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Eastern hemlock (*Tsuga canadensis*) regeneration in the presence of hemlock woolly adelgid (*Adelges tsugae*) and elongate hemlock scale (*Fiorinia externa*)

Evan L. Preisser, Mailea R. Miller-Pierce, Jacqueline Vansant, and David A. Orwig

Abstract: The hemlock woolly adelgid (*Adelges tsugae* Annand) is an invasive hemipteran that poses a major threat to eastern hemlock (*Tsuga canadensis* (L.) Carrière) forests in the United States. We conducted three surveys over a five-year period that assessed the density of hemlock woolly adelgid (HWA) and a second invasive pest, the elongate hemlock scale (EHS; *Fiorinia externa* Ferris), overstory hemlock mortality, and hemlock regeneration in ~140 hemlock stands (mean size, 44 ha; range, 7–305 ha) within a 7500 km² north–south transect of southern New England (USA). In each stand, we rated HWA and EHS density on 50 hemlock trees using a 0–3 scale (0, none; 1, 1–10 organisms/m branch; 2, 11–100 organisms/m branch; 3, >100 organisms/m branch). Data on the presence or absence of regeneration were taken in 2005; in 2007 and 2009, we quantitatively assessed regeneration by counting the number of hemlock seedlings in three 16 m² plots per stand. In 2005, 81% of sampled stands had HWA, 72% had EHS, and 66% had hemlock regeneration. In 2007, 86% of sampled stands had HWA, 79% had EHS, and 46% had hemlock regeneration. In 2009, 91% of stands had HWA, 87% had EHS, and 37% had hemlock regeneration. The proportion of stands with hemlock regeneration declined 46% between 2005 and 2009, and hemlock seedling density declined 71% between 2007 and 2009. A best-fit model selection algorithm found that this decrease was inversely correlated with stand-level adelgid density. There was no correlation between the change in seedling density and stand-level density of the elongate hemlock scale. The apparent decline in regeneration suggests that the ecosystem-level changes currently occurring in southern New England may be difficult to reverse.

Résumé : Le puceron lanigère de la pruche (*Adelges tsugae* Annand) est un hémiptère invasif qui représente une grave menace pour les forêts de pruche du Canada (*Tsuga canadensis* (L.) Carrière) aux États-Unis. Nous avons réalisé trois inventaires sur une période de cinq ans pour évaluer la densité du puceron lanigère de la pruche (PLP) et d'un second ravageur invasif, la cochenille de la pruche (CP) (*Fiorinia externa* Ferris), la mortalité de la pruche dans l'étage dominant et la régénération de la pruche dans ~140 peuplements de pruche (taille moyenne, 44 ha; étendue, 7–305 ha) à l'intérieur d'un transect nord–sud de 7500 km² dans le sud de la Nouvelle-Angleterre (É.-U.). Dans chaque peuplement, nous avons évalué la densité du PLP et de la CP sur 50 pruches en utilisant une échelle de 0 à 3 (0, aucun individu; 1, 1–10 individus/m de branche; 2, 11–100 individus/m de branche; 3, >100 individus/m de branche). Les données sur l'absence ou la présence de régénération ont été recueillies en 2005; en 2007 et 2009 nous avons évalué quantitativement la régénération en comptant le nombre de semis de pruche dans trois placettes de 16 m² par peuplement. En 2005, le PLP, la CP et la régénération de pruche étaient présents dans respectivement 81, 72 et 66 % des peuplements. En 2007, le PLP, la CP et la régénération de pruche étaient présents dans respectivement 86, 79 et 46 % des peuplements. En 2009, le PLP, la CP et la régénération de pruche étaient présents dans respectivement 91, 87 et 37 % des peuplements. La proportion de peuplements avec une régénération de pruche a diminué de 71 % entre 2007 et 2009. Un algorithme de sélection du meilleur modèle a montré que cette diminution était inversement corrélée avec la densité du puceron à l'échelle du peuplement. Il n'y avait pas de corrélation entre le changement dans la densité des semis et la densité à l'échelle du peuplement de la CP. Ce déclin apparent de la régénération indique que les changements en cours à l'échelle de l'écosystème dans le sud de la Nouvelle-Angleterre pourraient être difficiles à inverser.

[Traduit par la Rédaction]

Received 15 January 2011. Accepted 10 September 2011. Published at www.nrcresearchpress.com/cjfr on 22 November 2011.

E.L. Preisser, M.R. Miller-Pierce, and J. Vansant. Department of Biological Sciences, Woodward Hall, 9 East Alumni Avenue, University of Rhode Island, Kingston, RI 02881, USA.

D.A. Orwig. Harvard University, Harvard Forest, Petersham, MA 01366, USA.

Corresponding author: Evan L. Preisser (e-mail: preisser@uri.edu).

Introduction

The hemlock woolly adelgid (*Adelges tsugae* Annand; hereafter HWA) feeds on eastern hemlock (*Tsuga canadensis* (L.) Carriere) in the northeastern US. This hemipteran is native to Asia, with the invasion appearing to have originated from a single source location in southern Japan (Havill et al. 2006). HWA first appeared in Virginia in the 1950s and has since spread as far south as Georgia and as far north as Maine (Souto et al. 1996; U.S. Forest Service 2008). Although a “western” form of HWA is present on the west coast of the US, it is apparently endemic to the region and differs in a number of respects from the invasive adelgids present in the northeastern US (Havill et al. 2006). HWA is bivoltine and parthenogenetic in the invaded range and a specialist on eastern and Carolina hemlock (*Tsuga caroliniana*). Although the early-instar “crawler” phase can move between branches, between-tree dispersal occurs passively by wind or biotic agents (McClure 1990). The sessile adults feed at the base of hemlock needles on ray parenchyma (Young et al. 1995); HWA-infested trees can die in as little as four years, and few trees survive more than 10 years of infestation (McClure 1991; Orwig and Foster 1998). This invasive insect thus threatens to extirpate a long-lived “foundation species” from much or all of the invaded range, permanently altering native ecosystems in which hemlock provides critical wildlife habitat while shading and cooling headwater streams (Ellison et al. 2005).

Eastern hemlock is also threatened by a second invasive insect, the elongate hemlock scale (*Fiorinia externa* Ferris; hereafter EHS). This hemipteran (~1.5 mm adult) was introduced into New York City from Asia in 1908 (Sasscer 1912). Its range began to expand in the mid-1970s, and it is now found in 14 eastern states (Lambdin et al. 2005). It is found almost exclusively on eastern hemlock in the northeastern US (McClure and Fergione 1977). EHS reproduces sexually and is univoltine in the northeastern US. The eggs of overwintering adults hatch in late spring to produce crawlers that can move actively or be dispersed passively; the sessile adults suck fluids from the mesophyll on the underside of hemlock needles (McClure 2002). Although high-density EHS infestations (e.g., >1 scale/needle) can reduce branch growth (McClure 1980), research comparing the impacts of EHS with those of HWA has found that EHS has a much smaller impact on its host plant than does HWA (Miller-Pierce et al. 2010; Preisser and Elkinton 2008; Radville et al. 2011).

Although the damage done to hemlock forests by HWA (and, to a lesser extent, EHS) has been documented, data on hemlock mortality primarily address the fate of hemlock saplings and mature trees, and less attention has been paid to hemlock regeneration. Pests may, however, affect younger trees differently than older individuals: many pests and pathogens exhibit strong preferences for plants of a specific age or size. For example, the invasive balsam woolly adelgid (*Adelges piceae* Ratz.) feeds almost exclusively on Fraser fir (*Abies fraseri* (Pursh) Poir.) trees >4 cm diameter at breast height (dbh), leading to forest stands that contain few mature but many small trees (Smith and Nicholas 2000). Conversely, the chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) has eliminated mature American chestnut (*Castanea dentata* (Marsh.) Borkh.) trees but does not attack small stump

sprouts, allowing this former canopy-dominant tree to survive as a small understory shrub (reviewed in Ellison et al. 2005).

Although relatively little is known about the impacts of HWA or EHS on understory hemlock, there are a number of pathways by which HWA and EHS might potentially affect hemlock regeneration. Regeneration might be affected directly by pest colonization and mortality of seedlings or indirectly by (i) reduced seed production linked to the decline and death of mature trees, (ii) reductions in seed survival, persistence, or germination, or (iii) poor survival of germinated seedlings via changes in abiotic conditions caused by overstory hemlock mortality (Ellison et al. 2005). Stadler et al. (2005) and Small et al. (2005) both documented high hemlock sapling mortality in stands deteriorating from HWA in southern New England. We are aware of only a few papers that address hemlock regeneration in HWA-invaded areas and none that address the impact of EHS on regeneration. Although ongoing research has confirmed that both invasive species readily colonize and feed upon hemlock seedlings ~0.3 m in height (L. Gonda-King, unpublished data), we were unable to find any published research documenting this fact. Both Orwig and Foster (1998) and Kizlinski et al. (2002) mention, but do not quantify, the fact that seedling densities were lower in HWA-infested areas. In contrast, Eschtruth et al. (2006) observed an increase in overall frequency and cover of hemlock seedlings following overstory hemlock decline resulting from HWA. If HWA and EHS have minimal impacts on hemlock regeneration, any future discovery and release of successful biocontrol agents may allow surviving seedlings to mature and restore hemlock-dominated ecosystems. Conversely, if one or both insects eliminate seedlings as effectively as HWA does mature trees, then even successful biocontrol agents may prove insufficient at preventing the functional extirpation of hemlock from large portions of its range.

We present the results of three landscape-level surveys of the density of HWA and EHS, hemlock regeneration, and overstory hemlock mortality over a five-year period in a 7500 km² transect of southern New England. We found a decline in the proportion of hemlock stands with regeneration and the density of hemlock seedlings and a negative correlation between changes in seedling density and the degree of stand-level HWA infestation. Our findings suggest that even in areas where overstory hemlock decline is happening less rapidly than predicted, hemlock-dominated ecosystems are unlikely to persist over the long term.

Methods

We repeatedly surveyed ~140 hemlock stands (Fig. 1; Table 1) in a 7500 km² transect of southern New England stretching from Long Island Sound in southern Connecticut to the Vermont border in northern Massachusetts. Details of stand selection, as well as this region’s climate and geology, are given in Orwig et al. (2002). Stands were visited in June–July 2005 ($n = 137$), 2007 ($n = 140$), and 2009 ($n = 141$) to survey hemlock health, as well as stand-level infestation by HWA and EHS. Each time that a stand was visited, we selected 50 hemlocks (>2 m in height and >8 cm dbh) for branch-level sampling. This was done by choosing the nearest suitable hemlock, sampling it, locating the next nearest

Fig. 1. Presence or absence of *T. canadensis* regeneration (seedlings 0–1 m in height) in hemlock stands surveyed in 2005, 2007, and 2009.

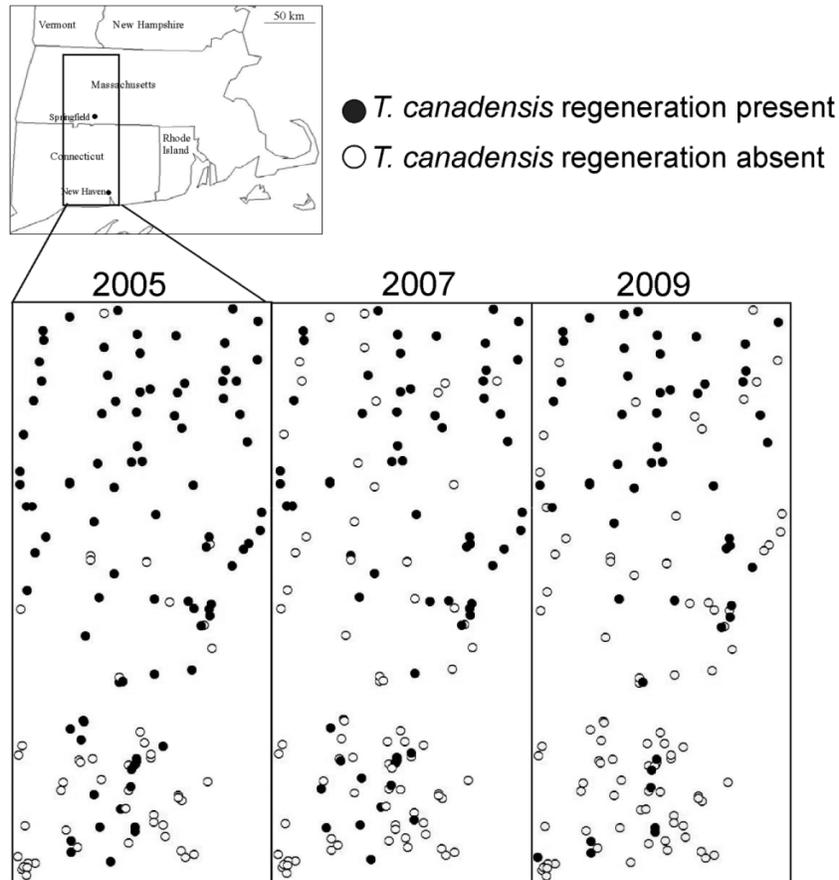


Table 1. Site and soil characteristics of eastern hemlock (*T. canadensis*) stands sampled in Massachusetts and Connecticut in 2005, 2007, and 2009.

Variable	Mean (SE)	Range
Stand size (ha)	44 (3)	7–305
Elevation (m above sea level)	142 (7)	15–378
Slope (%)	22 (1)	1–64
Tree basal area (m ² ·ha ⁻¹)	48.1 (1.0)	18.7–81.4
Tree stem density (ha ⁻¹)	923 (26)	350–2125
Hemlock RIV	63 (1)	22–90
Mean hemlock dbh (cm)	23.2 (0.4)	13–44
Humus depth (cm)	4.5 (0.2)	0.2–15.0

Note: SE, standard error; RIV (relative importance value) calculated as the sum of relative basal area derived from the variable radius plots and relative density derived from the fixed area plot in each stand (Orwig et al. 2002; D. Orwig, unpublished data); dbh, diameter at breast height.

hemlock and sampling it, and continuing this process until a total of 50 trees had been sampled. Both edge and interior trees were sampled within any given stand. Although we would have preferred to mark and resample the same trees in all three surveys, the majority of surveyed stands were on private land where landowners did not permit setting up permanent plot markers and tagging individual trees. On each of these trees, we examined the underside of 2 m long branches on approximately opposite sides of each tree that were reachable from ground level. Whenever possible, we chose branches with a similar amount of new growth for our sur-

veys. Each branch was examined for 1 min. After examining the two branches, we gave each tree HWA and EHS density ratings of 0–3 (0, none; 1, 1–10 organisms/m branch; 2, 11–100 organisms/m branch; 3, > 100 organisms/m branch). Data from the 50 sampled trees were averaged to generate mean HWA and EHS density ratings per stand per sampling date (Table 2). The percentage of dead standing hemlocks in each stand (mortality) was estimated to the nearest 10% based on a walk-through of the sampled portion of the stand; a minimum of 75 hemlock trees were observed during each walk-through. After each stand was sampled in the 2005, 2007, and 2009 surveys, we classified each stand as regeneration (defined as the presence of any hemlocks 0–1 m in height) either present or absent. In the 2007 and 2009 surveys, we quantitatively assessed hemlock regeneration in each stand by staking out a 4 × 4 m (16 m²) quadrat in a randomly chosen cardinal direction as close as possible to the first, 25th, and 50th surveyed hemlock trees. We then counted the number of hemlock seedlings 0–1 m in height within each quadrat. Data from the three quadrat surveys were averaged to generate a mean number of hemlock seedlings per square metre per stand per sampling date (Table 2).

As both HWA and EHS densities fluctuated over time (Table 2; also see McClure 1983, 1991), we averaged each stand’s HWA and EHS infestation ratings from 2005, 2007, and 2009 to calculate a mean HWA and EHS infestation rating for each stand over this five-year period. We also used previously gathered data that classified each stand according

Table 2. Mean (SE) results of stand-level surveys conducted in 2005, 2007, and 2009.

Variable	2005	2007	2009
Stands sampled	137	140	141
Stands with hemlock regeneration	90	66	55
Hemlock seedlings (m ⁻²)	ND	0.14 (0.029)	0.04 (0.006)
Proportion of hemlock trees dead	0.26 (0.022)	0.26 (0.017)	0.33 (0.022)
Stands with HWA	111	121	129
Stands with low (0 < HWA ≤ 1.49) rating	99	62	127
Stands with medium (1.5 ≤ HWA < 2.49) rating	11	49	2
Stands with high (2.5 ≤ HWA < 3.0) rating	1	10	0
Mean HWA density rating	0.45 (0.047)	1.23 (0.076)	0.34 (0.029)
Proportion of 50 sampled trees with HWA	0.26 (0.022)	0.63 (0.032)	0.26 (0.018)
Stands with EHS	98	110	122
Stands with low (0 < EHS ≤ 1.49) rating	24	24	44
Stands with medium (1.5 ≤ EHS < 2.49) rating	38	28	72
Stands with high (2.5 ≤ EHS < 3.0) rating	36	58	6
Mean EHS density rating	1.35 (0.100)	1.64 (0.102)	1.38 (0.076)
Proportion of 50 sampled trees with EHS	0.56 (0.039)	0.66 (0.037)	0.74 (0.034)

Note: HWA, hemlock woolly adelgid (*Adelges tsugae*); ND, data not taken during the survey year. Insect density ratings: 0, no insects detected; 1, 1–10 organisms/m branch; 2, 11–100 organisms/m branch; 3, >100 organisms/m branch.

Table 3. ANOVA assessing the relationship between the 2007–2009 change in hemlock regeneration and site-level predictive factors.

Factor	SS	F	df	p
Slope	0.003	0.034	1, 124	0.854
Humus depth	0.235	2.908	1, 124	0.091
HWA rating	0.498	6.149	1, 124	0.014*
EHS rating	0.286	3.529	1, 124	0.063
HWA rating × humus depth	0.616	7.617	1, 124	0.007*
EHS rating × humus depth	0.174	2.149	1, 124	0.145
EHS rating × slope	0.213	2.628	1, 124	0.107

Note: The best-fit model was selected from an array of initial predictive factors (mean HWA rating, mean EHS rating, latitude, longitude, aspect, average slope, elevation, organic horizon depth, hemlock relative importance value, stand area, and all two-way interactions) using a step-forward model selection algorithm (minimum AIC_c stopping rule). SS, sums of squares; F, F value; df, degrees of freedom; p, p value; *, significant at $\alpha = 0.05$.

to elevation, latitude, longitude, aspect, average slope, soil organic horizon depth, stand size, and hemlock relative importance value (Table 1). Detailed descriptions of each variable have been published elsewhere (Orwig et al. 2002; Preisser et al. 2008).

Statistical analysis

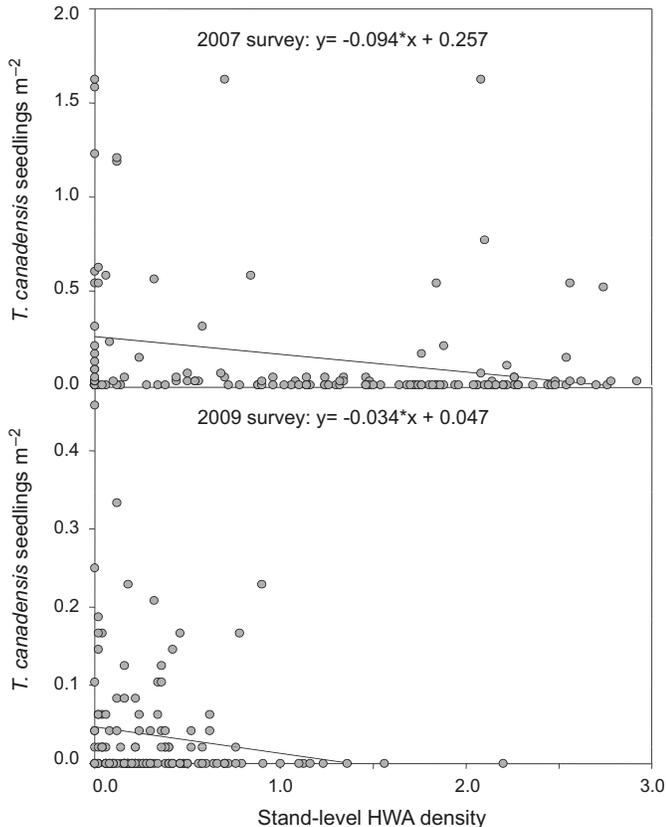
The dependent variable for our analyses was the change in number of hemlock seedlings per square metre per stand (calculated from the three 16 m² quadrat samples taken at each stand in 2007 and 2009). To avoid prejudicing our analyses either for or against a given hypothesis, we followed recommended procedures (Johnson and Omland 2004) and employed model selection to identify the best fit model. Specifically, we used the small sample unbiased Akaike information criterion approach (AIC_c), a modification of the standard AIC approach recommended when the number of free parameters exceeds (sample size)/40 (Hurvich and Tsai 1989). We used a step-forward model selection algorithm with a minimum AIC_c stopping rule to select the best-fit model from the following array of initial predictor variables: mean HWA infestation rating, mean EHS infestation rating,

latitude, longitude, aspect, average slope, elevation, humus depth, hemlock relative importance value, stand area, and all two-way interactions. We tested the resulting model using ANOVA in JMP 9.0.0 (SAS Institute Inc. 2010).

Results

The results of the 2005–2009 surveys are summarized in Table 2. From 2005 to 2009, the proportion of HWA- and EHS-infested stands increased (Table 2) while the proportion of stands with hemlock seedlings declined (Fig. 1; Table 2). This was particularly true in the southern portion of the study area, where both HWA and EHS have been present for the longest. When the quantitative data on change in seedling density from 2007 to 2009 were analyzed, the model selection algorithm identified four main effects: average slope, humus depth, mean HWA infestation rating, and mean EHS infestation rating (Table 3). There was a greater decrease in hemlock seedling density in stands with high mean HWA infestation ratings ($F_{[1,124]} = 6.15$, $p = 0.014$; Fig. 2). There was no relationship between changes in seedling density and the main effects of slope, humus depth, or mean EHS infestation rating (Table 3). There was a significant humus depth ×

Fig. 2. Stand-level relationship between eastern hemlock (*Tsuga canadensis*) seedlings m^{-2} and hemlock woolly adelgid (HWA, *Adelges tsugae*) density rating for the 2007 (top panel) and 2009 (bottom panel) surveys. The number of *T. canadensis* seedlings m^{-2} was calculated on the basis of three 16 m^2 quadrats; the HWA density rating was calculated by averaging data from 50 sampled trees per stand, where each tree was rated on a 0–3 scale (0, none; 1, 1–10 organisms/m branch; 2, 11–100 organisms/m branch; 3, >100 organisms/m branch).



HWA rating interaction: the effect of HWA infestation on seedling density was greater in sites with shallow versus deep humus deposits ($F_{[1,124]} = 7.62$, $p = 0.007$). There were no other significant two-way interactions.

Discussion

Our work documents a decline in hemlock regeneration throughout a large swath of southern New England, and our analysis suggests that chronic HWA infestation may be partially responsible for this pattern. This finding may appear surprising in light of recent work documenting a slower-than-expected decline in the health of southern New England hemlock stands (Preisser et al. 2008). One explanation for these divergent perspectives is the fact that because seedlings and mature trees differ in the amount of stored carbohydrate reserves, they often respond differently to herbivore infestation (Boege and Marquis 2005). Specifically, seedlings possess lower levels of stored reserves and are generally less tolerant of (and slower to recover from) herbivory than larger individuals of the same species. This should make seedlings more sensitive to herbivory than mature trees and less likely to re-

cover during or benefit from periodic reductions in HWA density (McClure 1991). Although we were unable to find any published literature confirming that HWA and EHS can feed on hemlock seedlings, ongoing research has demonstrated that both invasive species readily colonize and feed upon hemlock seedlings ~0.3 m in height (L. Gonda-King, unpublished data). Given both species' ability to utilize seedlings, herbivore-induced resource depletion could have a devastating effect on seedling survival.

The fact that HWA density was less correlated with changes in seedling density in stands with greater humus depths is consistent with our understanding of hemlock's response to HWA infestation. Adelgid-infested hemlocks growing in stressful conditions (hot, exposed slopes and (or) xeric conditions) often decline more quickly in health than trees in more suitable habitats (Royle and Lathrop 2000; Small et al. 2005). Deep organic horizons provide more moisture and better growing conditions for hemlocks, which improves their short-term prospects for survival. It is important to note, however, that this is only a temporary reprieve: even hemlocks growing under ideal conditions eventually succumb to adelgid damage (McClure 1991).

Even if HWA is not directly increasing seedling mortality, it could indirectly affect hemlock recruitment through overstory tree mortality that ultimately decreases hemlock seed production. This is especially likely in the southern portion of our survey area where high levels of overstory hemlock mortality have occurred (Preisser et al. 2008). Because hemlock seeds are viable for a relatively short period (1–4 years; Olson et al. 1959), seedling mortality unrelated to HWA may combine with a decreasing number of entering recruits to produce the observed pattern. HWA infestation of overstory trees may also lead to reductions in seed survival, persistence, or germination. It is also possible that HWA-mediated decline in overstory hemlock alters understory light and moisture conditions in such a way as to put hemlock seedlings at a competitive disadvantage. Overstory hemlock decline has been found to accelerate net nitrification and N mineralization while increasing understory light and temperature levels (Orwig et al. 2008). Because hemlock seedlings are particularly tolerant of cool, low-light conditions (Hadley 2000), a shift in understory conditions may well lead to the competitive release of deciduous species such as birch (*Betula* spp.) and maple (*Acer* spp.).

Although the range expansion and increased abundance of EHS on eastern hemlock (Preisser et al. 2008) make it another plausible explanation for continued hemlock decline in southern New England, we found only a marginally significant ($p = 0.063$; Table 3) relationship between EHS density and changes in seedling density. This suggests that, in contrast with HWA, this invasive species plays a relatively small role in the changes in the density of hemlock seedlings. This accords with research that found no stand-level correlation between overstory hemlock health and EHS density over an eight-year period (Preisser et al. 2008), as well as experimental work showing that multiple years of EHS infestation had minimal impacts on hemlock branch growth (Preisser and El-kinton 2008) and sapling growth (Miller-Pierce et al. 2010).

There are several alternative explanations for the observed change in the density of hemlock seedlings. Perhaps the most likely option involves another herbivore, the white-tailed deer

(*Odocoileus virginianus* Zimmerman). Deer browse can significantly reduce hemlock regeneration (Mladenoff and Stearns 1993), and portions of our study area have experienced more than a doubling of deer densities since 1980 (Kittredge and Ashton 1995). It is thus highly likely that deer browsing has reduced seedling densities in many of our study plots. Because we did not measure deer densities, we cannot exclude the possibility that increases in deer browsing are responsible for the changes in hemlock seedling density. Research has shown, however, that HWA-mediated canopy decline can magnify the impact of deer herbivory on hemlock and other seedlings and thus ultimately alter the trajectory of forest response (Eschtruth and Battles 2008). As a result, deer browse and HWA damage may interact synergistically to suppress regeneration more than either factor alone.

Our inability to distinguish between alternative explanations for our findings is one of several limitations of our work. Because most of our surveyed stands were on privately owned land where plot marking was not permitted, we could not conduct experimental manipulations (i.e., manipulate deer access via fencing) or repeatedly sample the same trees. As a result, our work identifies strong correlations but cannot be used to infer causation. A second problem involves the relatively small sizes (three 16 m² plots per stand) of the seedling-density plots used in 2007 and 2009. While we would have preferred to sample more and larger plots in each stand, our sampling design was intended to balance within-stand sampling effort with the need to survey ~140 stands spread across a 7500 km² area in a two-month period. This balancing effort also explains our failure to take pest-density data on hemlock seedlings. Although subsequent work has shown that adelgids settle and feed on rooted hemlock cuttings (Ingwell and Preisser 2011) and ongoing research has shown that both HWA and EHS settle and feed on hemlock seedlings (L. Gonda-King, unpublished data), we cannot confirm the presence of HWA- or EHS-infested seedlings in our surveys. It is also conceivable that climate, which is known to affect both hemlock recruitment and HWA overwintering survival, might act to synchronize both factors. Finally, seedling recruitment of late-successional trees such as hemlock can be highly variable across time; it is possible that even a five-year study such as ours may be too short to evaluate processes that may be manifest on a decadal scale.

Regardless of the cause, the observed changes in seedling density imply that the ecosystem-level changes associated with reduction in hemlock cover will be difficult to reverse. In the absence of seedlings or persistent seedbanks, regeneration cannot occur, and the ongoing changes to forest structure (Ellison et al. 2005) are unlikely to reverse themselves. This fact emphasizes the need for protective efforts that consider both the overstory and understory hemlock layers in threatened forests. Such an approach increases the odds for retaining a valuable forest species that currently faces such an uncertain future.

Acknowledgements

This research would not have been possible without the help of J. Backer, D. Cox, and J. Elkinton. Funding for this work was provided by an AES Hatch grant and NSF grant DEB-0715504 to E.P.

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