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A 20-year experiment on the effects of deer and hare on eastern hemlock regeneration

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ABSTRACT

Eastern hemlock (Tsuga canadensis) is a shade-tolerant, slow-growing tree once common in forests across the Great Lakes region. It was heavily exploited in the late 19th and early 20th centuries and now experiences limited regeneration across much of its range. This failure to regenerate has been ascribed to poor seedbed conditions, insufficient canopy openings, warmer climate, and browsing by white-tailed deer (Odocoileus virginianus) or snowshoe hare (Lepus americanus). To test whether deer or hare limit hemlock regeneration, we studied >2000 hemlock seedlings inside and adjacent to experimental deer exclosures at 59 sites randomly distributed across hemlock and hemlock-component stands in northern Wisconsin and the western Upper Peninsula of Michigan, U.S.A. We monitored local deer and hare abundance, seedling growth, and seedling survival for 20 years. Two First Nations reservations showed lower deer density and greater survival and growth of unprotected seedlings than three U.S. national forests. Cohorts of hemlock seedlings protected from deer survived at a rate 4x higher than those exposed to deer (59.3% vs. 15.0%) and shared a combined height 5.2x greater. Hare densities significantly affected seedling survival only within exclosures. This extensive, long-term study identifies deer as the primary factor constraining hemlock regeneration in the region.

Key words: exclosures, Great Lakes region, Odocoileus virginianus, tree regeneration, Tsuga canadensis
INTRODUCTION

Eastern hemlock (*Tsuga canadensis* L., Pinaceae) occurs as a long-lived tree across much of eastern North America. Before European settlement, hemlocks were a major component of the old-growth hemlock and hemlock-hardwood forest types that dominated many upland areas in the upper Great Lakes region (Finley 1976). They were co-dominant with sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) in forests that also supported red and white pines (*Pinus resinosa* Ait. and *P. strobus* L.), red oak (*Quercus rubra* L.), and other species (Curtis 1959). Hemlocks are shade tolerant, slow growing, and well adapted to forest understories, having a flexible leader-shoot and branches tolerant of falling branches and trunks that might otherwise cause “death from above” (Clark & Clark 1991). Timber harvest and bark extraction for the tanning trade eliminated more than 99% of the mature hemlock forests in the region, reducing their extent to just 0.5% of the landscape by the 1920s (Rogers 1978, Eckstein 1980). Because hemlock acts as a foundation species in ecosystems, mediating snow retention, stabilizing soil moisture, and moderating downstream water flows (Ellison et al. 2005), its absence has substantial ecological impacts.

The scarcity and biotic value of hemlock forests led several ecologists and foresters to express concerns about population declines and apparent lack of regeneration by the latter 20th century (e.g., Curtis 1959; Goder 1961; Hett & Loucks 1976; Anderson & Loucks 1979; Eckstein 1980; Frelich & Lorimer 1985; Leopold et al. 1988). Without active regeneration, we face the prospect that the scarce remnant stands may represent “living dead” (Janzen 1986), with long-lived adults in the canopy but insufficient seedlings or saplings to persist over time. Several mechanisms have been proposed to account for the
failure of hemlock regeneration at many sites, including lack of suitable climatic conditions, adequate seed dispersal, or appropriate seed beds (summarized in Mladenoff & Stearns 1993).

Three decades ago, evidence that white-tailed deer (*Odocoileus virginianus*) were contributing to the widespread lack of regeneration of eastern hemlock and white cedar (*Thuja occidentalis* L.) forests in the Great Lakes region was mostly descriptive and anecdotal (Alverson et al. 1988). Since then, data have accumulated indicating that sustained deer browsing often shifts patterns of tree recruitment and may eventually eliminate slow-growing species susceptible to deer browse, such as hemlock and yellow birch, from forest canopies (Salk et al. 2011). Deer are native to North America but now commonly occur at 2x-5x the density at which they occurred before European settlement (Garrott et al. 1993). At these densities, deer profoundly modify the density and diversity of shrubs and forest herb communities with ramifications on the physical and biotic structure of soils, bird and terrestrial vertebrate communities, and forest structure (e.g., Gill & Beardall 2001; Rooney 2001; Russell et al. 2001; Rooney & Waller 2003; Côté et al. 2004; Waller et al. 2009; Waller 2014). Thus, deer are a “keystone herbivore” (Waller & Alverson 1997). Recent results derived from U.S. Forest Service FIA plots spanning northern Wisconsin indicate that deer browsing has acted cumulatively over more than 40 years to depress sapling recruitment in hemlock, white cedar, yellow birch, northern red oak, and several other tree species (Bradshaw & Waller 2016). Deer browsing causes heavy impacts in forests across much of the eastern U.S. (Rawinski 2014).

Several mechanisms potentially limit the survival and recruitment of juvenile hemlocks in northern Wisconsin and the western Upper Peninsula of Michigan. Small- to
intermediate-sized seedlings (4-29 cm tall) are widely distributed in this region but occur more commonly on coarse woody debris, tip-up mounds, and in areas of high light and dense herb cover (Waller et al. 1996). These authors also found that, although seedling densities vary geographically, at least 100 seedlings/ha occurred at two-thirds of sites surveyed. Their survey of 140 hemlock stands confirmed that hemlock seedlings are widely distributed and relatively common (0.31/m²) but that survival and growth to larger sizes was being curtailed at sites of higher deer density and impacts. Hemlock seedlings often require 10 years to reach 30 cm in height and 23 years to reach 100 cm (Rooney & Waller 1998). Density of larger (30-300 cm) juveniles is unrelated to local site factors but conspicuously declines in plots with heavier deer browse (Rooney et al. 2000). These studies collectively suggest that deer have limited the ability of hemlock forests to recruit sub-canopy saplings in our region for several decades.

Snowshoe hare (*Lepus americanus*) and other Leporidae also browse woody seedlings, possibly limiting hemlock regeneration as well. Historically, exclosures were often fenced to exclude both deer and hare, placed within deer yards, and erected without replication. Such practices maximized demonstrative impact but limited their value to fairly assess deer and hare effects at a regional scale.

Here, we report the results from a 20-year experiment designed to: (a) rigorously assess the magnitude of deer effects on hemlock growth and survival using experiments where seedlings act as phytometers, and (b) discriminate between the effects of deer and hare browsing. Applying a careful experimental design replicated across a regional array of hemlock and hemlock-hardwood sites allows us to draw strong and general conclusions, a necessity for wisely managing this dwindling and threatened resource.
METHODS

Background, site selection, and experimental design

A previous study of the demography of naturally occurring hemlock seedlings included 118 randomly chosen, unbiased study sites in northern Wisconsin and the western Upper Peninsula of Michigan (Waller et. al. 1996). We initiated our experiment in September 1990 at a randomly selected subset of 60 of those sites. Our sites were stratified by ownership across three National Forests and two First Nation reservations (Fig. 1). At each site, we selected two 3-by-3m plots, as alike as possible with respect to slope, moisture, and canopy and sub-canopy cover. We then randomly selected one as the experimental (caged, exclosure) plot and the other as a control (uncaged and unprotected from deer). The exclosure cages were 2.4 m on a side and 1.3 m tall. Their sides and tops were constructed with rigid steel “cattle panels” with 15-by-20 cm openings that excluded deer but allowed free access for snowshoe hare and other small herbivores. The large mesh of the cattle panels sometimes allowed deer to browse foliage of seedlings around the periphery of the exclosure plot, but we considered that acceptable given that it reduced the likelihood that the exclosures would have a statistically significant effect.

Source, planting, and monitoring of hemlock seedlings

In spring 1991, we acquired four-year-old, bare-root hemlock seedlings from Flickinger’s Nursery in Pennsylvania, and wild hemlock seedlings dug (with root balls) from our study sites and nearby forests. The Pennsylvania (PA) seedlings were easier to obtain and transplant in large quantities but we used both types to test whether fertilized
nursery seedlings are more attractive to deer than wild (WI) seedlings. We transplanted
the hemlock seedlings into replicate 3-by-3 arrays in both the fenced and control plots at
each site, and then recorded each seedling’s height (maximum elevation from substrate),
length (longest distance along stem from base to any branch tip), and basal diameter. In
spring 1992, we added a second pair of plots at a random subset of sites (14 in number)
with seedlings from the opposite source as seedlings originally planted at that site (Fig. 1).
Some of the hemlocks planted in spring 1991 experienced transplantation shock by
spring 1992 but transplantation shock deaths declined thereafter. We replaced many of
these dead individuals by transplanting additional seedlings into sites where fewer than
five of the nine original individuals survived in either plot, always transplanting the same
number and kind of seedlings into both the caged and the control plots
measure and record seedling survival, diameter, height, length, and recent browse. We did
not resurvey the 13 sites on Menominee tribal lands after 1997 or the 16 sites on Ottawa
National Forest lands after 2007. In each spring census, exclosure cages were tilted onto
their sides to provide access for measuring the hemlock seedlings inside. All branches or
trees that had fallen onto the top of a cage were placed into the plot in positions similar to
those they occupied on that cage. Few were massive enough to kill hemlock seedlings,
though they sometimes inhibited growth by bending hemlocks onto their side. In a few
instances, heavy branches or trees crushed the cages. These were left in place, requiring us
to remove side panels to access the seedlings.
A few cages were moved or stolen. Stolen cages were replaced with the exception of
one remote site, which was abandoned (Fig. 1). Moved cages were returned to their
original positions, and we continued to score seedlings inside those plots as “caged” because the temporary exposure to deer would bias analyses towards rejecting a significant exclosure effect. Seedlings that were seriously damaged when cages were moved, or inside cages that could not be replaced, were excluded from analyses. Here, we focus on seedling height because it serves as the best indicator of a seedling’s ability to grow vertically and eventually escape browsing. Of the total of 2,014 hemlock seedlings tracked, we restricted analyses to a subset of 1,056 individuals (528 PA and 528 WI) that were 5-44 cm in height in spring 1992. The lower size limit was set at the minimum height of seedlings we observed to be browsed by deer and the upper limit was the height of the largest PA seedlings in spring 1992. This decision excluded: (a) 227 individuals alive in spring 1991 but dead or shorter than 5 cm in spring 1992; (b) 89 WI individuals alive in 1992 but taller than 44 cm; (c) individuals transplanted into sites to compensate for losses after spring 1992; and (d) all naturally occurring individuals first tracked in 1993 or later. Restricting analyses to this subset (53.4% of the total) ensured that all hemlock individuals were exposed to ambient levels of deer and hare browsing at the start of the experiment and that size differences were minimized across ownerships and origin classes (i.e., nursery versus wild sources). The 958 individuals not used in this study are being incorporated into a separate analysis of transit times through the height zone susceptible to deer browsing (5 – 200 cm) and how this varies across ownerships.

Estimating local deer and hare abundance

Alverson and Waller (1997) provide a full description of the pellet-count methods used here. During spring visits to each site, the same observer (WSA) recorded the number
of fresh deer-pellet groups in eight, circular, 0.01-acre sample “points” (totaling 4049 m² per site). These counts reflect the number of pellets deposited during the winter season between leaf fall (October) and snowmelt (mid-April to mid-May). We sought to obtain relative estimates of deer abundance across our study sites, not absolute numbers.

Using the same eight sample points within each site, we also obtained two estimates of relative Leporid abundance (mostly snowshoe hare but some eastern cottontail rabbits, *Sylvilagus floridanus*), which were highly correlated (*R*²=0.92, *p*<0.0001, *n*=56 sites). One method ("independent hare pellets" or HPEL) better differentiated sites with high and very high densities of hare, so that metric was used in analyses here: We tallied the total number of hare pellets at least 0.5 m distant from any other hare pellets within the eight sample points during each census.

**Statistical analyses**

After initial exploratory data analysis with JMP Pro v. 14.0 (SAS Institute 2018), we applied one-way ANOVAs to compare average deer and hare pellet counts among ownerships. We also plotted mean values over time by ownership. To control for potentially confounding variables and effects of initial differences in seedling source or condition, we included seedling origin (PA or WI), whether a seedling had been transplanted or not, and initial height whenever it was appropriate to do so. We included ownership as a fixed factor because we designed the experiment around this factor and it had only five categories.

We initially focused on the growth of individual plants but the death of many individuals in uncaged plots reduced our ability to assess the effect of exclosures. Instead,
we calculated log response ratios for each site by using the summed height of all seedlings in the exclosure plots relative to the summed height of seedlings in control plots. This variable averaged effects across seedlings within each plot including seedlings that died (height 0). Log response ratios are useful in exclosure and trophic-cascade studies because they capture proportional changes attributable to an experimental manipulation (Flagel et al. 2016). We computed log response ratios for each site and census period using the formula:

\[
\log_{10}\left(\frac{1 + \text{pooled heights of hemlocks in exclosure cage}}{1 + \text{pooled heights of hemlock juveniles in uncaged control plot}}\right)
\]

Sites where exclosures have no effect have log response ratios of zero, and positive log response ratios indicate greater summed hemlock heights within the exclosures. We analyzed mean log response ratios across census years using a general linear mixed model (mixed model ANCOVA) to test the effects of exclosure and initial seedling size while controlling for ownership.

We also analyzed cumulative height results across years with repeated measures MANOVA, using time, local densities of deer and hare (mean pellet densities averaged across all census periods), and their product (testing for interactive effects) as predictors. Because seedling heights deviated from normality and were not linearly related to the predictors, we log transformed the height values as of 2007 (the last year we gathered both deer- and hare-pellet data):

\[
\log (H_{07S}) = \ln (\text{summed height in 2007} + 10 \text{ cm})
\]

To evaluate how hare affect hemlock growth in the absence of deer, we separately analyzed log sums of seedling heights for plots protected from deer. Our first models
included the effects of initial seedling size, ownership, and deer and hare pellet counts. Ownership accounted for 8%-10% of the total variance but also absorbed some of the effect of the deer and hare predictors, leading us to delete this variable. Initial seedling size and deer were not significant, so we also dropped these predictors.

To complement these growth-based analyses, we analyzed survival of caged versus unprotected hemlock seedlings across varying levels of deer and hare presence, and among ownerships. The absence of data from 13 sites within Menominee tribal lands after 1997 and 16 sites in the Ottawa National Forest after 2007 presented a challenge. We applied Cox proportional hazard analysis, a statistical method often used in human health studies that allows “right-censoring” when individuals alive at one census point are later lost to the study (with unknown fates). We analyzed two sets of Cox Proportional Hazard models using JMP Pro v. 14.0 and SAS v. 9.4 (SAS Institute Inc. 2018). In the first, we used models with “static” pellet values for hare and deer at each site, i.e., the mean pellet values observed at that site across all census periods. In the second set of analyses, we included pellet values that varied over time based on either the specific values observed in each census or the sum of pellet values for both the previous and current census periods. Here, we report only results from models using “static” pellet values because they had more explanatory power.

Finally, we performed model selection of survivorship with linear models in R-3.5.2 (R Core Team 2018). The model set included all combinations of the fixed effects of deer abundance (estimated by the average number of deer pellet groups at a site over the course of the experiment) and hare abundance (estimated similarly), site ownership, seedling origin, and seedling transplant status. Interaction terms were included between deer and
hare presence with each other, and with the other three effects. Akaike’s Information Criterion (AIC; Akaike 1974) was used to identify more parsimonious yet effective models for survival. Model selection was also checked using Bayesian information criterion (BIC), as AIC tends to select more complex models when dealing with large amounts of data (Hooten & Hobbs 2015).

RESULTS

Testing lack of bias

In spring 1992, fertilized, nursery-grown (PA) seedlings were taller, on average, than the wild (WI) seedlings (mean 22.7 cm, SE 0.37 vs. 15.5 cm, SE 0.41, both n=528; t test, p<0.0001) and less skewed in their height distribution (Fig. 2a). Despite this, our efforts to match the number, sizes, and origin of individuals in adjacent pairs of plots within sites succeeded in eliminating significant differences (Fig. 2b; caged mean 19.2 cm, SE 0.42 vs. uncaged mean 18.9, SE 0.42; t-test NS). Summed heights in caged plots averaged 173.9 cm (SE 11.1) versus 177.0 cm (SE 11.1) in the control plots (Fig. 2c; t-test NS). By-site differences of summed heights in caged vs. uncaged plots were mostly small and symmetrically distributed around zero (Fig. 2d). Across ownerships, mean heights differed slightly (16.4 cm in NNF vs. 21.1 cm in MEN and ONF). As of spring 1992, 68% of sites had some PA seedlings and 56% had some WI seedlings; 26 sites had only PA seedlings, 19 only WI seedlings, and 14 both kinds (Fig. 1). PA and WI seedlings were represented in every ownership but proportions varied, which reinforced our decision to include seedling source and transplant status as factors in our analyses.
**Deer and hare pellet counts**

The overall mean number of deer pellet groups per site per census was 7.64 (SE 0.98, median 4.33, range 0 – 25.25, with census-specific maximums of 0-89). This indicator of deer abundance varied among ownerships (1-way ANOVA p=0.0009, df 58), with tribal lands and the NNF falling below the other ownerships (Fig. 3a). The overall mean number of hare pellets per site per census was 4.26 (SE 1.06, median 0.14, range 0 – 36, with census-specific maximums of 0-111). Overall mean hare pellets per site also varied among ownerships (1-way ANOVA p=0.0172, df 58), and westerly ownerships (CNF and LDF) had more hare (Fig. 3b). There was no correlation between the experiment-long mean indices of deer and hare abundance (Fig. 4) nor between deer and hare pellet counts within any of the seven census periods from 1991 to 2007 in which we gathered both kinds of pellet data. Notably, there were many sites with little or no hare presence, in contrast to deer (Fig. 4). The five ownerships spanned all four possible combinations of deer and hare relative abundance: above average deer and hare (CNF), above average deer / below average hare (ONF), below average deer / above average hare (LDF), and below average deer and hare (MEN and NNF).

**Differences in growth**

Seedling heights were starkly higher inside the exclosures (Fig. 5a). After 9, 15, and 19 years, hemlock seedlings inside the exclosures were, in aggregate and on average, 3.3x, 6.5x, and 5.2x taller than otherwise matched seedlings outside. Plotting the log response ratios of the protected and unprotected seedlings reveals that these differences grew quickly for 13-14 years and then appeared to level out (Fig. 5b). This may reflect the limit
for this composite variable once seedlings in control plots exposed to abundant deer have
died and seedlings in caged plots (as well as control plots exposed to relatively few deer)
continue to grow at slow to moderate rates. The general linear mixed model (Fig. 5c)
showed the effects of exclosure and initial seedling size to be highly significant (F=34.8 and
36.7, respectively). This difference was already apparent by 1995, just three years into the
experiment when summed seedling heights within exclosures were 54% larger, on average,
than those outside (F=19.18, p<0.001, $R^2=0.65$ in ANCOVA controlling for initial 1992
seedling height).

Repeated measures MANOVA analysis gave similar results. Inferred deer density
alone covaried significantly with differences in growth across the exclosure fences among
sites (Exact F=8.147, p=0.009). Within sites, differential growth inside and outside the
exclosure reflect both period (Exact F=3.37, p=0.021) and cross-census variation in local
deer density (Exact F=3.21, p=0.025). In contrast, local hare density was insignificant. Re-
running the repeated measures analysis without the hare predictor again revealed effects
of local deer density both across and within sites (Exact F=7.77 and 3.01, p=0.010 and
0.029, respectively). Hare only had strong effects in plots protected from deer, in which
heights declined sharply as hare densities increased by 2007 (the last year with hare
abundance data; $R^2 = 0.277$, p=0.0003).

Differences in survival

Of the 1 056 juvenile hemlocks alive in spring 1992, 40.9% were still alive 19 years
later in spring 2011. Total “death from above” mortality was small and randomly
distributed, so we did not adjust for it. Seedling origin and transplant status did affect
survival and so were included as factors in our analyses.

Hemlocks protected within the deer exclosures survived at far higher rates than
those exposed to both hare and deer in the control plots (59.3% vs. 15.0%, $X^2=169.7$,
p<0.0001; Fig. 6a). Naturally occurring, non-transplanted WI seedlings survived better
than transplanted PA and WI seedlings (53.2% vs. 31.9%, $X^2=46.0$, p<0.0001, Fig. 6b), and
wild (WI) individuals (in-situ or transplanted) survived better than PA (bare-root nursery)
seedlings (41.2% vs. 31.5%, $X^2=25.8$, p<0.0001, Fig. 6c). Ownership affected survival of
hemlocks protected from deer within exclosures to some degree ($X^2=16.7$, p=0.002; Fig.
6d), but hemlocks exposed to deer herbivory in the control plots showed far greater
differences ($X^2=59.1$, p<0.0001; Fig. 6e). Tribal (LDF and MEN) lands had the best survival
rates in control plots (33.5%) and a national forest (NNF) the worst (0.0%).

Cox proportional hazard analyses indicated that deer impacts on hemlock survival
supersede all other factors. When all seedlings were analyzed together, excluding deer had
the greatest effect on seedling survival (Table 1a): The exclosure effect was almost five
times larger than the next most important predictor, ownerships (which also reflects
variation in deer abundance). Excluding ownership from the analyses (not shown here)
yielded the same overall result except for reordering the importance of deer abundance
and seedling origin.

Sites with higher local hare densities also showed reduced seedling survival but
only for seedlings protected within the exclosures (Table 1b). Outside the exclosures, local
hare density had no effect, even as other variables sustained their effects (Table 1c). Within
exclosures, ownership also affected seedling survival as did transplant status (with non-
transplanted seedlings having higher survival). Surprisingly, local deer density had an apparent positive effect on hemlock seedling survival inside the exclosures (Table 1b). Excluding ownership from these analyses of seedling survival gave essentially the same results.

After ranking the Cox proportional hazard models by their explanatory power (Chi-square values) and simplicity (incorporating only significant predictive covariates), we assessed a fuller range of survival models using Akaike’s Information Criterion (AIC) and the Bayesian (Schwarz) Information Criterion (BIC). These analyses included models with additional explanatory variables and interactions. For seedlings protected from deer within exclosures, AIC supported a model of survival that included local deer and hare abundance, ownership, seedling origin, and the interaction between deer and origin (Table 2a). Hemlock seedling survival inside cages declined at sites with more hare (effect size=-0.26, p<0.001; Table 3a) but increased at those with more deer (effect size=0.21, p<0.001). This highest strength model (51.3%) had twice the evidence of the next best model (25.7%), which included transplant status. In these exclosure plots, BIC converged on the same top model with even greater strength of evidence (67.8%).

In the control plots exposed to deer, the best AIC model included deer, seedling origin, ownership, and the interaction between deer and ownership (Table 2b). This model’s evidence (46.4%) was slightly above the next best model (36.4%), which included hare abundance. This second model showed a negative effect size for hare presence on survival (effect size=-0.04, p>0.10), but it was small relative to the large effect size of deer abundance (effect size=-0.40, p<0.001). BIC converged on three of the four same top
models for the control plots, including the top two, and showed a greater strength of evidence for the top model (74.3%).

DISCUSSION

For any tree to regenerate successfully, its seedlings must pass through a series of stages and trials, any of which alone, or in combination, could preclude growth into the canopy. This experiment focused on seedlings that were at least several years old and so did not test whether a scarcity of new seedlings (due, e.g., to impaired seed sources, poor dispersal, or inadequate microsites for seedling germination and establishment) or poor early survival (of seedlings less than 5 cm tall) might be causing failures in hemlock regeneration before deer can become an important source of mortality. However, in the context of these hemlock and hemlock-hardwood stands, those questions were already resolved in a previous study that included all of the current field sites (Waller et al. 1996). That study of 140 hemlock and hemlock-hardwood stands in the region concluded that, “Small- to intermediate-sized seedlings (4-29 cm tall) are widely distributed.” and that, “... at least 100 seedlings/ha occurred at two-thirds of sites surveyed.”

Given that small seedlings occur at most of the sites (which our field observations confirmed), our current analyses of the growth and survival of juvenile hemlocks clearly and consistently indicate that elevated deer presence suppresses or eliminates regeneration in most hemlock stands in our region. Because our sites were well dispersed and chosen randomly, they represent broad regional ambient conditions through the 1990s and 2000s. These findings undermine the conclusions of Mladenoff and Stearns (1993), who used computer simulations to argue that evidence from particular stands could not be
extrapolated to explain regional failures of hemlock regeneration and that “browsing [by deer] is not the critical step blocking hemlock forest re-establishment on a regional scale.” Our experiment, focused on existing hemlock and hemlock-component forest stands, demonstrates instead that deer indeed limit hemlock growth and survival to such a great extent as to curtail effective regeneration in three national forests. And, although one might hope that hemlock retains the ability to colonize other forest types in the region, recent analyses of 40 years of U.S. Forest Service FIA data from 13 105 plots extending to all forest types reveal that hemlock (and several other vulnerable woody species) are failing to regenerate throughout our region (Bradshaw and Waller 2016).

We noticed during fieldwork that some sites with few (or no) deer pellet groups showed evidence of deer browse, suggesting that our pellet-group counts may underestimate deer impacts: Deer may pass through some “patrol” sites where they browse but do not linger. We were surprised to see positive associations of deer presence with hemlock survival within the exclosure cages. A likely explanation for this is that higher deer densities eliminate low and mid-story vegetation adjacent to the exclosure cages, thus increasing light available to caged hemlocks. Notably, long-term average counts of deer and hare pellets for each site provided better results in our survival analyses than did the use of deer and hare pellet counts specific to each census period. In addition to reducing sampling variance, the long-term estimates may better reflect the cumulative, deleterious effects of browsing on tree seedlings, with consequences delayed to later census periods (cf. experimental work by Canham et al. 1993).

Hare reduced seedling survival inside the exclosures while deer but not hare reduced survival outside. Although hare limited or eliminated regeneration at some sites,
this was far less common than deer suppressing hemlock growth and survival. As evident in Fig. 4, many sites had few or no hare (despite the fact that our experiment covered at least two hare population cycles) but very few sites lacked deer. By 2007 (year 15 in these analyses), hemlock seedlings disappeared from only 6 sites within exclosures (13% of the 47 study sites extant at that time) vs. 26 sites (55%) in the control plots. (Of these 26 sites, only 4 also were limited by hare.) Our subjective assessment during fieldwork in 2007 was that hare were suppressing or preventing regeneration at 11 sites (23%), 10 of which had above-average hare presence, but that deer suppressed or prevented regeneration in at least 36 (77%) of the sites.

Eastern hemlock’s ecological and life history traits adapted it to live in forest conditions prevalent before European settlement, with mature, continuous canopies that provided scarce light to sparse understories, and abundant coarse woody debris. Such conditions also constrained deer population densities. Less browsing by deer increased the probability that slow-growing hemlock juveniles had time to become tall enough to escape herbivory, which can take a century in dense shade (Eckstein 1980). These same traits may now threaten the ability of hemlock populations to persist. Young, actively managed forests are more open, which allows additional light for the understory and increases food available to larger deer populations, which in turn increases the probability that juvenile hemlocks will be browsed. Mature trees are removed from managed forests, reducing the amount of coarse woody debris available as substrates for hemlock recruitment and compounding population declines (Waller et al. 1996). Mature hemlock trees can remain in the canopy for 600-900 years (Eckstein 1980), so re-establishing the historic structure of these forests will require long-term planning.
Evidence consistently and repeatedly points to elevated deer populations as a critical factor in regional failures of hemlock regeneration (McWilliams et al. 2018). Whitetailed deer function as a keystone herbivore in these areas, profoundly affecting the current and future structure of populations and entire communities, yet few efforts have been made to address these impacts. Hemlock is now experiencing new challenges as well, including the spread of hemlock wooly adelgid and warmer and drier climates (Ash et al. 2017). But, if the widespread and pernicious effects of chronically high deer populations are not addressed as a necessary precondition for hemlock regeneration, viable populations of eastern hemlock are unlikely to persist in most hemlock and hemlock-hardwood stands in our region.

ACKNOWLEDGMENTS

This work was funded by grants from the National Science Foundation (BSR-90000102), the U.S. Department of Agriculture (Forest/Rangeland/Crop Ecosystem 93-00648), and the W. F. Vilas Trust Estate (University of Wisconsin-Madison) to DMW, WSA, S. Solheim, and E. Judziewicz. Additional fieldwork was carried out by M. Leach, E. Judziewicz, R. Barloga, K. Frerker, T. Schappe, A. Bastin, and D. Foster. T. Brandner managed data in the early stages of the project. We thank the staffs of the Chequamegon-Nicolet and Ottawa National Forests, and the Menominee and Lac du Flambeau Ojibwe tribal councils, for their interest and permission to work on their lands. R. Hewitt, Wisconsin Department of Natural Resources, offered facilities for cold storage of our bare-root seedlings. T. Cook, Dept. of Biostatistics and Medical Informatics, UW-Madison, and J. Beck provided advice on survival analyses. S. Friedrich prepared the graphics. The Trout

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Lake Biological Station, Boulder Junction, WI, provided lodging during our spring field surveys. Thanks also are due the Field Museum for allowing WSA to take time from other responsibilities to conduct field surveys in 2001 and 2007.
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Mroz and J. Martin. Department of Forestry, Michigan Technical University, Houghton, MI. pp. 73–90.

TABLES

Table 1. Results from Cox proportional hazards analyses of hemlock seedling survival of (a) all seedlings (n = 1 056, $X^2 = 253.2$, p < 0.0001); (b) seedlings protected from deer browsing inside exclosures (n = 500, $X^2 = 120.7$, p < 0.0001); and (c) seedlings exposed to deer in control plots (n = 556, $X^2 = 104.4$, p < 0.0001). Deer and hare abundance were estimated by the average number of deer pellet groups and hare pellets deposited at any given site over the course of the experiment (see Methods).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Predictor</th>
<th>Chi-square value*</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Combined</td>
<td>Exclosure</td>
<td>146.6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Ownership</td>
<td>31.5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Hare abundance</td>
<td>26.5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Transplant status</td>
<td>18.9</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Deer abundance</td>
<td>4.7</td>
<td>0.031</td>
</tr>
<tr>
<td></td>
<td>Seedling origin</td>
<td>4.6</td>
<td>0.033</td>
</tr>
<tr>
<td>(b) Exclosure plots</td>
<td>Hare abundance</td>
<td>69.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Transplant status</td>
<td>31.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Deer abundance</td>
<td>15.6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Ownership</td>
<td>13.1</td>
<td>0.011</td>
</tr>
<tr>
<td>(c) Control plots</td>
<td>Deer abundance</td>
<td>35.4</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Ownership</td>
<td>29.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Transplant status</td>
<td>18.4</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Deer x Deer</td>
<td>13.9</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Hare abundance</td>
<td>---</td>
<td>NS</td>
</tr>
</tbody>
</table>

* Derived from effect-likelihood ratio tests.
Table 2. Selection of linear mixed effect models predicting years of survival using Akaike’s Information Criterion (AIC) and Bayesian (Schwarz) Information Criterion (BIC) in (a) exclosure plots and (b) control plots. Variables: AveDeer, AveHPEL (deer and hare abundance; see Methods), OWN (ownership), ORIGN (nursery stock versus wild origin), TRANS (transplanted versus seedlings growing in situ).

(a)

<table>
<thead>
<tr>
<th>Models for seedlings protected from deer:</th>
<th>df</th>
<th>Δ weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>OWN+ ORIGN+ AveHPEL+ AveDeer+ AveDeer:ORIGN</td>
<td>10</td>
<td>0.513</td>
</tr>
<tr>
<td>OWN+ ORIGN+ TRANS+ AveHPEL+ AveDeer+ AveDeer:ORIGN</td>
<td>11</td>
<td>1.382 0.257</td>
</tr>
<tr>
<td>OWN+ ORIGN+ TRANS+ AveHPEL+ AveDeer+ AveDeer:ORIGN+ AveDeer:OWN</td>
<td>15</td>
<td>3.456 0.091</td>
</tr>
<tr>
<td>OWN+ ORIGN+ AveHPEL+ AveHPEL:OWN+ AveDeer</td>
<td>13</td>
<td>4.481 0.055</td>
</tr>
</tbody>
</table>

(b)

<table>
<thead>
<tr>
<th>Models for seedlings vulnerable to deer:</th>
<th>df</th>
<th>Δ weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>OWN+ ORIGN+ AveDeer+ AveDeer:ORIGN</td>
<td>12</td>
<td>0.464</td>
</tr>
<tr>
<td>OWN+ ORIGN+ AveHPEL+ AveDeer+ AveDeer:ORIGN</td>
<td>13</td>
<td>0.483 0.364</td>
</tr>
<tr>
<td>OWN+ ORIGN+ TRANS+ AveHPEL+ AveDeer+ AveDeer:ORIGN</td>
<td>14</td>
<td>2.311 0.146</td>
</tr>
<tr>
<td>OWN+ TRANS+ AveDeer+ AveDeer:OWN</td>
<td>12</td>
<td>6.170 0.021</td>
</tr>
</tbody>
</table>

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Table 3. Summary statistics of the top selected AIC and BIC models for (a) seedlings protected from deer browsing inside exclosures; and (b) seedlings exposed to deer in control plots. Deer and hare abundance were estimated by the average number of deer pellet groups and hare pellets deposited at any given site over the course of the experiment (see Methods).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Predictor</th>
<th>Effect size</th>
<th>Std. Error</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Exclosure</td>
<td>Hare abundance</td>
<td>-0.26</td>
<td>0.03</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Deer abundance</td>
<td>0.21</td>
<td>0.04</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Ownership: LDF</td>
<td>1.07</td>
<td>0.85</td>
<td>0.210</td>
</tr>
<tr>
<td></td>
<td>MEN</td>
<td>-9.87</td>
<td>0.78</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>NNF</td>
<td>-1.88</td>
<td>0.85</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>ONF</td>
<td>-2.11</td>
<td>0.67</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Seedling origin: WI</td>
<td>3.64</td>
<td>0.68</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Deer x Origin: WI</td>
<td>-0.18</td>
<td>0.06</td>
<td>0.004</td>
</tr>
<tr>
<td>(b) Control</td>
<td>Deer abundance</td>
<td>-0.40</td>
<td>0.06</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Ownership: LDF</td>
<td>-1.80</td>
<td>1.08</td>
<td>0.095</td>
</tr>
<tr>
<td></td>
<td>MEN</td>
<td>-8.93</td>
<td>0.97</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>NNF</td>
<td>-4.63</td>
<td>1.13</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>ONF</td>
<td>-3.24</td>
<td>1.11</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Seedling origin: WI</td>
<td>1.59</td>
<td>0.45</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Deer x Ownership</td>
<td>0.67</td>
<td>0.27</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>MEN</td>
<td>0.50</td>
<td>0.10</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>NNF</td>
<td>0.04</td>
<td>0.13</td>
<td>0.763</td>
</tr>
<tr>
<td></td>
<td>ONF</td>
<td>0.24</td>
<td>0.08</td>
<td>0.003</td>
</tr>
</tbody>
</table>
FIGURE LEGENDS

**Figure 1.** Map of the randomly selected set of 59 sites used in this study, which sampled five ownerships in northern Wisconsin and the western Upper Peninsula of Michigan: two First Nation reservations on Lac du Flambeau Ojibwe lands (LDF, 8 sites) and Menominee lands (MEN, 13); and what were at the time three separate national forests, the Chequamegon (CNF, 12), the Nicolet (NNF, 10), and the Ottawa (ONF, 16).

**Figure 2.** Contrasts of heights of hemlock seedlings in spring 1992: (a) Individual, nursery-grown (PA) seedlings versus wild (WI) seedlings (means 22.7 cm and 15.5 cm were significantly different; t-test, p<0.0001); (b) Individual seedlings in exclosure cages versus seedlings in uncaged control plots (means 19.2 cm and 18.9 cm, n. s. different); (c) Summed heights by site of all seedlings in the exclosure plots versus the uncaged control plots (means 173.9 cm versus 177.0 cm, n. s. different); (d) By-site differences in the summed total heights of all seedlings in the exclosure plots versus the control plots.

**Figure 3.** One-way analyses of variance across ownerships of (a) the mean number of deer pellet groups per site 1991–2011, and (b) the mean number of hare pellets per site 1991–2007; tribal lands include Lac du Flambeau Ojibwe (LDF) and Menominee (MEN), and national forest lands Chequamegon (CNF), Nicolet (NNF), and Ottawa (ONF).

**Figure 4.** Scatterplot of the experiment-wide mean values of deer pellet groups and independent hare pellets (HPEL, see Methods) at each of the 59 sites from 1991-2007.
(Deer pellet groups by-site mean 7.64, SE 0.98, range 0 – 25.25; hare pellets by-site mean 4.26, SE 1.06, range 0 – 36.)

**Figure 5.** Growth of hemlock seedlings in- and outside the deer exclosures: (a) Mean summed heights of all surviving seedlings present in each plot inside the exclosures (above) and outside (below); (b) Log response ratios of mean summed seedling heights inside vs. outside the exclosure over time plotted with their standard errors (positive log response values reflect greater heights in the caged plots); and (c) Results from the mixed-model ANCOVA showing summed heights (adjusted plot means) in 2011 as a function of the exclosure treatment (left) and initial seedling size (summed seedling heights in that plot in 1992).

**Figure 6.** Contrasting survival curves of hemlock seedlings from 1992-2011 for (a) caged (exclosure) plots and uncaged (control) plots; (b) naturally occurring (non-transplanted) and transplanted seedlings; and (c) wild (WI) seedlings and nursery stock (PA). Mean seedling survivorship also varied among ownerships for (d) caged seedlings, and especially for (e) uncaged seedlings. Ownerships: (CNF) Chequamegon National Forest, (LDF) Lac du Flambeau Ojibwe, (MEN) Menominee, (NNF) Nicolet and (ONF) Ottawa National Forests.
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