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Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid

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Abstract

Aim The hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), a small, aphid-like insect native to Japan, is currently migrating northward through eastern North America and threatens to eliminate eastern hemlock [*Tsuga canadensis* (L.) Carriere], one of the most abundant, long-lived shade tolerant species, across its range. The major objectives of this study were: (1) to characterize the pre-HWA distribution, composition, and structure of hemlock stands; (2) to characterize the spatial patterns of damage generated by HWA across southern New England since the time of its arrival in 1985; and (3) to examine environmental and stand factors that are associated with declines in crown vigour and mortality of hemlock.

Location Our study was conducted in a 4900-km^2 study region extending from Long Island Sound northward to the Massachusetts border and including the Connecticut River Valley in Connecticut, USA.

Methods Aerial photographs and extensive field study were used to map and develop GIS overlays of 1000 hemlock stands in our study region. Intensive sampling of a random selection of 114 hemlock stands across the study area was used to document patterns of hemlock infestation, vigour, and mortality in relation to stand and site characteristics. Mantel tests were utilized to assess the relative importance of environmental and stand variables in controlling the intensity of HWA infestation and damage.

Results Most stands were located along ridge tops, steep hillsides and narrow valleys. Hemlock importance values ranged from 22 to 96% and stand densities varied from 300 to 1450 stems ha^{-1}. Adelgid presence and adelgid-induced hemlock mortality were found in 88 and 74% of the sampled forests, respectively. Approximately 25% of stands were logged recently, ranging in intensity from partial hemlock cutting to large clearcuts. A geographical trend in reduced HWA infestation intensity and tree mortality and enhanced crown vigour of overstory and understory hemlock occurs from south to north, coincident with the temporal colonization pattern of HWA. Mantel analyses indicated that patterns of HWA infestation, hemlock mortality, and crown vigour were most strongly correlated with latitude. Mortality was also weakly related to aspect and stand size. Average mortality was highest on western aspects but exceeded 20% on most slopes. Remaining trees averaged over 50% foliar loss, with no significant difference among aspects.

Main conclusions Results suggest that as HWA becomes abundant, stands on xeric aspects succumb rapidly, but that stand and landscape variables such as overstory composition and structure, slope, and elevation, exert little control over susceptibility or eventual mortality. Ultimately, duration of infestation controls the intensity of hemlock decline and mortality. Over 4290 ha of hemlock forest have been eliminated by logging or HWA just within the southern part of our transect since the mid-1980s, and we

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predict continued HWA infestation will lead to unprecedented hemlock loss throughout the north-eastern USA, regardless of site conditions or location.

Keywords
Hemlock woolly adelgid, infestation dynamics, hemlock mortality, tree vigour, landscape patterns, logging, Connecticut, Mantel test.

INTRODUCTION

Forest infestation by introduced pathogens and pests and the resulting selective decline in dominant tree species is an important ecological, economic and evolutionary process that alters ecosystem structure, function and dynamics (Castello *et al*., 1995; Enserink, 1999; Everett, 2000). Infestations may also exert devastating impacts on natural resources and aesthetic conditions by initiating dramatic shifts in forest composition, altering ecosystem processes such as nutrient cycling and retention, and increasing ecosystem susceptibility to further disturbances, including fire and invasion by exotic plants and animals (Vitousek, 1986; Ramakrishnan & Vitousek, 1989; Mack *et al*., 2000). In the north-eastern USA, pest and pathogen outbreaks have occurred through geological time but have increased in the last century (Castello *et al*., 1995; Liebhold *et al*., 1995; O'Keefe & Foster, 1998). Nearly 5000 years ago, a range-wide, 1000-year decline in hemlock is hypothesized to have been caused by insect outbreaks (Davis, 1981; Bhiry & Filion, 1996) whereas recent declines have occurred in such dominant species as chestnut [*Castanea dentata* (Marshall) Borkh.], elm (*Ulmus* L. spp.), and beech (*Fagus grandifolia* Ehrh.) (Liebhold *et al*., 1995) from introduced pathogens.

The hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) a small, aphid-like insect native to Japan, is currently spreading unimpeded across the eastern USA and threatens the widespread decline or elimination of eastern hemlock [*T. canadensis* (L.) Carriere], one of eastern North America's most important tree species (Orwig & Foster, 1998). Hemlock is one of the most abundant, long-lived and shade-tolerant trees in the North-east and consequently it plays a unique role in forest ecosystems (Rogers, 1978). The deep shade and acidic litter characteristic of hemlock stands result in cool, damp microclimates, low light availability, depauperate understories and slow rates of nitrogen cycling (Lutz, 1928; Rogers, 1978, 1980; Aber & Melillo, 1991; Abrams & Orwig, 1996). HWA infestation may therefore initiate community and ecosystem responses that are substantially greater in magnitude and aesthetic impacts than those resulting from previously mentioned, pathogen-induced tree declines (Jenkins *et al*., 1999; Foster, 2000; Yorks *et al*., 2000).

HWA was first reported in north-western North America during the 1920s (Annand, 1924) and in the eastern United States near Richmond, VA in the early 1950s (Souto *et al*., 1996). Since then, HWA migrated to southern New England by 1985, produced localized mortality by 1988 (McClure, 1990), and currently occurs in every town in Connecticut (McClure *et al*., 2000; Fig. 1). In Connecticut, HWA infestation was limited to the southern third of the state from 1985 to 1989, moved to the entire central portion of the state by 1994 and then lastly to the north-eastern and north-western corners of the state by 1999 (McClure *et al*., 2000). Woolly adelgid is now found in over 160 towns ($>40\%$) in Massachusetts (Fig. 1; C. Burnham, unpublished data) and recently migrated successfully to Portsmouth, NH (Anonymous, 2001). The temporal and spatial pattern of spread of HWA is unpredictable and the rate of stand deterioration following infestation can be extremely variable (Souto *et al*., 1996).

Adelgids feed on the ray parenchyma cells of young hemlock twigs and may inject a toxic saliva, thereby causing needle loss and bud, branch and eventual tree mortality within 4–10 years (McClure, 1991; Young *et al*., 1995; Orwig, 2002). HWA is a devastating pest because it is parthenogenetic, reproducing rapidly with two generations per year, is easily transported by wind, birds, mammals and humans, can infest and kill hemlocks of all sizes and age classes, and is migrating at a rate of approximately 30 km year^{-1} (McClure, 1989, 1990, 1991). To date, there are no effective native predators in the eastern USA and hemlock has shown no resistance to HWA or recovery following heavy, chronic infestation (McClure, 1995a; Orwig & Foster, 2000). Extreme winter temperatures below –30 °C have led to high HWA mortality levels (Parker *et al*., 1998, 1999), although residual HWA populations recover quickly to injurious levels and may eventually develop even greater cold tolerance as it migrates northward (McClure & Cheah, 1999).

Because of difficulty in obtaining adequate coverage of horticultural soaps and oils on large trees and the high per tree costs associated with these applications, biological control is the only potentially viable option for managing HWA populations in forest ecosystems (McClure, 1995b; McClure & Cheah, 1999). Efforts are underway in many mid-Atlantic and New England sites to release HWA-specific insect predators native to Asia (McClure *et al*., 2000; Montgomery *et al*., 2000). Preliminary field results suggest one of these exotic predators, *Pseudoscymnus tsugae* (Sasaji and McClure), reproduced, successfully overwintered, dispersed and reduced HWA densities by as much as 88% on infested branches (McClure *et al*., 2000). However, it is still uncertain what the long-term prognosis of this biocontrol agent will be within a stand and across large landscapes. The ability to anticipate stand susceptibility and landscape to

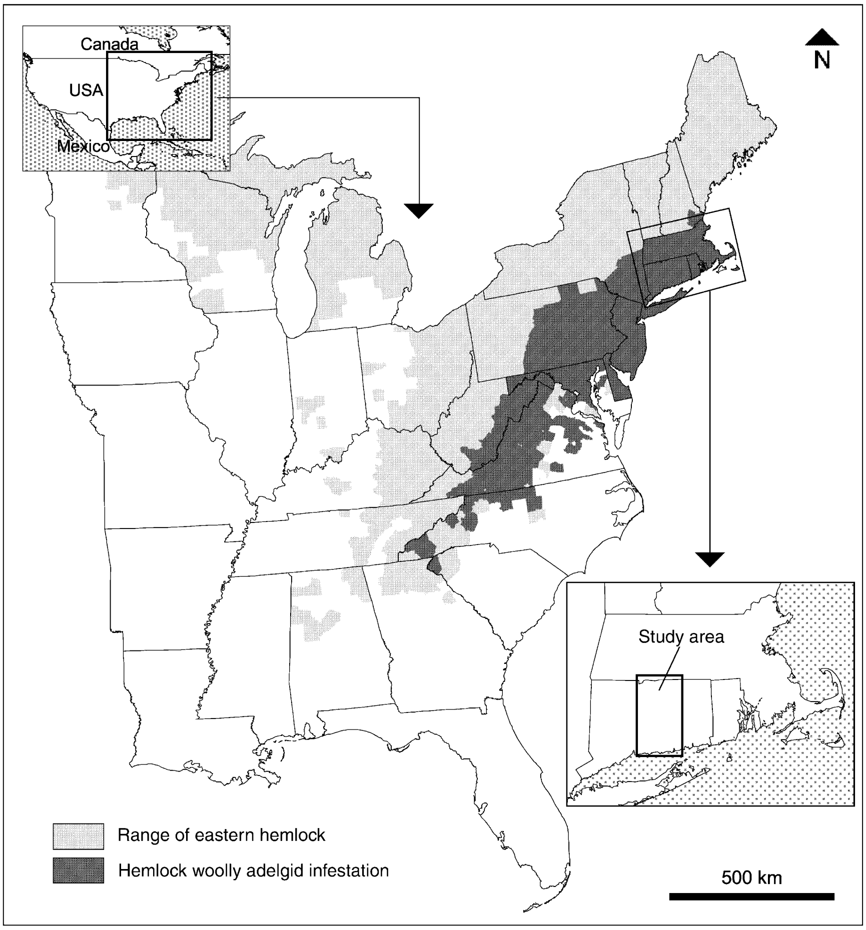

Figure 1 Hemlock woolly adelgid (*Adelges tsugae* Annand) distribution map by county in the eastern USA during 2002 (adopted from USDA, 2002). Inset map shows location of study transect in central Connecticut.

regional dynamics of HWA and hemlock mortality is critical for assessing ecological risk, determining effective release sites and planning future management efforts (Gray & Salom, 1996).

Landscape and local edaphic and biotic factors have been shown to play important roles in pest and pathogen spread and impact by influencing pathogen dispersal and population growth (Eager, 1984; Mitchell & Preisler, 1991), host distribution (Smith & Nicholas, 1998) and susceptibility (Liebhold *et al*., 1994; Trial & Devine, 1994; MacLean & MacKinnon, 1997; Powers *et al*., 1999). Although the general extent of HWA distribution is broadly monitored at a state level, there is little information on the influence of landscape or stand factors on infestation patterns, tree health, or tree mortality. Recent studies based on satellite imagery and tree crown surveys of infested forests of the Mid-Atlantic and southern New England regions suggest that xeric ridges and slopes may have been more severely impacted by HWA than others, but these studies highlight the need for additional investigations of site factors (Royle & Lathrop, 1997, 2000; Bonneau *et al*., 1999a,b; Young *et al*., 2000). By analysing the abundance and distribution of hemlock and HWA impact in southern New England, we sought to define the patterns rigorously, to undertake quantitative analyses of the factors associated with hemlock decline and mortality and to develop a sound prognosis of hemlock's future role in the region.

Our major objectives in this study are: (1) to characterize the pre-HWA distribution, composition and structure of hemlock stands; (2) to characterize the spatial patterns of damage generated by HWA across southern New England since the time of its arrival and (3) to examine environmental and stand factors that are associated with declines in crown vigour and mortality in hemlock. Our initial observations and surveys (Orwig & Foster, 1998, 2000) led us to several expectations that are examined in this study:

1. A broad latitudinal pattern of decreasing extent and severity of HWA impact from the southern New England coast inland is controlled by dispersal rates since HWA arrived initially in southern Connecticut in 1985.
2. HWA-associated stress and mortality is controlled broadly by duration of infestation and is unrelated to landscape or site factors including elevation, slope, aspect, or density and arrangement of hemlock stands.
3. Hemlock forest susceptibility to HWA is independent of stand history, composition, or structure (e.g. species composition or stand size).

Study area

The study focused on a 4900-km^2 study region extending from Long Island Sound northward to the Massachusetts border and including the lower Connecticut River Valley and portions of the eastern uplands and coastal slopes (Figs 1 and 2a; Bell, 1985). The region encompasses considerable variation in physiography, vegetation, land-use history and incidence of HWA infestation and is characterized by a humid, continental climate with long, cool winters and short mild summers (Hill *et al*., 1980). Elevations range from 0 to 300 m a.s.l and soils are formed primarily from glacial deposits of weathered gneiss, schist, and granite (Reynolds, 1979). The region is located at the southern limits of the hemlock–white pine–northern hardwood vegetation type (Nichols, 1935) and the northern limit of Braun's (1950) oak–chestnut type.

METHODS

Aerial photo interpretation

Leaves off, black and white aerial photographs (1 : 80,000) taken in 1980 were obtained from the Connecticut Department of Environmental Protection to produce a base map of hemlock distribution prior to the arrival of HWA. 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 min topographic maps with the aid of a zoom transfer scope and scanned into vector format. The abundance of hemlock in each polygon was assigned to two broad cover classes: 10–50% and > 50%. A total of 1000 hemlock polygons were mapped in the study region (Fig. 2a), with the vast majority (78%) less than 20 ha in size. Three hundred and nine stands were mapped as containing > 50% hemlock cover, while 691 contained 10–50% hemlock.

Data collection

During the summers of 1997 and 1998, we visited 206 stands representing almost 9000 ha of the 16,541 ha mapped as hemlock in the entire study region (Fig. 2a and b): 114 were correctly identified and undisturbed by recent human activities, fifty-three were misidentified, thirteen had been developed for housing, twenty were clearcut within the last 6 years (see results for additional logging information), three had burned and three were inaccessible. Over half of

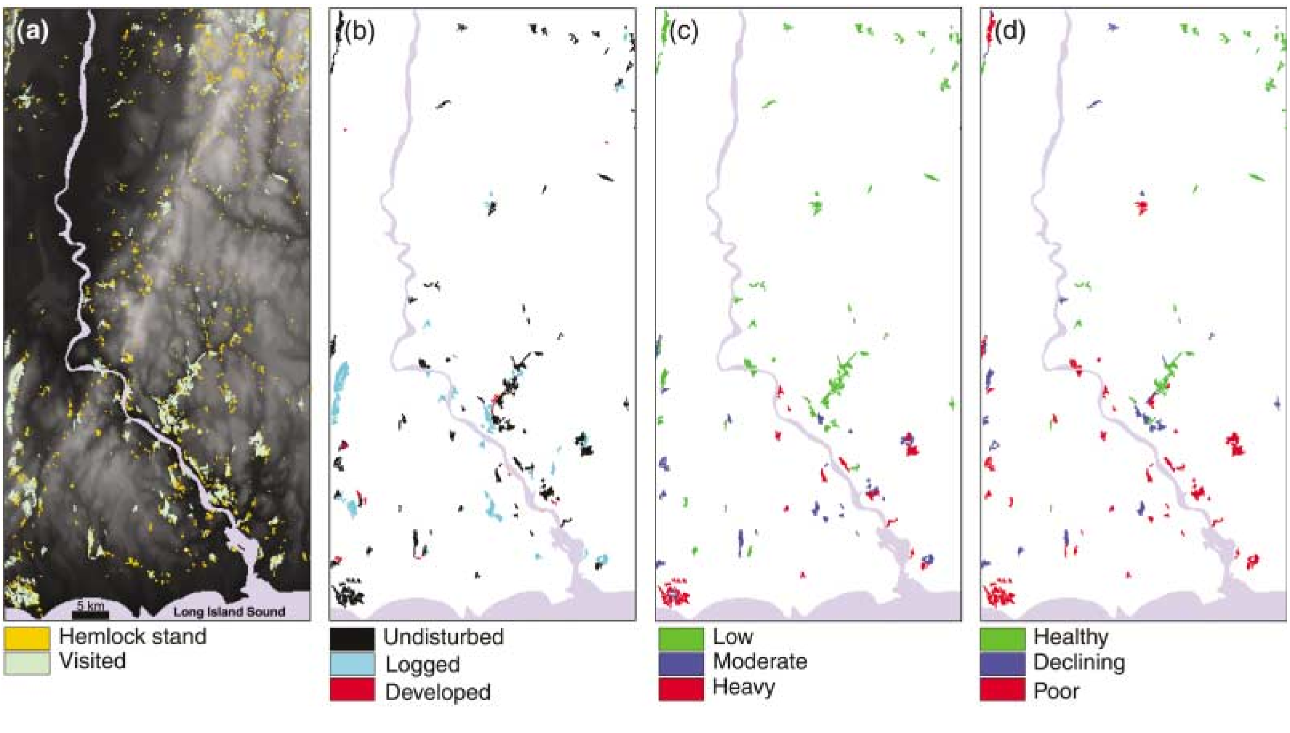

Figure 2 Spatial patterns of hemlock [*Tsuga canadensis* (L.) Carriere] distribution and associated hemlock woolly adelgid (HWA) damage in the Central Connecticut study transect. (a) Location of 1000 hemlock stands mapped from aerial photographs and the stands visited in this study. Elevation ranges from 0 (black) to 300 m a.s.l. (white). (b) Location of the 114 stands sampled in this study and the stands that were undisturbed, logged, or developed since 1980. (c) Mean overstory hemlock mortality resulting from HWA infestation. Mortality levels were classified as: low = 0–20%; moderate = 21–60%; and heavy = > 60%. (d) Mean overstory hemlock vigour (crown health) resulting from HWA infestation. Vigour ratings were based on the amount of foliage remaining on the tree and were classified as: low = 100–75%; moderate = 74–25%; and heavy = < 25%.

the misidentified stands were < 20 ha and the majority were located in the northern portion of the transect. Species mistaken for hemlock in these small-scale photos included white pine (*Pinus strobus* L.), eastern redcedar (*Juniperus virginiana* L.), and mountain laurel (*Kalmia latifolia* L.). Because of the large number and size distribution of mapped polygons, we concentrated our field sampling efforts in stands > 20 ha, regardless of cover class designation, which made up 10,680 ha or 65% of the total acreage mapped as hemlock. Large hemlock stands represent some of the most unusual habitat elements interspersed within the deciduous hardwood matrix across the landscape and they have the potential to undergo the greatest structural and ecosystem changes associated with HWA-induced decline and mortality.

One hundred and fourteen hemlock stands were quantitatively sampled for the intensity of HWA infestation and stand and site characteristics. Nineteen stands < 20 ha were also included in this sample, several of which have been examined in previous HWA studies (Orwig & Foster, 1998; D.A. Orwig *et al.*, unpublished data). To assure adequate coverage of large areas, vegetation was sampled in one fixed-area (20 × 20 m) plot and five to ten variable-radius plots located every 30–50 m along a transect orientated through the long dimension of the forest in each stand. In fixed-area plots, all trees [stems at least 8 cm diameter breast height (d.b.h.)] were tallied by species and d.b.h., and assigned a canopy position based on a visual estimation of the amount of intercepted light received by the tree crown (Smith, 1986). Hemlocks that died within the previous 2–4 years, which were identified by extensive retention of fine twigs in the crown, were tallied to determine species composition prior to HWA infestation. Crown vigour classes were assigned to each hemlock tree based on the amount of retained foliage: 1 = 76–100%; 2 = 51–75%; 3 = 26–50%; 4 = 1–25%; 5 = dead (Orwig & Foster, 1998). Presence and intensity of infestation by HWA were estimated from the number of egg sacs present on branches from several trees in each plot and categorized as: 0 = absent; 1 = low density; 2 = moderate density; or 3 = heavy density, or egg sacs at the base of almost all the needles.

All saplings (less than 8 cm d.b.h. and over 1.4 m tall) were tallied by species. Nomenclature follows Gleason & Cronquist (1991). Overstory species composition, degree of hemlock mortality and basal area were also assessed within variable radius plots using the Bitterlich method with a 5 or 10 basal area factor gauge (Wenger, 1984). Slope, aspect, topographic position, elevation, depth of the soil organic horizon to the nearest 0.5 cm and presence of historical and recent logging activity were recorded at each sampling point. A relative importance value was calculated for each overstory species in every stand by summing the relative basal area derived from the variable radius sampling and the relative density derived from the fixed-area plots. Values for hemlock included both live and recently dead trees to represent 'pre-HWA' importance.

We attribute observed hemlock damage and mortality to HWA, although additional factors exacerbated hemlock decline, including summer drought, scale insects [*Fiorinia externa* Ferris and *Nuculaspis tsugae* (Marlatt)], and hemlock looper (*Lambdina fiscellaria* Guen.) (McClure, 1989; Benzinger, 1994; Evans *et al.*, 1996). We assume that hemlock damage and mortality is overwhelmingly due to HWA, although the effect of other insects on hemlock susceptibility to HWA remains uncertain (Evans *et al.*, 1996; McClure *et al.*, 2000).

Data analysis

GIS overlays and digital elevation models (1 : 250,000 scale DEM; USGS, unpublished data) were analysed in ArcView to determine the size, patch characteristics and spatial distribution of pre-HWA hemlock stands and the subsequent patterns of decline and mortality. To assess the relative importance of environmental and stand variables in controlling the intensity of infestation, we utilized Mantel tests (Mantel, 1967; Manly, 1997a), which includes space (i.e. geographical location) as a predictor variable in the analysis. This technique performs a linear regression on distance matrices generated from dependent variables (hemlock importance value, HWA infestation level, overstory and sapling mortality levels, and average crown health, or vigour) and predictor variables (space, latitude, slope, aspect, elevation and stand size). Prior to analysis, aspect values were transformed from circular variables to a measure relevant to vegetation as: aspect = cosine (45 – azimuth degrees) + 1 (Beers *et al.*, 1966). Values range from 0 on south-western slopes commonly exposed to the sun to 2 on the least exposed north-eastern slopes. In addition, latitude and longitude were converted to distance measures with the same units (i.e. km from the equator or prime meridian, respectively).

The Mantel coefficient of a variable vs. location is a measure of the spatial autocorrelation of that variable; a positive value indicates that points close together geographically tend to have similar values and a negative value indicates that points close together tend to have dissimilar values. If there is no spatial autocorrelation, then the value of the observed r should not be statistically different from zero. Partial Mantel coefficients were also calculated (e.g. hemlock mortality vs. elevation controlling for location) to assess the relative contributions of various factors influencing the analysis. Mantel test coefficients and significance levels were calculated with Manly's RT randomization program (Manly, 1997b), with 1000 randomizations for each test.

RESULTS

Stand structure and composition

Hemlock stands in the study area varied considerably in size and structure (Fig. 2; Table 1). Sampled stands occupied 5854 ha representing 39% of the area of hemlock forest. Average stand size was 51 ha, hemlock overstory basal area ranged from 19 to 75 m^2 ha^{-1} and overstory stem densities averaged 834 ha^{-1}. Based on importance values, ninety-two

Table 1 Characteristics of hemlock [*Tsuga canadensis* (L.) Carriere] forest stands sampled in southern New England ($n = 114$)

	Mean ± SE	Range
Area (ha)	51 ± 4	10–242
Elevation (m a.s.l.)	95 ± 6	12–259
Slope (%)	22 ± 1	1–61
Tree basal area (m^2 ha^{-1})	45 ± 1	19–75
Tree stem density (ha^{-1})	834 ± 26	300–1450
Hemlock R.I.V.*	64 ± 1	22–96
Mean hemlock d.b.h. (cm)	23.8 ± 0.5	13.7–44.4
Hemlock sapling density (ha^{-1})	314 ± 60	0–5750
Organic litter depth (cm)	3.7 ± 0.2	0.2–7.7

*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.

stands (81%) contained > 50% hemlock. Black birch (*Betula lenta* L.) was the second most important overstory species in these forests, occurring in 91% of the stands (Table 2). Various oak (*Quercus* L. spp.), maple (*Acer* L. spp.), and hickory (*Carya* Nutt. spp.) species were also common in the overstory, but occurred at lower densities. Hemlock saplings were found in 80% of the stands, averaging 314 stems ha^{-1} (Table 1), although seedlings were present in less than half of the stands.

Field inspection indicated that these hemlock forests had experienced a wide range of historical land uses. Although many developed from woodlots that showed evidence of past oak and chestnut cutting (50%), successional stands were also common (42%) in which hemlock and other species have established on land that had been previously cleared for pasture or tillage.

Table 2 Overstory species composition of hemlock forest stands sampled in southern New England (114 stands). Only species occurring in at least seventeen stands (15%) are shown

	% Occurrence ($n = 114$)	Relative importance value* Mean ± SE
Tsuga canadensis	**100**	**64.0 ± 1.4**
Betula lenta L.	91.2	8.6 ± 0.7
Quercus rubra L.	89.5	4.4 ± 0.5
Q. alba L.	80.7	3.1 ± 0.3
Acer rubrum L.	79.8	4.2 ± 0.4
Q. velutina Lam.	75.4	4.6 ± 0.6
Carya Nutt. spp.	60.5	3.8 ± 0.5
A. saccharum Marshall	53.5	5.2 ± 0.9
Fagus grandifolia L.	45.6	3.0 ± 0.5
B. alleghaniensis Britton	37.7	3.9 ± 0.6
Q. prinus L.	28.1	8.5 ± 1.4
Fraxinus americana L.	25.4	2.0 ± 0.4
Pinus strobus L.	18.4	4.5 ± 1.5
Liriodendron tulipifera L.	15.8	1.4 ± 0.3

*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. Values are calculated from number of stands in which the species is present.

Regional and landscape distribution of hemlock

Overall, 15,108 ha of hemlock forest were mapped in the study region, with higher concentrations in the south and north-eastern corner (Fig. 2). The scarcity of hemlock stands along the north-western edge of the transect is because of the presence of large urban areas including Hartford and Middletown. A large number of stands are located primarily on ridge tops, steep hillsides and narrow valleys (Fig. 2). Forty-six percent of the stands were located on western or north-western slopes, 31% were located on northern or north-eastern slopes, and fewer were found on southern or eastern slopes (Table 3). Mantel analysis indicated that pre-HWA hemlock importance value exhibited no spatial autocorrelation within the study area and was not significantly correlated with any of the environmental variables examined (Table 4). Hemlock stand elevation was the only environmental variable that exhibited spatial autocorrelation in the study area ($r = 0.367$), with higher elevations occurring in the northern locations (Table 4; Fig. 2a).

Spatial pattern of HWA and hemlock decline

Hemlock woolly adelgid occurred in almost 90% of the sampled stands and HWA-induced mortality was recorded in two-thirds. Mantel analysis indicated that HWA infestation level was spatially autocorrelated in the study region ($r = 0.239$; Table 4). Partial mantel analysis (HWA/Env) suggests that, despite weak correlations with aspect, slope and location, HWA infestation level was most strongly related to latitude ($r = 0.248$). Hemlock mortality was also spatially autocorrelated, indicating that geographically adjacent stands exhibited similar values of hemlock mortality. In particular, hemlock mortality of trees > 8 cm d.b.h. showed a broad geographical pattern, with moderate to high mortality (i.e. 20–60% and > 60%, respectively) occurring in southern stands and low levels (i.e. 0–20%) in most northern stands (Fig. 2c). With respect to environmental variables, partial Mantel coefficients indicate that the pattern of both overstory and sapling mortality is strongly and positively correlated with latitude, and less strongly related to aspect (Table 4). Average mortality levels were higher on W and SW aspects, although most aspects exhibited mortality rates exceeding 20% (Table 3). Overstory mortality patterns were also weakly but significantly correlated with stand size ($r = 0.138$, $P < 0.017$).

Overall hemlock health, as indicated by crown vigour ratings of live trees, also displayed significant spatial autocorrelation in the study area ($r = 0.256$, $P < 0.001$), with the majority of trees classified as 'poor' vigour found in the southern stands (Fig. 2d). Crown vigour exhibited weak correlations with elevation and slope, although the relationship with slope was non-significant when other variables were controlled for (Table 4). Patterns of hemlock crown vigour were most strongly related to latitude ($r = 0.363$, $P < 0.001$). Mean crown vigour did not differ among aspects and averaged 3.5, or roughly 60% foliar loss (Table 3).

Table 3 Hemlock stand distribution and mean overstory hemlock mortality and crown vigour among slope aspect classes in hemlock stands sampled in southern New England ($n = 114$)

Slope aspect	Frequency of stand occurrence (%)	Mean overstory mortality (±SE)	Mean overstory crown vigour* (±SE)
N (337.5–22.5°)	14.0	26.6 ± 6.8ab	3.9 ± 0.4a
NE (22.5–67.5°)	16.7	18.0 ± 5.3ab	3.3 ± 0.4a
E (67.5–112.5°)	11.4	5.0 ± 2.0a	3.2 ± 0.4a
SE (112.5–157.5°)	7.0	31.1 ± 13.6ab	3.8 ± 0.7a
S (157.5–202.5°)	0.1	0	2.45a
SW (202.5–247.5°)	3.5	39.0 ± 19.9ab	4.7 ± 0.6a
W (247.5–292.5°)	20.2	45.0 ± 7.7b	4.6 ± 0.3a
NW (292.5–337.5°)	26.3	25.7 ± 5.4ab	3.6 ± 0.3a

Aspect values in a column with the same letter are not significantly different at $P < 0.01$.
*Crown vigour classes were assigned to each hemlock tree based on the amount of retained foliage: 1 = 76–100%; 2 = 51–75%; 3 = 26–50%; 4 = 1–25%; 5 = dead (Orwig & Foster, 1998).

Table 4 Correlation of overstory hemlock importance value (HEMIV), hemlock woolly adelgid (HWA), overstory mortality (OVERMORT), sapling mortality (SAPMORT) and crown vigour in 114 Connecticut hemlock stands with latitude, aspect, slope, elevation and geographical location, where *r* is the Mantel coefficient and *P* is the significance after 1000 randomizations

	Location		Latitude		Aspect		Slope		Elevation		Stand size	
Variable	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Location	–	–	0.708	0.001	NS		NS		0.367	0.001	NS	
HEMIV	NS		NS		NS		NS		NS		NS	
HEMIV | Location*	–	–	NS		NS		NS		NS		NS	
HEMIV | Envir.†	NS		NS		NS		NS		NS		NS	
HWA	0.239	0.001	0.298	0.001	–0.049	0.049	0.097	0.011	0.090	0.019	NS	
HWA | Location	–	–	0.236	0.001	NS		0.097	0.008	NS		NS	
HWA | Envir.	0.090	0.027	0.248	0.001	–0.046	0.044	0.082	0.022	NS		NS	
OVERMORT	0.112	0.011	0.165	0.001	0.121	0.001	NS		NS		0.138	0.016
OVERMORT | Location	–	–	0.173	0.002	0.125	0.001	NS		NS		0.130	0.020
OVERMORT | Envir.	NS		0.205	0.002	0.132	0.001	NS		NS		0.137	0.017
SAPMORT	NS		NS		0.063	0.022	NS		NS		NS	
SAPMORT | Location	–	–	NS		0.064	0.022	NS		NS		NS	
SAPMORT | Envir.	NS		0.101	0.046	0.068	0.019	NS		NS		NS	
Vigour	0.256	0.001	0.352	0.001	NS		0.049	0.047	0.100	0.002	NS	
Vigour | Location	–	–	0.337	0.001	NS		0.049	0.031	NS		NS	
Vigour | Envir.	NS		0.363	0.001	NS		NS		–0.087	0.002	NS	

NS indicates values of r that are not significant ($P > 0.05$).
* | Location indicates a partial correlation controlling for location.
† | Envir. indicates a partial correlation controlling for the other four predictor variables.

Only a few groups of stands remain with predominantly healthy trees. These occur primarily in the north-east corner of the transect and in the centrally located Salmon River Valley. Stand size was not significantly correlated with observed tree vigour. To date, infestations have been chronic, with progressive tree decline. We have not detected any evidence of resistance or recovery in any populations or on any sites.

Logging, development and hemlock loss patterns

Directly through decline and mortality or indirectly through the stimulation of logging of infested stands, HWA has generated a profound change in hemlock forests in southern New England. Logging activity ranged from thinning of infested trees to complete removal of all overstory hemlock and many hardwoods. Hemlock had been partially logged in the past 6 years from twenty of the 114 sampled forests and clearcut in twenty additional stands, precluding data collection on forest structure and composition. The majority of logged stands were located in the southern portion of the study area, where HWA infestation has occurred for the longest period of time and vigour of remaining trees is the lowest (Fig. 2b). In terms of area impacted, 1058 ha were partially logged (based on a conservative estimate of half of the acreage of those stands) and 1352 ha were clearcut for a total of 2410 ha of hemlock forest lost to logging in the last 6 years. An additional 296 ha of hemlock forest was developed since 1980, primarily for housing (Fig. 2b).

Over 25% of the stands sampled, representing 1880 ha, have already lost more than half of their hemlock cover because of HWA-induced mortality. Remaining trees in all stands with HWA continue to be infested and deteriorate. When HWA-induced mortality, logging and development are combined, 30% of the area mapped as hemlock in 1980 has been converted to other land cover types. At the present time, a considerably larger extent of hemlock forest is infested with HWA and is rapidly deteriorating in the remainder of this study area.

DISCUSSION

Across southern New England, HWA is generating a profound change in the amount and vigour of hemlock and threatens to eliminate this important long-lived and shade tolerant species (Fig. 3). Information on variation in tree mortality, defoliation level, or crown health resulting from pest and pathogen infestations is critical for assessing pest migration rates, extent of tree damage and decline and the specific factors responsible for the observed patterns (Mitchell & Preisler, 1991; Liebhold *et al.*, 1995; Luther *et al.*, 1997; MacLean & MacKinnon, 1997; Powers *et al.*, 1999; Radeloff *et al.*, 2000). Such spatial and stand-level information is also invaluable for anticipating future patterns of infestation and decline and for prioritizing management efforts suitable for vulnerable and/or susceptible stands (Gage & Pijanowski, 1993; Liebhold *et al.*, 1995). Understanding the factors that control the pattern and rate of spread of HWA is one of the most important components for developing successful pest management programmes (Gray & Salom, 1996).

Factors controlling the regional status of hemlock and HWA impacts

We observed a distinct pattern of high hemlock mortality and low tree vigour in the south and decreasing mortality and improved tree vigour in the north. This trend supports our initial expectations and is consistent with the significant Mantel correlation between HWA infestation level and latitude and the predominantly south to north migration pattern of HWA since its arrival in New England (McClure *et al.*, 2000). In addition, the spatially autocorrelated mortality and vigour patterns observed in this study suggest that geographically adjacent stands exhibited similar patterns of mortality and decline. Many southern stands were infested during the mid- to late 1980s (McClure *et al.*, 2000) and despite differences in composition and site-related factors, most stands experienced decline and heavy mortality with continued HWA infestation. The only areas within our study region containing predominantly healthy hemlock forests were located in the north-eastern corner and in the centrally located Salmon River Valley. These locations were only recently infested (Orwig & Foster, 1998; McClure *et al.*, 2000) and therefore remain in better overall health.

Our results suggest that latitude is the most important environmental factor associated with HWA infestation level, hemlock decline (vigour) and mortality, although some environmental and site factors exhibited weaker, but significant relationships. Contrary to our second expectation, both overstory and understory hemlock mortality were associated with topographical aspect, with higher levels observed on south-western and western slopes. Mayer *et al.* (1996) and Bonneau *et al.* (1999a) also found poorer hemlock health of infested trees on south-westerly slopes. These slopes are relatively warmer and more xeric, conditions that may impose an additional stress on shallow-rooted, drought-sensitive hemlock, making them more vulnerable to HWA attack (Souto & Shields, 2000). Additional site-related factors not measured in our study, such as depth to bedrock, soil type, or soil nutrient status may also have been associated with mortality and warrant further investigation (cf. Bonneau *et al.*, 1999a).

There was no relationship between hemlock vigour or mortality and stand-level hemlock abundance or percentage hardwood overstory, as indicated by low correlations with hemlock importance values. This finding supports our expectations and suggests that hemlock-hardwood stands are just as susceptible to infestation as hemlock dominated stands. This contrasts with other coniferous pests such as spruce budworm [*Choristoneura fumiferana* (Clem.)] or balsam woolly adelgid (*A. piceae* Ratz.), which typically cause more intense damage with higher host concentrations (MacLean & Ostaff, 1989; Nicholas *et al.*, 1992). Unlike pests such as mountain pine beetle (*Dendroctonus ponderosae* Hopkins) or balsam woolly adelgid that preferentially damage and kill large-diameter trees (Witter & Ragenovich, 1986; Mitchell & Preisler, 1991), HWA attacked all size classes and both overstory and understory hemlocks exhibited crown damage and mortality. In addition, the intensity and spatial distribution of sapling mortality was similar to that of overstory trees. The significant relationship between stand size and overstory mortality was unexpected, even when both location and other environmental factors were controlled for, and may signify that HWA populations reach large stands more quickly or they increase and spread more rapidly and efficiently within large contiguous stands.

An additional factor that may be contributing to the hemlock mortality observed in this study is the interaction between HWA and the introduced elongate hemlock scale, whose distribution currently overlaps with the northern distribution of HWA (McClure, 1989; McClure *et al.*, 2000). We observed scale predominantly in the southern half of our study area. Although the interplay of these two pests is not well known (Evans *et al.*, 1996; McClure *et al.*, 2000), it is believed that the added stress of two insects attacking hemlock simultaneously further weakens the tree and leads to more rapid mortality (McClure *et al.*, 2000).

Logging and indirect consequences of HWA

The extent of hemlock decline and mortality observed in our study also contributed to increased cutting in the area. Of forty stands visited that experienced logging, thirty-six were located in the southern half of the transect. Because of

Figure 3 Composite figure of site photos. (a) Aerial view of widespread hemlock mortality resulting from hemlock woolly adelgid infestation in southern Connecticut. (b) Thinning hemlock crowns associated with HWA infestation and classified as poor vigour. This condition was observed throughout the transect but was prevalent in the southern stands. Note the loss of foliage from the interior portions of crown branches and the tufts of needles remaining on the branch tips. (c) Stand of dead and dying hemlock trees following several years of heavy HWA infestation in southern Connecticut. Prolific establishment of black birch (*Betula lenta* L.) seedlings is replacing hemlock trees.

the relatively low value of hemlock timber resulting from ring shake, hemlock has not historically been a commercially desirable species (Baumgras *et al*., 2000; Howard *et al*., 2000). However, HWA infestations have led to unprecedented rates of presalvage removals across New England (Foster, 2000; Kizlinski *et al*., 2002). In our transect the intensity of logging is greatest in the south, suggesting that land managers and owners are responding to reduced vigour and increasing mortality observed in these stands. Importantly, increased logging has occurred throughout Connecticut and Massachusetts or is planned as loggers and foresters are anticipating the arrival of HWA and forest decline (Donnelly, 1994; Cox & Mauri, 2000). In many areas logging is a major indirect consequence of HWA that will exert a great impact on regeneration dynamics, future forest composition and structure, wildlife habitat and landscape pattern. The contrasts and interactions between HWA-induced mortality and logging are largely unknown, but initial results suggest that both disturbances lead to profound changes in the structure and composition of these forests (Kizlinski *et al.*, 2002; Orwig & Kizlinski, 2002).

Management implications

Although the exact timing and location of HWA arrival and eventual hemlock mortality are unpredictable at any specific location, our results suggest that, within 15 years of initially entering southern Connecticut, HWA migrated into every town and damage intensity broadly mirrored the overall south to north migration pattern (McClure *et al.*, 2000). These observations provide a practical timeline for anticipating hemlock deterioration and resulting landscape patterns that can be beneficial for land and resource managers. Although we focused primarily on stands > 20 ha, our sampling and observations in dozens of smaller stands reveal similar patterns of decline and mortality (Orwig & Foster, 1998). Ridgetop and topographically exposed sites appear most susceptible to rapid adelgid-induced decline and may also be the most difficult to protect because of location and stressful growing conditions. In addition, mixed hardwood–hemlock stands are just as likely to succumb to extended infestation as predominantly hemlock stands. Therefore, we suggest that large tracts of hemlock-dominated forest located at the northern extent of the adelgid's range should be given high priority when planning biocontrol release sites. These sites appear most vulnerable to rapid HWA infestation, tree decline, and dramatic ecological change and would incur the greatest benefit of protection. In addition, these sites have the best chance of protection if efforts begin immediately after HWA is detected. Forest monitoring and early detection will be critical for control efforts to have any chance. We believe that without control, prolonged, heavy infestations will lead to severe or complete hemlock mortality on all site types in southern New England.

The loss of hemlock will lead to a much more homogenized landscape with respect to species composition and structure. Species already in the canopy of these forests and poised to replace hemlock include birch, maple and oak species. Many infested stands have already experienced prolific black birch establishment (Fig. 3), a trend we predict will continue based on this species' high annual seed production and its close association with hemlock forests (Ward & Stephens, 1996).

CONCLUSION

Eastern hemlock is a long-lived, shade tolerant species that plays a unique ecological role in forested areas across eastern North America. As a late successional conifer it is often an important component of old-growth and mature forests and it provides important wildlife habitat. In addition, hemlock casts deep shade and creates cooler microenvironments in riparian and wetland habitats. Although hemlock abundance declined dramatically with land clearance, forest utilization and increased fire following European settlement, it has been increasing with regional reforestation and changes in forestry practices and is highly valued for its ecological and aesthetic attributes. Ironically, this tree species, which oftentimes is concentrated on sites least affected by direct human activity, is now threatened across its range.

Hemlock woolly adelgid occurs in most of the stands across our southern New England region and the geographical pattern of mortality and tree vigour is coincident with the temporal migration patterns of HWA from south to north. Factors other than latitude, such as topographically exposed slopes and large stand size only exhibit minor, although significant relationships. The low vigour of most remaining trees suggests that site and environmental variables will exert little influence on stand susceptibility or eventual mortality. Over 4290 ha of hemlock forest has been eliminated by logging or HWA just within the southern part of our transect since the mid-1980s, and we predict continued HWA infestation will lead to unprecedented hemlock loss throughout the north-eastern USA, regardless of site conditions or location.

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