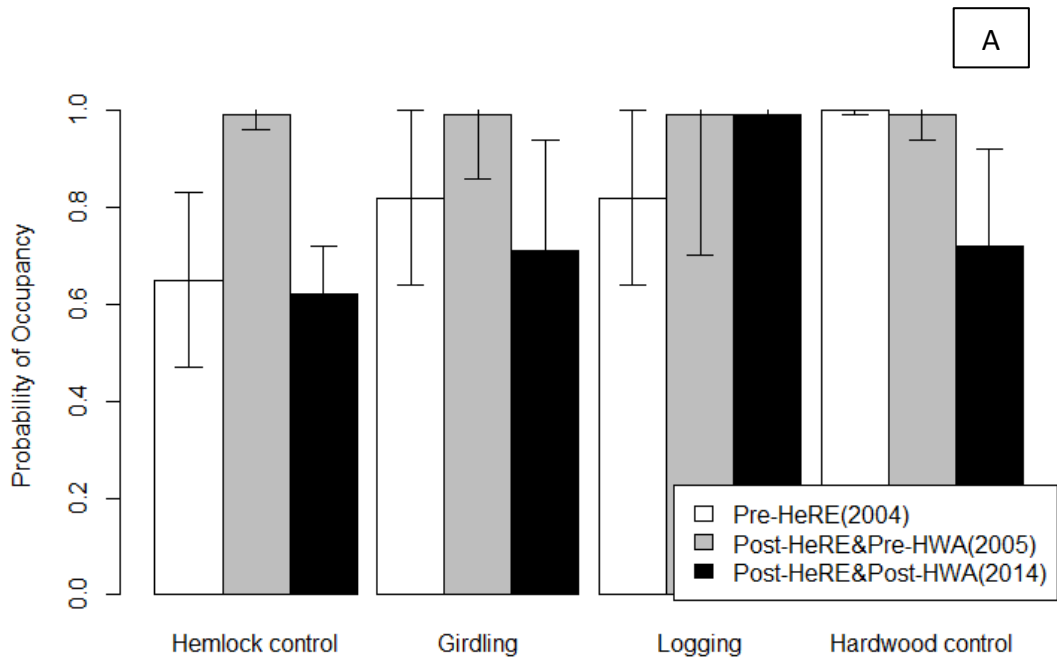
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## Figure legends

Figure 1. Occupancy (A), detection probabilities (B), and relative abundance (C) of *P. cinereus* in Harvard Forest before and after canopy manipulations simulating adelgid outbreak. Error bars represent standard errors of the means of the estimates.

Figure 2. Top: Average relative abundance (density/ m<sup>2</sup>) of *N. viridescens* at Harvard Forest before and after canopy manipulations simulating adelgid outbreak. Bottom: Occupancy and detection probability of *N. viridescens* in 2014, ten years after canopy manipulations simulating adelgid outbreak in Harvard Forest. Error bars represent standard errors of the means of the estimate

Fig. 1



C

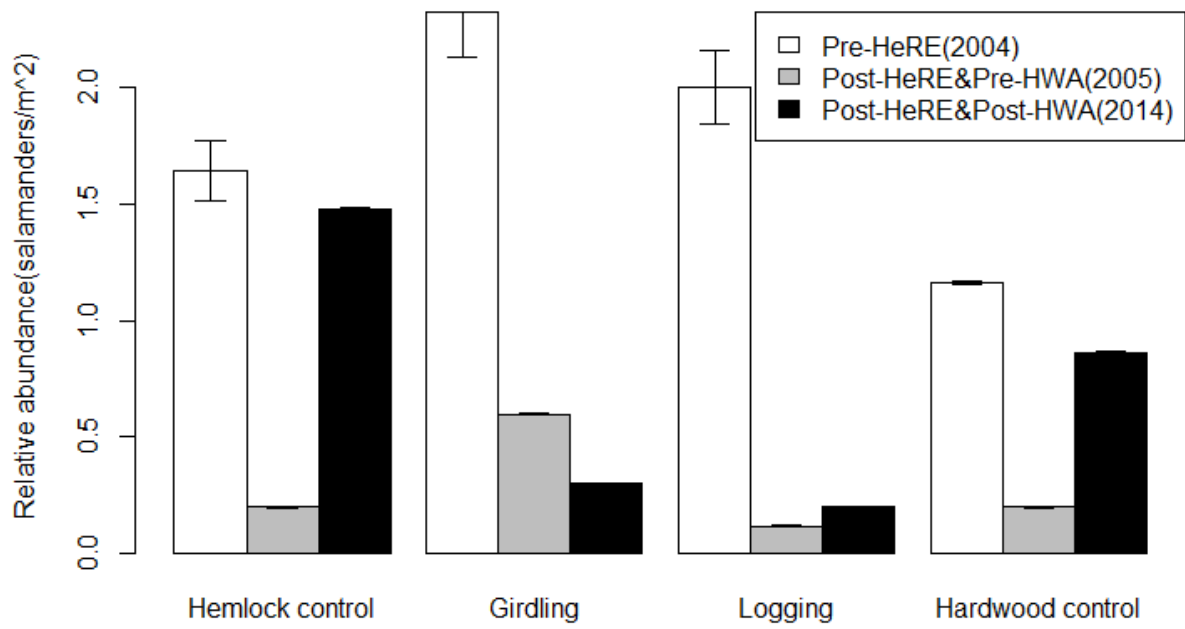




Figure 2

