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

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Abstract

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

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

Introduction

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

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

Tsuga canadensis also is declining throughout its range. The nonnative insect *Adelges tsugae* Annand (hemlock woolly adelgid), introduced to the US from Japan in the early 1950s, is killing hemlock seedlings, saplings, and mature trees (Ellison et al. 2010). In addition, many landowners and land managers have been logging *T. canadensis* prior to the arrival of the adelgid (Orwig et al. 2002, Foster and Orwig 2006). In New England, as *T. canadensis* declines or is logged out, it has been replaced by deciduous species including *Acer rubrum* L. (red maple) *Betula lenta* L. (black birch), and *Quercus rubra* L. (northern red oak) (Orwig and Foster 1998, Orwig 2002, Brooks 2004).

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

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

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

Materials and Methods

Study site and experimental design

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

Study species

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^2 for males and juveniles and 24 m^2 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

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

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

Sampling

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

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

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

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

Habitat characteristics

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

Estimation of detection and occupancy probabilities and relative abundance

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

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

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

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

Data availability

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

Results

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

One year after the canopy-manipulation treatments had been applied, the occupancy probability of red-backs had substantially increased to almost 100% in all plots (Fig. 1A). The associated standard errors of these occupancy estimates were 0.03 in hemlock-control plots and 0.05 in the hardwood plots, but they were wider in the girdled and logged plots (0.13 and 0.29, respectively). In contrast, the detection probability of red-backs declined significantly in all plots following canopy manipulation, although the magnitude of change was lower in the hardwood plots. The relative abundance of red-backs also decreased dramatically in all plots (including the hemlock control plots) after the manipulations: from 2.0 to 0.1 individuals/m^2 in the logged plots, from 2.4 to 0.6 individuals/m^2 in the girdled plots, from 1.6 to 0.2 individuals/m^2 in the hemlock-control plots, and from 1.2 to 0.2 individuals/m^2 in the hardwood control plots.

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

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

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

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

Discussion

This study provides a glimpse into three possible futures for populations of terrestrial salamanders in stands currently dominated by *T. canadensis* in central New England. The first two views are of what populations of salamanders may look like in ten years following two modes of *T. canadensis* loss – direct mortality caused by the adelgid and pre-emptive salvage logging. The third is a vision of what populations of salamanders will look like 50 – 70 years from now, when stands previously dominated by *T. canadensis* are succeeded by mixed deciduous stands. Our results suggest that all three potential future forests will have fewer salamanders.

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

Our results also suggest that the relative abundance of red-backs will take at least 50 years to recover to their relative abundance observed prior to logging if the 40% rate of increase observed between one-year post-treatment and ten years’ post-treatment continues (Fig. 1C). The partial recovery of these populations observed in the logged plots could have been due to availability of dense understory vegetation in these plots (Orwig et al. 2013, Ellison et al. 2016), even though this variable did not have statistically significant effects on salamander abundance (Table 3). It is also possible that no recovery has occurred in the logged plots at all, as the relative abundance of red-backs in the logged plots was 40% lower than in the control plots in 2005, but was 86% lower in 2014 (Fig. 1C). Further sampling in the girdled plots will be required to determine whether red-backs are increasing or decreasing in these plots, since the treatment had just been applied in 2005, and we cannot yet determine whether relative abundance is still declining or whether it reached its lowest point somewhere between one and 10 years after the experimental treatments were applied.

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

Declines in the relative abundance of both species of salamanders in both the hemlock- and hardwood-control plots between 2004 and 2014 also suggests that populations of both species may be experiencing declines caused by factors other than logging or simulated adelgid infestation. A far-ranging study assessing populations of plethodontid salamanders in 22 eastern North American states reported declines in the relative abundance of 180 out of 205 populations, but only 22 could be attributed to habitat destruction; soil acidification was one potential explanation for these declines (Highton 2005). Increases in temperatures or changes in precipitation are other potential causes. Another potential explanation, at least in our hemlock-control plots, is that adelgid infestation is causing changes in habitat that may have indirect negative effects on the relative abundance of each species. Finally, we note that sampling in control plots may not have been conducted far enough away from logged and girdled plots so as to eliminate edge effects; the abundance of salamanders in disturbed habitats can be impacted up to 34 m into the surrounding forest (Hocking et al. 2013). However, we carefully considered the assumptions of modeling occupancy and detection probability in estimating these quantities, and subsequent estimates of abundance, from our data. Because each survey was done in a single season, we were unlikely to have violated the closure assumption. Surveys were done from late May – July, when adults are dispersing but red-backs juveniles have not yet emerged, reducing the influence of the latter in our estimates (Gotelli and Ellison 2012). Second, as our ACOs were more widely separated from one another (15 m apart) than the home range (~ 3×3m) of red-backs, it was reasonable to consider them as independent replicates. Due to the large home range of red efts we are not expecting this assumption to hold though. Finally, we accounted for habitat heterogeneity by including habitat characteristics in the statistical models.

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

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

States. Along with relative abundance, occupancy probability, and detection probability, future investigations should examine other state variables, including age/stage structure, sex ratio, and body conditions so as to better describe the changes in these populations due to such habitat disturbances. Finally, our results add to the growing body of literature reporting on how the loss 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
P. cinereus	2004 May - July	CB	3	68	Abundance, occupancy and detectability
	2005 May - July	CB	5	69	Abundance, occupancy and detectability

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
N. viridescens	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	**32.98**
		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	**33.3**
		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	**36.18**
		Relative humidity	0.81	0.17			37.61

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

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

		Block only	0.99	0.26			21.88
		Block, Relative humidity	0.99	0.06			23.01
	Hemlock control	Intercept only	0.42	0.11	0.76	0.13	45.66
		Relative humidity	0.41	0.11			**43.95**
		Block only	0.42	0.12			49.66
		Block, Relative humidity	0.4	0.11			47.5
2014	Hardwood control	Intercept only	0.99	0.03	0.16	0.03	**91.94**
		Relative humidity	0.99	0.03			93.91
		Block only	0.99	0.02			93.93
		Block, Relative humidity	1	0.02			95.91
	Logged	Intercept only	0.98	0.78	0.01	0.01	**15.2**
		Relative humidity	0.98	0.78			15.8
		Block only	0.99	0.28			16.97
		Block, Relative humidity	0.99	0.47			17.57
	Girdled	Intercept only	0.44	0.19	0.2	0.09	**62.01**
		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
	Hemlock control	Intercept only	0.83	0.09	0.48	0.06	**130.83**
		Relative humidity	0.82	0.09			132.83
		Block only	0.83	0.09			133.81
		Block, Relative humidity	0.82	0.09			135.81
Red efts							
2014	Hardwood control	Intercept only	1	0.01	0.26	0.04	96.11
		Relative humidity	0.99	0.02			**95.12**
		Block only	1	0.01			98.04
		Block, Relative humidity	0.99	0.03			97.05
	Logged	Intercept only	1	0.009	0.17	0.04	78.2
		Relative humidity	0.99	0.01			**72.87**
		Block only	1	0.008			80.19
		Block, Relative humidity	0.99	0.02			74.86

Girdled	Intercept only	0.86	0.36	0.16	0.07	67.94
	Relative humidity	0.85	0.36			69.94
	Block only	1	0.02			**67.34**
	Block, Relative humidity	0.99	0.05			69.35
Hemlock control	Intercept only	0.99	0.01	0.32	0.05	104.49
	Relative humidity	0.99	0.04			**101.82**
	Block only	1	0.004			105.98
	Block, Relative humidity	1	0.005			102.84

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.

Model: *P. cinereus* ~ Treatment * (density + cover + RH) + year

	DF	**Sum Sq.**	**Mean Sq.**	**F-value**	**P-value**
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		

Model: *N. viridescens* ~ Treatment * year

	DF	**Sum Sq.**	**Mean Sq.**	**F-value**	**P-value**
Year	1	0.0025	0.0025	28.890	0.0007 ***

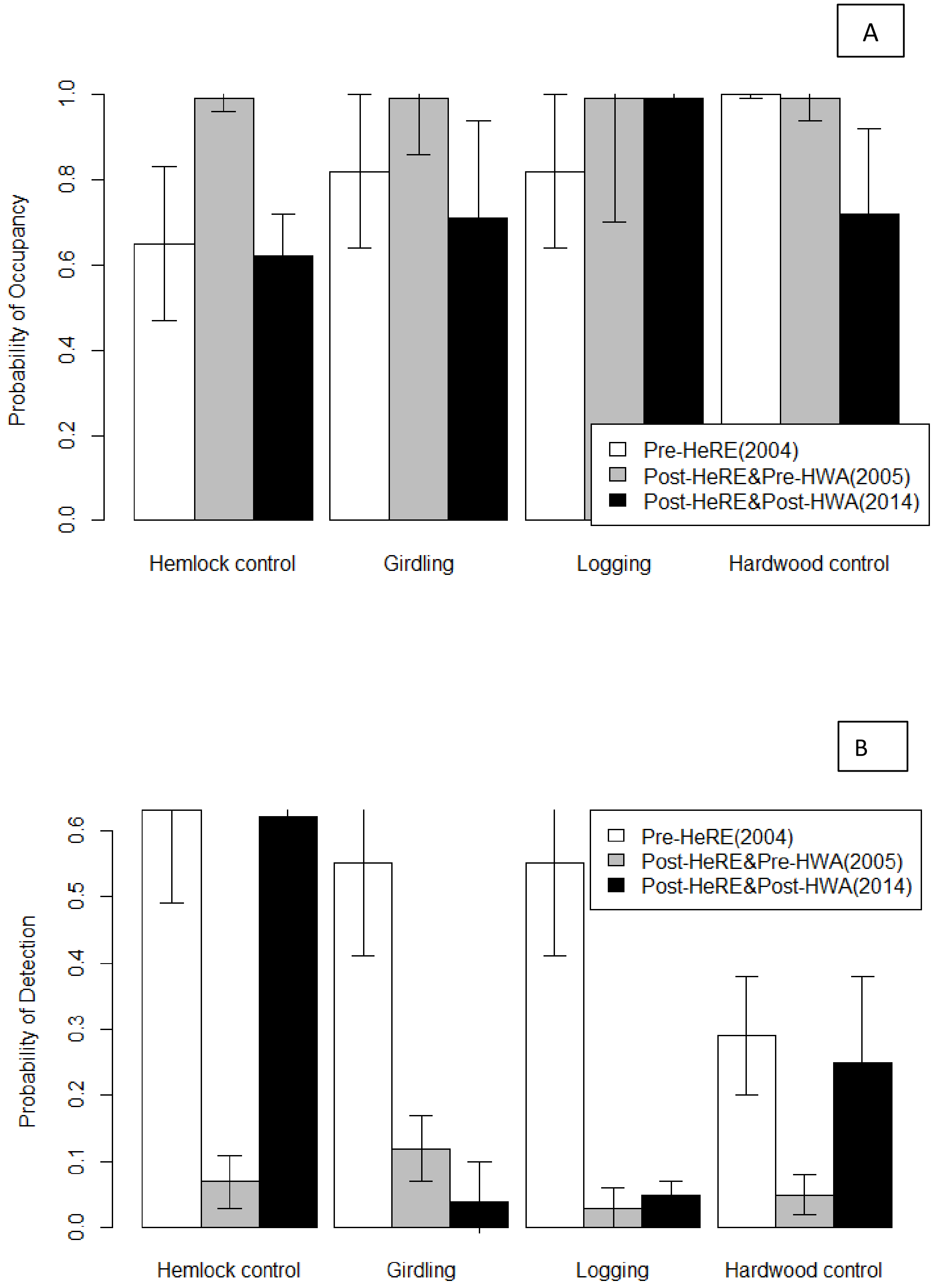
Treatment	3	0.0004	0.0001	1.621	0.2597
Treatments: year	3	0.0010	0.0003	3.832	0.0571
Residuals	8	0.0007	0.0001		

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^2)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


A
Probability of Occupancy
0.0
0.2
0.4
0.6
0.8
1.0
□ Pre-HeRE(2004)
▨ Post-HeRE&Pre-HWA(2005)
■ Post-HeRE&Post-HWA(2014)
Hemlock control
Girdling
Logging
Hardwood control
B
Probability of Detection
0.0
0.1
0.2
0.3
0.4
0.5
0.6
□ Pre-HeRE(2004)
▨ Post-HeRE&Pre-HWA(2005)
■ Post-HeRE&Post-HWA(2014)
Hemlock control
Girdling
Logging
Hardwood control

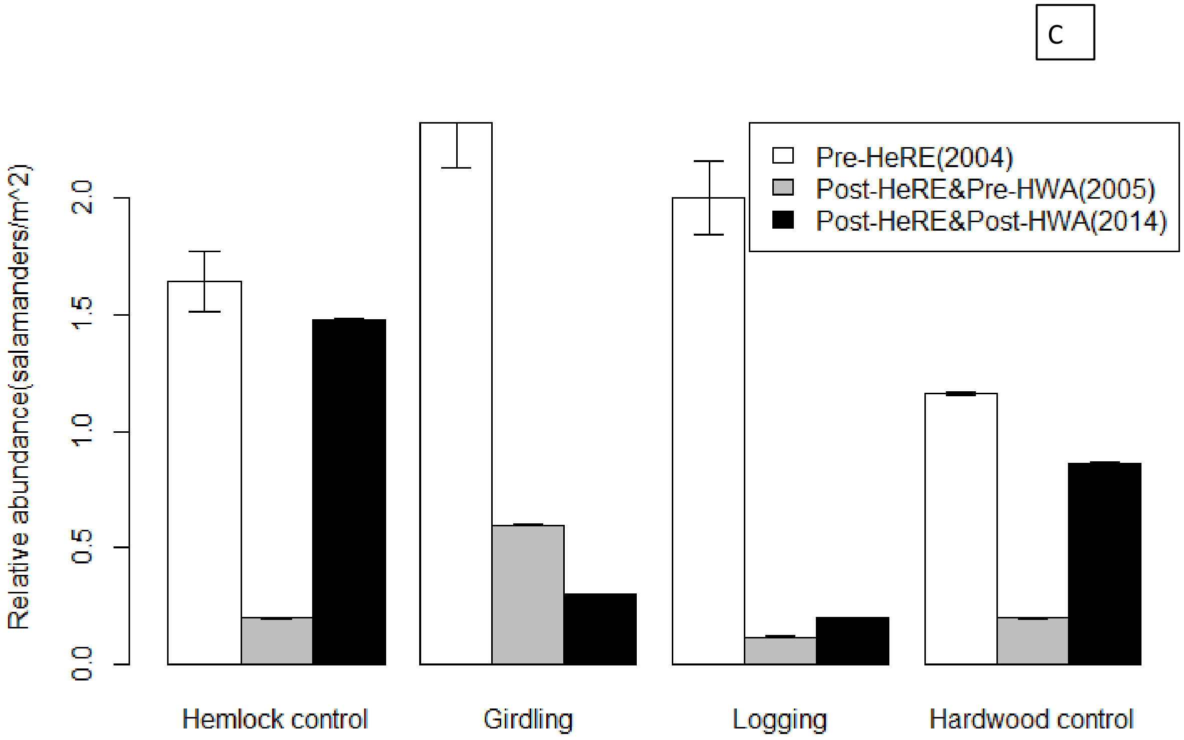
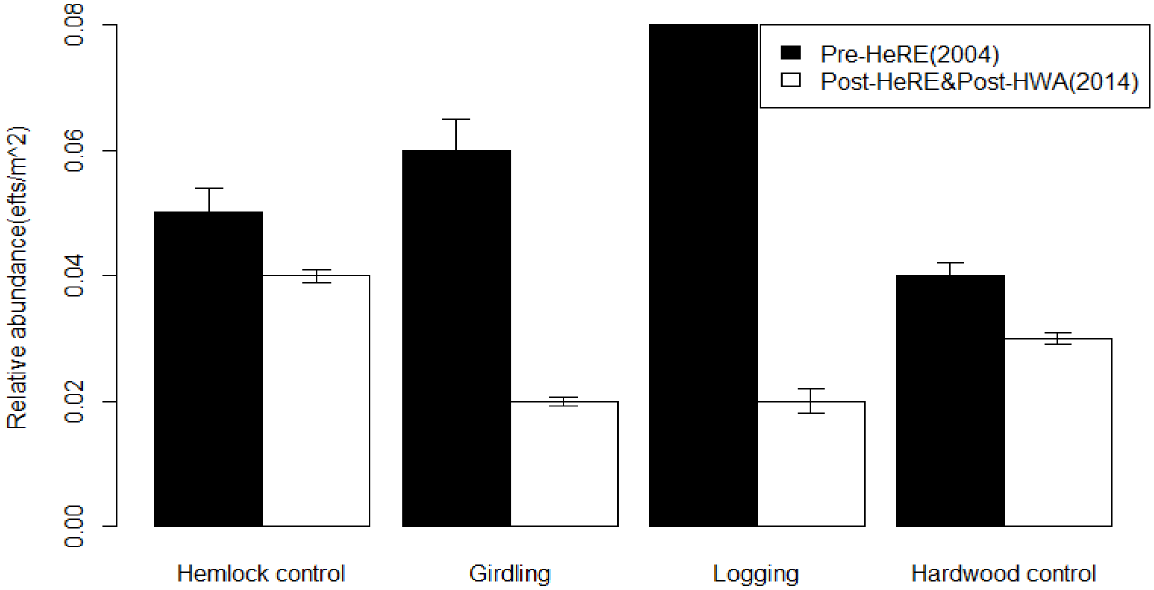

c
Relative abundance(salamanders/m^2)
0.0
0.5
1.0
1.5
2.0
☐ Pre-HeRE(2004)
▨ Post-HeRE&Pre-HWA(2005)
■ Post-HeRE&Post-HWA(2014)
Hemlock control
Girdling
Logging
Hardwood control

Figure 2



Relative abundance(efts/m^2)
0.00
0.02
0.04
0.06
0.08
■ Pre-HeRE(2004)
☐ Post-HeRE&Post-HWA(2014)
Hemlock control
Girdling
Logging
Hardwood control