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A foundation tree at the precipice: *Tsuga canadensis* health after the arrival of *Adelges tsugae* in central New England

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Abstract. Hemlock (*Tsuga canadensis*) plays a unique role in Eastern forests, producing distinctive biogeochemical, habitat, and microclimatic conditions and yet has begun a potentially irreversible decline due to the invasive hemlock woolly adelgid (*Adelges tsugae*; HWA) that causes foliar damage, crown loss, and mortality of host trees. Understanding the regional, landscape, site, and stand factors influencing HWA spread and impact is critical for predicting future landscape dynamics and directing effective management. Using aerial photographs, we documented hemlock distribution throughout central Massachusetts and subsampled 123 stands to examine the spatial pattern of HWA and its impact on tree vigor and mortality since its arrival in 1989. In the study region, over 86,000 ha of hemlock forest were mapped in 5,127 stands. White pine (*Pinus strobus*), red oak (*Quercus rubra*), red maple (*Acer rubrum*), and black birch (*Betula lenta*) were common overstory associates. Hemlock abundance increased from south to north, commonly on western and northwestern slopes. Average stand size was 55 ha, overstory basal area ranged from 23 to 55 m^2 ha^{-1} and overstory stem densities averaged 993 ha^{-1}.

By 2004, 40% of sampled stands were infested, but most stands remained in good health overall; only 8 stands contained high HWA densities and only two had lost >50% overstory hemlock. Out of fifteen stand and landscape predictor variables examined, only latitude and winter climate variables were related to HWA density. Cold temperatures appear to be slowing the spread and impact of HWA at its northern extent as HWA infestation intensity and hemlock mortality and vigor were significantly correlated with average minimum winter temperature. Contrary to predictions, there was no regional increase in hemlock harvesting. The results suggest that regional HWA-hemlock dynamics are currently being shaped more by climate than by a combination of landscape and social factors. The persistence and migration of HWA continues to pose a significant threat regionally, especially in the northern portion of the study area, where hemlock dominates many forests.

Key words: *Adelges tsugae*; hemlock woolly adelgid; infestation dynamics; landscape patterns; logging; Mantel test; Massachusetts; regression tree analysis; tree vigor; *Tsuga canadensis*.

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INTRODUCTION

In many forested ecosystems, individual species play a prominent role in defining the structure and composition of the forest and controlling important ecosystem processes. These foundation species are often locally abundant and influence both terrestrial and aquatic habitats (Ellison et al. 2005). Globally, many foundation taxa are experiencing declines due to overharvesting, irruptions of native pests, and the introduction of pests and pathogens. In the eastern U.S., hemlock (*Tsuga canadensis*) is a quintessential foundation species, creating cool, dark microenvironments, acidic soils, and unique habitat for diverse understory herbs and shrubs (D'Amato et al. 2009) and wildlife (Snyder et al. 2002, Tingley et al. 2002, Ross et al. 2003, Rohr et al. 2009). In the mosaic of eastern forests, stands of hemlock provide stark contrast to the matrix of deciduous and pine forests. In riparian areas, where they often dominate, hemlocks moderate stream flow and diurnal temperature fluxes (Ellison et al. 2005, Hadley et al. 2008).

For decades ecologists have monitored the spread of the invasive insect, the hemlock woolly adelgid (*Adelges tsugae*; HWA) as it progressively removes this foundation species and reshapes the Eastern forest landscape (McClure 1989, Orwig et al. 2002). In central New England, hemlock has begun what is thought to be an irreversible decline. Due to hemlock's unique characteristics (extraordinary shade tolerance; longevity; importance in old-growth, riparian, and wetland forests; nutrient poor and acidic litter) its loss would lead to major species' shifts in local abundance and distribution and be a dominant driver of ecosystem processes over future decades (Jenkins et al. 1999, Lovett et al. 2006, Orwig et al. 2008, Nunez et al. 2010). Given the absence of large-scale, effective biological or chemical control, and hemlock's abundance in New England ($>4.3 \times 10^9$ cubic feet; 10–43% of total softwood growing stock), the potential ecological, economic, and aesthetic losses are enormous (Smith et al. 2009, Holmes et al. 2010).

Despite decades of research examining various aspects of HWA biology (McClure 1989, 1990, 1991, Young et al. 1995) and related forest impacts (Orwig and Foster 1998, Jenkins et al. 1999, Orwig et al. 2002, 2008, Eschtruth et al. 2006), the pattern and rate of hemlock decline is still not well understood. Better knowledge of the regional, landscape, and site factors that control the impact of HWA and the subsequent response of forest ecosystems to its damage across a range of spatial and temporal scales is necessary to forecast future dynamics of forest change associated with this pest. Since it entered Richmond, VA in the early 1950s (Souto et al. 1996), HWA has spread via wind, birds, deer and humans rapidly to the north and recently to the more scattered stands in the south (McClure 1990, Morin et al. 2009). Current rates of HWA dispersal are estimated to be between 8 and 13 km yr^{-1} (Evans and Gregoire 2007). However, recent examination of county-level HWA detection throughout the eastern U.S. suggested that HWA spread has slowed in its northern range in central New England and along the ridges of the Appalachian Mountains north of Tennessee while spread to the south continues unabated (Fitzpatrick et al. 2010).

The current study is part of a lengthy (>15 year) investigation examining factors that lead to the decline of hemlock in the eastern U.S. Shortly after HWA entered southern New England in the mid-1980s, McClure (1991) concluded that hemlock succumbed within four years of initial infestation. Based on this expectation, we established permanent plots throughout southern Connecticut to document hemlock's immediate demise and replacement (Orwig and Foster 1998) and across an additional 100 hemlock stands statewide to examine patterns of HWA infestation and hemlock decline (Orwig et al. 2002). We observed a latitudinal pattern of HWA abundance and hemlock mortality that broadly mirrored the insect's migration northward into Massachusetts; however, the dispersal and spatial distribution of HWA were erratic and patchy. Some stands in Connecticut deteriorated rapidly and suffered >90% hemlock mortality within several years, whereas others sustained modest levels of mortality and contained many live and healthy trees after a decade of infestation (Orwig and Foster 1998). We also documented that over a quarter of stands experienced intense salvage or pre-emptive logging (Orwig et al. 2002).

Based on this experience and with HWA migrating northward, the intent of this study was to document the landscape status of hemlock in Massachusetts before widespread mortality has transformed the forest. Our broad objective was to document the pace, process and extent of forest landscape change wrought by this insect invasion. Within a 50 km-wide band through central Massachusetts that included the northern extent of HWA distribution in New England we sought to: (1) document and sample the distribution of hemlock; (2) examine the spatial pattern of HWA and its impact on tree vigor and mortality since its arrival in the study area in 1989 (cf. C. Burnham, *unpublished data*); and (3) interpret the environmental, stand, landscape, and climatic factors controlling the spread and impact of HWA. Due to the larger and more continuous extent of hemlock forest in Massachusetts than Connecticut we predicted that HWA would spread rapidly and that hemlock mortality would be progressive and rapid over the span of a few years. Based on previous experience (Kizlinski et al. 2002, Orwig et al. 2002) and greater overall rates of timber harvesting in this study region (Thompson et al. 2011), we predicted even more pre-emptive and salvage logging.

METHODS

Study area

The study focused on a 4,060 km^2 region in central Massachusetts, extending from the southern to northern state boundaries and including the Connecticut River Valley (Fig. 1). The region encompasses considerable variation in physiography, vegetation and land-use history, comprises portions of the Worcester/Monadnock Plateau, Lower Worcester Plateau/Eastern Connecticut Upland, and Connecticut Valley ecoregions (Griffith et al. 1994) and is characterized by a humid, continental climate with long, cool winters and short, mild summers (Taylor 1998). Land cover in 1999 was 70% forest, 17% developed, 8% agriculture, and 5% water (MassGIS: www.mass.gov/mgis). The vegetation is broadly classified as either Transition or Central hardwoods with white pine and hemlock (Westveld et al. 1956) across elevations ranging from 20 to 465 m a.s.l. Soils formed primarily from glacial deposits of weathered gneiss, schist, and granite are predominantly Inceptisols, with valley floodplains dominated by Entisols (Mott and Fuller 1967, Swensen 1989, Taylor 1998).

Aerial photo and other landscape data

To produce a map of hemlock distribution contemporaneous with the arrival of HWA in 1989, we manually interpreted color infrared (CIR) photographic overlays (1:40,000) taken on several dates in March or April of 1990–1993. All stands greater than 1.3 ha and estimated to contain at least 10% hemlock cover were delineated onto acetate overlays, transferred to USGS 7.5 minute topographic maps with the aid of a zoom transfer scope, and digitized into a GIS. The abundance of hemlock in each polygon was assigned to two broad cover classes: 10–50% hemlock and >50% hemlock.

In addition to field measurements several spatial data layers were used to interpret the landscape and bio-physical context of hemlock stands and the status of HWA (Table 1). Factors evaluated included elevation and aspect calculated from a 10-m digital elevation model (MassGIS web site); distance from field plots to permanent streams and major water bodies (e.g., Quabbin Reservoir; Massachusetts DEP 1:25,000 hydrography layer); distance to primary roads (www.census.gov/geo/www/tiger/); and minimum January temperature, maximum July temperature and mean annual precipitation from 1971–2000 (PRISM Climate Group 2010).

Field data collection

During the summers of 2002–2004, 150 hemlock stands representing almost 7,900 ha were randomly selected from the map of hemlock distribution (Fig. 1): 123 stands were subsequently sampled, 17 were not sampled due to lack of landowner access, 8 were mis-identified stands of white pine, and 2 had been cleared for housing. Due to the large number and size distribution of mapped polygons, we concentrated field sampling (80%) in stands >20 ha of both hemlock abundance classes. Large hemlock stands are commonly interspersed within the deciduous hardwood-white pine matrix across the Massachusetts landscape and have the potential to undergo major structural and ecosystem changes associated with HWA-induced decline and mortality. Focusing on many large stands allowed us to address the goal of identifying the factors that are important in controlling the rate of HWA

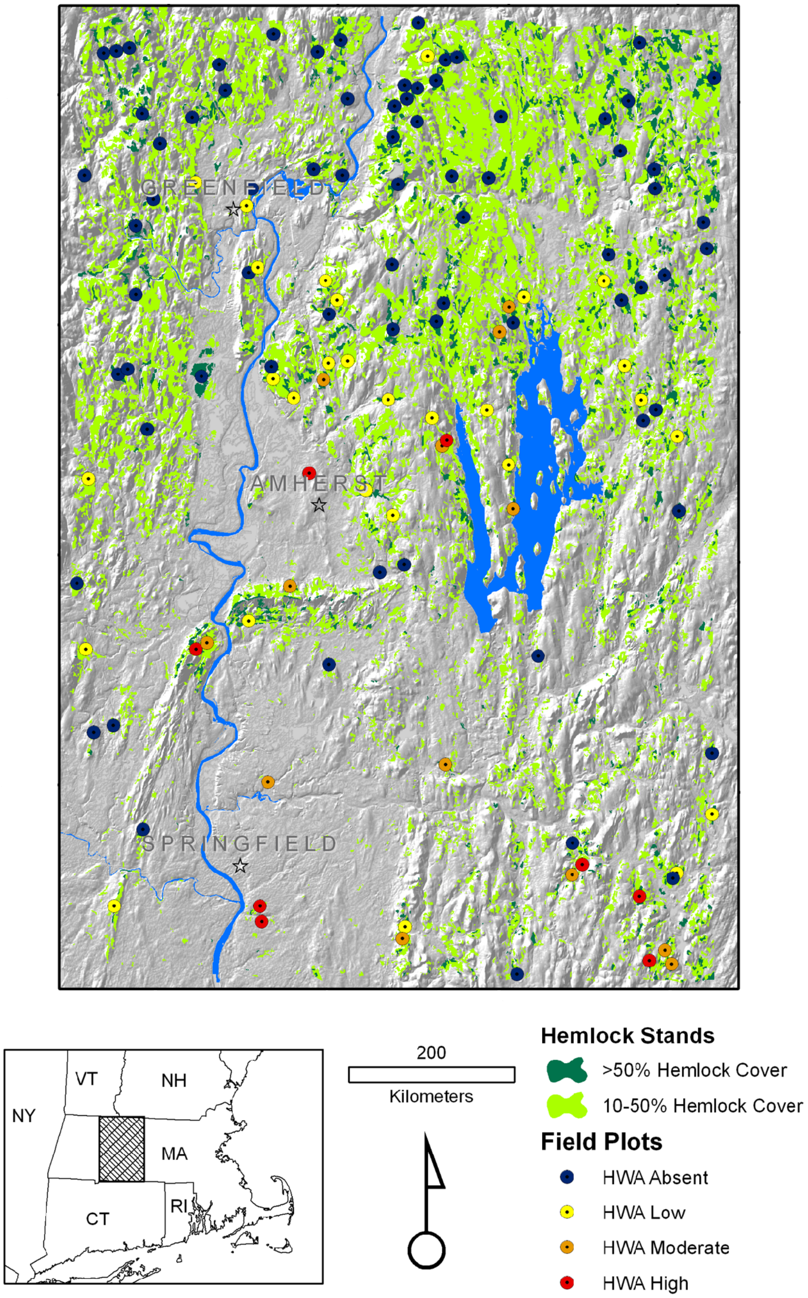

Fig. 1. Study region with location of hemlock stands mapped from aerial photographs. Stands are classified as containing >50% or 10–50% overstory hemlock, and are superimposed on topography derived from a digital elevation model. Plot locations are color coded to indicate the density of HWA found in the field. Inset map shows location of study area within New England.

infestation and hemlock decline.

To assure adequate sampling across large stands, vegetation was sampled in one fixed-area (400 m^2) plot and 5–10 variable-radius plots located every 30–50 m along a linear transect spanning the long dimension of each stand. In fixed-area plots, all trees (stems ≥8 cm diameter breast height (dbh)) were tallied by species and

Table 1. Average, SD, minimum, and maximum values of field sampled hemlock stand characteristics used as predictor variables in regression tree and Mantel analyses.

Hemlock stand characteristic	Mean	SD	Min	Max
Stand size (ha)	54.8	56.8	6.7	317.8
Aspect†	1.01	0.65	0	1.99
Elevation (m)	218	79	47	408
Slope (%)	22	12.1	0	64
Total overstory basal area (m^2/ha)	37.25	6.7	23	55.1
Trees per hectare	993	319	400	2125
Hemlock basal area (m^2/ha)	21.03	6.9	8.6	38.4
Understory richness	13	6.5	3	38
Organic matter depth (cm)	5	2.2	1	15
Organic C:N	26	3.6	17	36
Max July temperature (°C)‡	27.4	0.68	25.9	28.9
Min January temperature (°C)‡	−11.21	0.79	−12.6	−9.0
Mean annual precipitation (cm)‡	121.3	4.2	113.2	134.3
Proximity to road (m)§	373	230	0	976
Proximity to water (m)¶	362	280	0	1234

† Values transformed according to Beers et al. (1966).

‡ Obtained from the PRISM Climate Group (2010).

§ Primary Roads (classes A1 to A30) in U.S. Census TIGER data.

¶ Permanent streams and major water bodies as defined by Mass DEP hydrography layer (www.MassGIS.gov).

dbh, and assigned a canopy position based on a visual estimation of the amount of intercepted light received by the tree crown (Smith 1986). All saplings (<8 cm dbh and >1.4 m tall) were tallied by species and percent cover of herb and shrub species was estimated. Overstory species composition and the amount of hemlock mortality and basal area were also assessed in variable radius plots using the Bitterlich method with a 5 or 10 basal area factor gauge (Wenger 1984). Nomenclature follows Gleason and Cronquist (1991).

Dead hemlocks retaining extensive fine twigs were identified as dying within the previous 2 to 4 years and included in the tally of species composition prior to HWA infestation (cf. Orwig and Foster 1998). Crown vigor classes were assigned to each hemlock tree based on the amount of foliar loss: 1, 0–25 %; 2, 26–50%; 3, 51–75%; 4, 76–99%; and 5, dead (Orwig and Foster 1998). Presence and intensity of HWA infestation were estimated from several trees in each fixed- and variable-radius plot based on the number of egg sacs present and categorized as: 0, absent; 1, low density (1–10 ovisacs/m branch); 2, moderate density (11–100 ovisacs/m branch); or 3, high density (>100 ovisacs/m branch). A relative importance value was calculated for each overstory species by summing the relative basal area derived from the variable radius sampling and the relative density derived from the fixed-area plots (cf. Orwig et al. 2002). Values for hemlock included both live and recently dead trees to represent "pre-HWA" importance.

Based on field examination and extensive experience we attributed almost all hemlock damage and mortality to HWA while recognizing the uncertain role that other insects and factors may play in exacerbating hemlock decline, including summer drought, scale insects (*Fiorinia externa* and *Nuculaspis tsugae*), and eastern hemlock looper (*Lambdina fiscellaria*) (cf. McClure 1989, Evans et al. 1996, McClure et al. 2000, Preisser and Elkinton 2008, Preisser et al. 2008).

Four subsamples of organic and mineral soils were pooled by horizon, air dried, and analyzed for carbon (C) and nitrogen (N) at the University of Georgia Stable Isotope Laboratory (Athens, GA). Slope, aspect, topographic position, elevation, depth of the soil organic horizon (O-A) to the nearest 0.5 cm, and presence of historical (<50 years) and recent (within last 10 years) harvesting were recorded at each sampling point.

Data analysis

GIS overlays were analyzed to determine the size, patch characteristics, and spatial distribution of hemlock stands and the patterns of decline and mortality associated with HWA where present. We used Mantel tests and partial Mantel tests to assess relationships between the condition of hemlock stands (HWA density, hemlock importance values, hemlock vigor, and overstory and understory hemlock mortality) and several environmental and stand level predictor variables (Table 1). A Mantel test describes the correlation between two distance matrices (Mantel 1967), while a partial Mantel test describes the residual correlation between two distance matrices after accounting for the effect of the third (Smouse et al. 1986). Because Mantel r coefficients are calculated from distance matrices rather than vectors, they typically are much smaller in magnitude than conventional (e.g., Pearson) correlation coefficients, even when highly statistically significant (Dutilleul et al. 2000). By including a geographic distance matrix within the Mantel tests, we tested for spatial autocorrelation in the response variables. Similarly, by including a geographic distance matrix in the partial Mantel tests, we tested for a correlation between variables after accounting for the potential influence of spatial autocorrelation (Urban et al. 2002). We used Euclidian distance matrices for the response variables, the standardized environmental variables, and the GPS coordinates of the plots. We conducted Mantel tests using the Vegan Community Ecology Package (Oksanen et al. 2008) within the R statistical language (R Development Team 2008).

We used regression tree analysis (RTA) to model relationships between HWA density (modeled as an ordinal categorical variable) and 15 potential predictor variables (Table 1). RTA is a non-parametric technique for recursively partitioning a dataset based on values of predictors that maximize the homogeneity of the response (Breiman et al. 1984). RTA is useful for identifying complex and hierarchical relationships when there are many potential predictor variables that have non-normal distributions and are correlated among themselves (De'ath and Fabricius 2000). However, most implementations of RTA exhibit a selection bias toward predictors with many possible splits (e.g., continuous over categorical variables) and also tend to overfit to a given dataset by creating partitions that do not significantly reduce the variance (Breiman et al. 1984). Trees are typically pruned to include only those partitions assumed to be valuable beyond the sample data. We used an implementation of RTA, called conditional inference trees, within the PARTY library (Hothorn et al. 2006) of the R statistical Language (R Development Team 2008) that requires a statistically significant difference between the resulting subsets of the response ($\alpha < 0.05$ from a Monte Carlo randomization with 10,000 iterations). This modification minimizes bias and prevents over-fitting and the need for pruning (Hothorn et al. 2006).

RESULTS

Landscape distribution of hemlock

Hemlock were an important component of the forest within approximately 30% of the study region ($\sim$86,000 ha) typically making up 10 to 50% of the forest cover when present (Fig. 1). Some of the scarcity of hemlock in the southwestern corner of the region may be attributed to sprawling urban areas, including Springfield and Holyoke. Over 60% of hemlock stands were small, occupying less than 5 ha in size (Fig. 2A). Hemlock occurrence and abundance increased

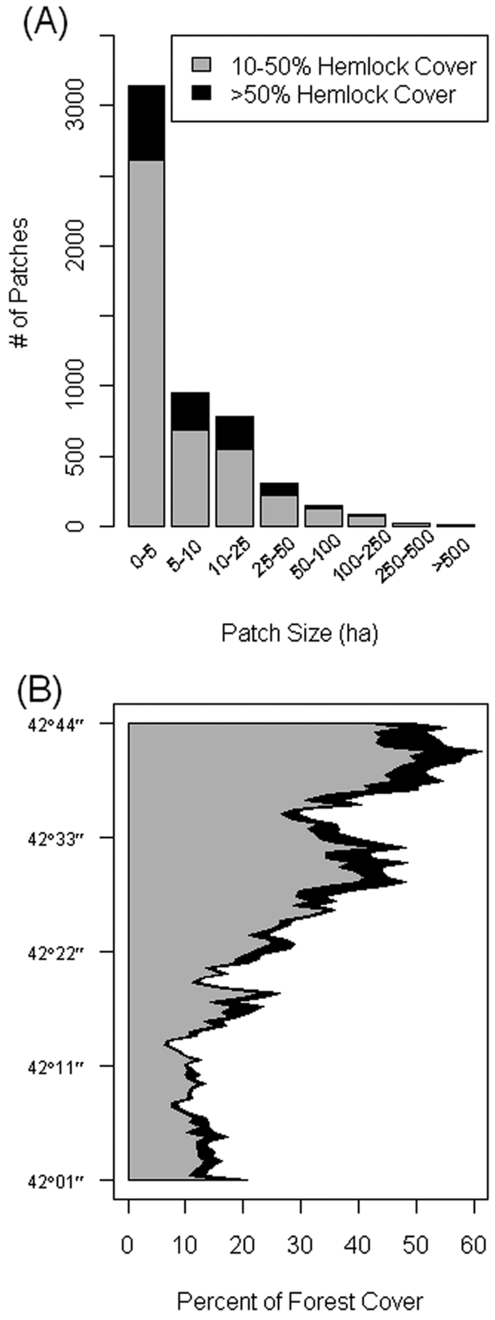

Fig. 2. Average size (A) and latitudinal (B) distribution of 5,127 polygons mapped as containing either 10–50% or >50% hemlock forest in the Massachusetts study area.

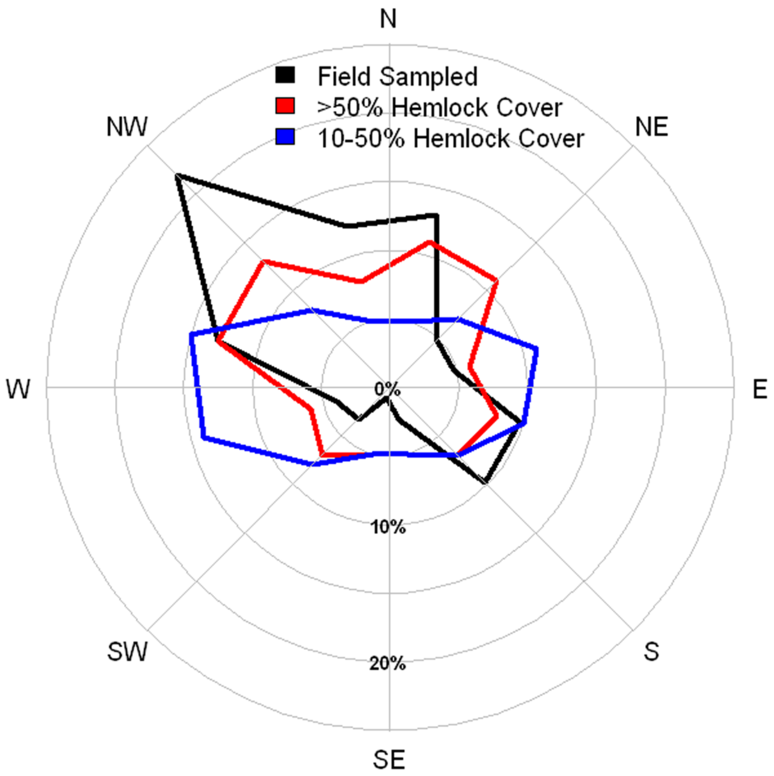

Fig. 3. Distribution of field sampled and mapped hemlock stands by slope aspect in the Massachusetts study area.

dramatically in the northern half of the study area (Fig. 2B), primarily on western to northwestern facing slopes (Fig. 3). Ten percent of the 3,035 km of the mapped streams in the study area flowed through stands containing 10–50% hemlock cover, while 14% of mapped streams flowed through stands with >50% hemlock cover.

Sampled stand structure and composition

Sampled stands ($n = 123$) occupied 6,740 ha, or 8% of the total area of hemlock forest (Fig. 1). Two-thirds of the stands contained >50% hemlock and the remainder contained 10–50% hemlock. Hemlock stand elevation ranged from 47 m to 408 m (Table 1). Average stand size was 55 ha, overstory basal area ranged from 23 to 55 $m^2\ ha^{-1}$ and overstory stem densities averaged 993 ha^{-1} (Table 1). Average hemlock overstory diameter was 22.7 ± 0.5 cm dbh. Fifty percent of the stands were located on western or northwestern slopes, and 27% were located on northern and eastern slopes (Fig. 3). Annual precipitation ranged from 113 to 134 cm and minimum annual temperatures ranged from 0.6 to 3.6°C across stands.

Average overstory hemlock importance value across stands was 60% and ranged from 25–89% (Table 2). Black birch (*Betula lenta*), red oak (*Quercus rubra*) and red maple (*Acer rubrum*) occurred with hemlock in the overstory in more than 90% of the sampled stands, each with importance values of 6–8%. White pine (*Pinus strobus*) also occurred with hemlock in over 80% of the sampled stands, with an average importance value of 6%. The sapling layer of these forests was dominated by hemlock, which was present in 97% of sampled stands at an average density of 452 stems ha^{-1} (Table 2). Red maple and black birch were also common sapling layer inhabitants, but at much lower densities.

Understory vegetation cover was low across most sites, as total seedling, shrub and herb cover each averaged around 5% (Table 2). Red maple

Table 2. Relative overstory importance values, abundance of saplings, and percent cover of understory vegetation in 123 hemlock stands in Massachusetts (mean ± SD). Species occurring in at least 30 stands are included.

Species	Frequency (out of 123)	Importance value (%)	Sapling density (ha^{-1})	Cover (%)
Trees				
Tsuga canadensis	123	59.9 ± 12.3	452 ± 377	1.7 ± 4.3
Quercus rubra	116	8.9 ± 8.0	...	0.3 ± 0.7
Acer rubrum	117	8.2 ± 5.8	22 ± 51	0.6 ± 1.5
Betula lenta	111	6.6 ± 5.9	42 ± 160	0.4 ± 1.5
Pinus strobus	99	6.0 ± 7.0	...	0.4 ± 1.9
Betula papyrifera	73	1.7 ± 2.6	...	...
Betula alleghaniensis	42	1.4 ± 2.8	...	...
Fagus grandifolia	46	1.2 ± 2.5	...	0.3 ± 1.4
Quercus alba	53	1.2 ± 2.2	...	...
Shrubs				
Kalmia latifolia	36	...	...	1.5 ± 4.9
Mitchella repens	71	...	...	0.7 ± 2.4
Hamamelis virginiana	36	...	...	0.5 ± 2.0
Gaultheria procumbens	45	...	...	0.4 ± 1.5
Viburnum acerifolium	32	...	...	0.3 ± 1.4
Vaccinium angustifolium	34	...	...	0.3 ± 1.4
Herbs/Ferns				
Maianthemum canadense	58	...	...	1.1 ± 4.3
Dennstaedtia punctilobula	53	...	...	0.9 ± 3.9
Trientalis borealis	47	...	...	0.2 ± 0.4
Medeola virginiana	33	...	...	0.1 ± 0.3
Uvularia sessilifolia	33	...	...	0.1 ± 0.2

and hemlock were the most common seedlings but only averaged 0.6% and 1.7% cover, respectively. Mountain laurel (*Kalmia latifolia*) was the only shrub species averaging >1% cover, and partridgeberry (*Mitchella repens*) and witch hazel (*Hamamelis virginiana*) were also frequently encountered in the shrub layer. Hay-scented fern (*Dennstaedtia punctilobula*) and Canada mayflower (*Maianthemum canadense*) were the most abundant herb species, but each averaged only 1% cover. Total species richness varied considerably across sites, averaging 13 species and ranging from only 3 up to 38 species.

Organic matter depth ranged from 1 to 15 cm and averaged around 5 cm in the study area (Table 1). Overall, average C:N values did not differ much across the landscape as organic matter C:N values averaged 26.1 while mineral soil C:N values averaged 25.6.

Spatial patterns of hemlock, HWA, and hemlock decline

Pre-HWA hemlock abundance (HEMIV) was not spatially autocorrelated within the study area and was not significantly correlated with any of the environmental variables examined (Table 3). Hemlock stand elevation ($r = 0.18$) and minimum winter temperature ($r = 0.68$) were the only environmental variables that exhibited spatial autocorrelation in the study area, with higher elevations and colder winter temperatures occurring in the more northern locations (Table 4). HWA occurred in almost 40% of the sampled stands although average HWA densities were low across most sites; only 8 stands contained high HWA densities (Fig. 1).

Mantel analysis indicated that HWA infestation level was spatially autocorrelated (SAC) within the study region ($r = 0.27$, $P = 0.001$; Table 3), indicating that geographically adjacent stands exhibited similar values of HWA density. HWA infestation was also correlated with elevation, but partial Mantel analysis suggests that this was attributable to SAC. After controlling for SAC (HWA|location), HWA infestation level was strongly correlated with latitude ($r = 0.21$) and minimum January temperature ($r = 0.21$), and weakly correlated with distance to roads ($r = 0.08$). Regression Tree Analysis (RTA) of HWA density identified three significant partitions resulting in four terminal nodes (Fig. 4). The top split partitioned the sampled stands based on latitude, with stands south of 42°35′ generally having higher levels of HWA density. Both the

Table 3. Mantel correlation coefficients (*r*) and significance (*P*) after 9999 randomizations of hemlock importance value (HEMIV), hemlock woolly adelgid density (HWA), overstory mortality (OVERMORT), and crown vigor (VIGOR) with location, latitude, and slope in 123 Massachusetts hemlock stands.

	Location		Latitude		Slope	
Variable	*r*	*P*	*r*	*P*	*r*	*P*
Location	1	0.001	0.88	0.001	...	NS
HEMIV	...	NS	...	NS	...	NS
HEMIV | Location†	NA	NA	...	NS	...	NS
HEMIV | Env.‡	...	NS	...	NS	...	NS
HWA	0.27	0.001	0.33	0.001	...	NS
HWA | Location	NA	NA	0.21	0.001	...	NS
HWA | Env.	0.23	0.001	0.32	0.001	...	NS
OVERMORT	0.074	0.073	0.079	0.062	0.098	0.064
OVERMORT | Location	NA	NA	...	NS	0.096	0.056
OVERMORT | Env.	...	NS	...	NS	0.1	0.054
VIGOR	0.12	0.009	0.14	0.005	0.089	0.078
VIGOR | Location	NA	NA	0.072	0.071	0.086	0.08
VIGOR | Env.	0.061	0.081	0.12	0.012	0.092	0.069

Note: NA = Non-applicable statistic; NS indicates values of *r* (. . .) that are not significant ($P > 0.10$).
† | Location indicates a partial correlation controlling for location.
‡ | Env. Indicates a partial correlation controlling for all other predictor variables.

Table 4. Mantel correlation coefficients (*r*) and significance (*P*) after 9999 randomizations of hemlock importance value (HEMIV), hemlock woolly adelgid density (HWA), overstory mortality (OVERMORT), and crown vigor (VIGOR) with elevation, minimum January temperature and distance to road in 123 Massachusetts hemlock stands.

	Elevation		Min. Jan. Temp		Distance to Road	
Variable	*r*	*P*	*r*	*P*	*r*	*P*
Location	0.18	0.001	0.68	0.001	...	NS
HEMIV	...	NS	...	NS	...	NS
HEMIV | Location†	0.057	0.078	...	NS	...	NS
HEMIV | Env.‡	...	NS	...	NS	...	NS
HWA	0.069	0.046	0.33	0.001	0.063	0.08
HWA | Location	...	NS	0.21	0.001	0.075	0.037
HWA | Env.	...	NS	0.31	0.001	0.057	0.077
OVERMORT	0.14	0.004	0.20	0.006	...	NS
OVERMORT | Location	0.13	0.013	0.20	0.002	...	NS
OVERMORT | Env.	0.13	0.023	0.18	0.007	...	NS
VIGOR	0.086	0.059	0.25	0.001	...	NS
VIGOR | Location	...	NS	0.23	0.001	...	NS
VIGOR | Env.	...	NS	0.23	0.001	...	NS

Note: NS indicates values of *r* (. . .) that are not significant ($P > 0.10$).
† | Location indicates a partial correlation controlling for location.
‡ | Env. Indicates a partial correlation controlling for all other predictor variables.

northern and southern branches of the regression tree were further partitioned based on the minimum January temperature and in both instances colder areas had lower levels of HWA infestation. Surprisingly, none of the remaining thirteen stand and landscape variables were significant predictors of HWA density.

Despite the duration of HWA infestation in MA, overstory hemlock mortality (MORT) was quite low overall, with only 2 infested stands exhibiting average mortality >50% and 1 additional infested stand experiencing >30% mortality. With respect to environmental variables, partial Mantel coefficients indicate that overstory mortality was significantly correlated with average minimum January temperature ($r = 0.18$) and elevation ($r = 0.13$) (Table 3). Hemlock sapling mortality patterns were low across the study area, averaged 13% in both infested and uninfested stands, and were not significantly related to any of the variables examined in this study (data not shown).

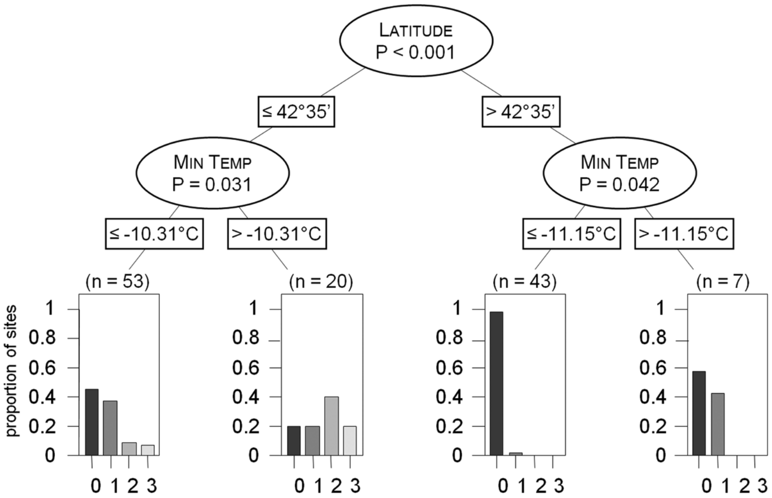

Fig. 4. Regression tree for HWA density within the Massachusetts study area using predictor variables from Table 1. All predictor variables were tested with a Monte Carlo randomization test at each node in the tree with the lowest significant P values resulting in a new node. Boxes with bar graphs represent proportion of stands with various HWA densities at that terminal node of the regression tree. Average stand HWA density values = 0, absent; 1, low density (1–10 ovisacs/m branch); 2, moderate density (11–100 ovisacs/m branch); or 3, high density (>100 ovisacs/m branch).

Overall hemlock health, as indicated by crown vigor ratings of live trees, displayed significant SAC in the study area ($r = 0.12$, $P = 0.009$). Six stands containing trees classified as "poor" vigor (i.e., <25% foliage remaining) were found in the southern half of the study area (data not shown). After controlling for SAC, crown vigor was also most strongly related to minimum January temperature ($r = 0.23$) and weakly correlated with latitude ($r = 0.07$) (Tables 3 and 4). Average stand size, distance to major stream or river, and organic layer soil C:N were not significantly related to HWA density, overstory hemlock mortality, or average hemlock crown vigor (data not shown).

Logging, other pests, and development

The majority of stands visited (87%) had some evidence of historical (10 to ~50 years since harvesting) forest cutting. Hemlock logging was also widespread across the study region, occurring in 76% of the sampled stands, regardless of pest presence or tree health (data not shown). Logging activity included selective cutting of uninfested hemlock, thinning of HWA-infested trees, and high intensity (up to 90%) removal of all overstory hemlock and many hardwoods in portions of the stands. Hemlock cutting during the past 10 years, estimated from stump deterioration, occurred in portions of 59 of the 123 sampled forests, although only 30 stands were actually infested with HWA. We estimate that a total of 1148 ha of uninfested hemlock forest and 605 ha of HWA-infested hemlock forest were removed by logging during the last 10 years. Evidence of hemlock harvesting >10 years prior to sampling was also observed in 28% of stands. At the time of sampling in 2004, the co-occurring invasive pest, the elongate hemlock scale (*Fiorinia externa*; EHS), was only observed in six stands and the native secondary pest, the hemlock borer (*Melanophila fulvoguttata*) was seen in 4 HWA-infested stands. Only two stands (37 ha) were developed for housing since 1993.

DISCUSSION

Managing invasive species poses many challenges including understanding and predicting the impacts on native communities (Parker et al. 1999, Strayer et al. 2006) and forecasting subsequent future dynamics of forest change. These challenges are exacerbated by the fact that the impact of an invasive insect may vary over time and geographically (Strayer et al. 2006). Our results suggest that, compared to other locations, the spread of HWA across New England is leading to unanticipated and highly variable dynamics and impacts on the region's forests. To assess the current status of HWA impacts in central New England, we discuss the various factors controlling HWA dynamics in the region. We then examine the likely future compositional changes by describing the potential replacement species already present in these forests. The impacts of logging and other indirect impacts of HWA are then reviewed, and we close by using our findings to make predictions of HWA dynamics and impacts across the region.

Factors controlling regional HWA impacts

Since its initial infestation into Massachusetts near Springfield, MA in 1989, HWA has migrated north and infested hemlock stands across the study area and the eastern two-thirds of the state. By 2004 (15 years later), 40% of sampled stands were infested, although most remained in good health overall. Despite the much greater abundance and continuity of hemlock forest in this region, HWA migration rate and tree damage are substantially lower than those observed to the south in Connecticut. Within the first 15 years of infesting Connecticut forests, HWA had spread to every town in the state and generated substantial overstory and sapling mortality and poor hemlock health across much of the southern half of the state (Orwig et al. 2002, Small et al. 2005, Stadler et al. 2005). High overstory mortality levels over similar infestation times have also been observed in New Jersey and Pennsylvania (Mayer et al. 2002, Eschtruth et al. 2006). Even more rapid deterioration of hemlock has been observed in the southeastern U.S., where hemlock productivity (Nuckolls et al. 2009) and crown density (Siderhurst et al. 2010) exhibited significant declines and tree mortality increased after only 3–6 years of HWA infestation (Ford et al. 2011, Krapfl et al. 2011).

The slower rates of HWA spread and tree deterioration in Massachusetts are likely due to cold winter temperatures. The sensitivity of HWA to temperatures below −25°C is documented by controlled environment studies (Parker et al. 1998, 1999, Skinner et al. 2003) and corroborated by growing field evidence. Depressed rates of spread (Evans and Gregoire 2007, Morin et al. 2009, Fitzpatrick et al. 2010) and low winter survival of HWA (Paradis et al. 2008, Trotter and Shields 2009) have been associated with cold winter temperatures. In this study, HWA exhibited a strong latitudinal pattern of infestation and a pattern of tree damage and mortality that paralleled the timing of infestation and corresponded with the northward temperature gradient. Our findings of very low HWA presence in the north, despite higher overstory and understory hemlock abundance, which should facilitate HWA spread, add further evidence that the colder climate of central New England has slowed the spread and impact of this pest at the northern extent of its current range.

The future of this latitudinal pattern of HWA infestation and tree mortality is uncertain, especially with a warming climate. Climate projections for New England suggest the average temperature will continue to increase by 2.1 to 5.3°C over the next century (Hayhoe et al. 2007), potentially allowing greater HWA survival across most of the range of hemlock and increasing the rate of spread and impact (Paradis et al. 2008, Dukes et al. 2009, Albani et al. 2010). Under a lower emissions scenario (2°C increase), the Massachusetts climate would be similar to current-day New Jersey, while a higher emissions scenario (5°C increase) would lead to a southern Appalachian climate (Frumhoff et al. 2007). Under either scenario conditions would be conducive to rapid HWA migration, high HWA survival, and heavy damage to hemlock forests.

With the exception of latitude and cold temperatures, none of the remaining variables were significant predictors of HWA infestation. In other regions, latitude was also a strong predictor of HWA presence (Orwig et al. 2002, Faulkenberry et al. 2009) and in regions with considerably more topographic relief and site variation, slope and elevation were useful predictors of HWA infestation (Young and Morton 2002, Koch et al. 2006). Although 25% of mapped streams ran through hemlock forests in our study area, distance to stream or major water body were not significant predictors of HWA, as documented by Koch et al. (2006) in areas where hemlock was more restricted to riparian areas. The lack of strong relationships between HWA and distance to streams or roads in our study suggests that these types of corridors were either not important for spread, or that HWA and the corridors were both highly dispersed throughout the study area, masking any spatial pattern of these potential relationships.

Less than 2% of the stands sampled, representing only 52 ha, lost more than half of their hemlock cover due to HWA-induced mortality. Similarly, remaining trees in most stands with HWA continue to be infested at low densities and are in good health; only 5 stands contained trees with less than 25% foliage remaining in the southern half of the study area. Minimum winter temperature had the strongest relationship with hemlock mortality and vigor, as southern stands were warmer, had higher HWA survival and longer HWA infestation times.

At the time of this study, the invasive elongate hemlock scale (*Fiorinia externa*; EHS) was found in low abundance in a few of the southern stands. Subsequently, we have observed a rapid increase in EHS abundance and spread in the study area (Preisser et al. 2008, 2011). HWA populations have also recently increased in density due to several consecutive warm winters, although some stands continue to have live hemlock trees despite the lengthy presence of both insects (Preisser et al., *unpublished data*). Increases in co-occurring pests could lead to more rapid tree decline, or in some cases slower tree decline (cf. Preisser and Elkinton 2008), making predictions about the rate and extent of future tree decline tenuous.

Potential replacement species

Hemlock forests in our study area commonly contain overstory white pine, red oak, red maple, and black birch. All of these are poised to be successful replacement species for hemlock in our study area. Birch and the other hardwood species have already begun to replace hemlock in southern New England and the mid-Atlantic region (Orwig et al. 2002, Small et al. 2005, Eschtruth et al. 2006) and are predicted to replace hemlock across much of the eastern U.S. (Kincaid 2007, Albani et al. 2010, Spaulding and Rieske 2010). In terms of understory vegetation, many of the forests we examined had low species richness and abundance, conditions that are common in healthy hemlock forests (Rogers 1980, D'Amato et al. 2009). With continued HWA feeding we expect hemlock regeneration to decline and eventually disappear and diversity and cover of understory species to exhibit large increases (Orwig 2002, Small et al. 2005, Eschtruth et al. 2006, Spaulding and Rieske 2010, Preisser et al. 2011). Species already present on many sites with the ability to increase following canopy openings include partridgeberry (*Mitchella repens*), witch hazel (*Hamamelis virginiana*), mountain laurel (*Kalmia latifolia*), and hay-scented fern (*Dennstaedtia punctilobula*).

Logging and indirect consequences of HWA

Logging was widely distributed in the study area, although no large clearcuts occurred and less than 1% of mapped hemlock forest was selectively cut during the last 10 years due to HWA. In the last 10 years hemlock was harvested in approximately half of stands visited even though only half of these were infested with HWA. Some of the infested stands were cut in response to perceived HWA-induced hemlock decline, although further social science research will be required to determine how widespread this motivation is. The relatively low harvesting intensity stands in contrast to the widespread pre-emptive and salvage cutting observed during the late 1990s in Connecticut where intensive salvage logging involved many large clearcuts and the removal of 15% of the area mapped as hemlock over a 6 year period (Kizlinski et al. 2002, Brooks 2004, Orwig et al. 2002). The harvesting of hemlock observed in the current study is consistent with overall harvesting trends in the region, where frequent, low intensity harvests have occurred over the last 20 years (McDonald et al. 2006, Thompson et al. 2011; D. Orwig et al., *unpublished manuscript*). Statewide, hemlock consistently represented approximately 5–7% of the total annual cut volume during the period 1984–2003, and there were no recent increases that could be attributed to HWA or other causes (McDonald et al. 2006).

Regional predictions of HWA dynamics

We can compare the unanticipated slow decline in hemlock found in this study with results from other geographical areas to begin to make regional predictions about the importance of landscape, climatic, and social factors leading to HWA spread, damage, and the trajectory of hemlock decline. For example, in the southeastern U.S., warmer winter temperatures, higher HWA survival (Trotter and Shields 2009), and faster dispersal rates (Evans and Gregoire 2007, Fitzpatrick et al. 2010) all contribute to rapid hemlock decline and extensive hemlock mortality (Nuckolls et al. 2009, Siderhurst et al. 2010, Evans et al. 2011, Ford et al. 2011, Krapfl et al. 2011). In contrast, New England hemlock forests experience periodic cold temperatures that reduce HWA survival (Paradis et al. 2008, Trotter and Shields 2009) and dispersal rate (Evans and Gregoire 2007), allowing for longer hemlock survival in the presence of HWA. Forests in the mid-Atlantic and New York regions should experience rapid HWA dispersal and hemlock mortality at most sites, and prolonged hemlock survival in the Allegheny and Adirondack Mountains of the region due to colder winter temperatures (Dukes et al. 2009). A combination of many other factors can also alter rates of HWA dispersal and hemlock decline within a geographical region including the number, size, and connectivity of hemlock stands, drought, co-occurring pests with HWA like EHS, topographic features like mountain ranges and site-specific factors like soil depth and aspect, and social attitudes towards management (to cut or not cf. Foster and Orwig 2006).

CONCLUSION

HWA has not yet generated a significant change in many hemlock forests in central New England; this is counter to predictions made in the mid-1990s when it was believed that hemlock stands would deteriorate rapidly as was observed in some mid-Atlantic and southern New England locations. Since 1989, HWA has spread throughout central MA and recently, over the border into Vermont, New Hampshire, and Maine. However, HWA damage appears to have been constrained by cold winter temperatures, which were more important in affecting HWA dynamics than landscape, ecological, and biological factors, regional differences in management attitudes, and landowner response to this pest. Although HWA has not yet resulted in widespread hemlock mortality, the persistence of HWA in the region's forests coupled with warming winter temperatures continues to pose a significant threat, especially in the northern portion of the study area, where large, hemlock dominated forests are very abundant.

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