Biol Invasions (2008) 10:201–213
DOI 10.1007/s10530-007-9123-z

ORIGINAL PAPER

Range expansion and population dynamics of co-occurring invasive herbivores

Evan L. Preisser · Alexandra G. Lodge · David A. Orwig · Joseph S. Elkinton

Received: 20 December 2006 / Accepted: 8 May 2007 / Published online: 20 June 2007

Abstract Although a range of studies have suggested that competition plays a critical role in determining herbivore assemblages, there has been little work addressing the nature of interactions between competing invasive herbivores. We report the results of research on the hemlock woolly adelgid *Adelges tsugae* ('HWA') and elongate hemlock scale *Fiorinia externa* ('EHS'), invasive herbivores that both feed on eastern hemlock (*Tsuga canadensis*). HWA has been linked to hemlock mortality throughout the East Coast of the US; the loss of hemlock threatens to permanently alter surrounding ecosystems. We assessed the spread and impact of both species by resurveying 142 hemlock stands across a 7,500 km^2 latitudinal transect, running from coastal CT to northern MA, for HWA and EHS density as well as hemlock mortality. These stands had been previously surveyed in either 1997–1998 (CT) or 2002–2004 (MA). While the number of HWA-infested stands has increased, per-stand HWA density has substantially decreased. In contrast, EHS distribution and density has increased dramatically since 1997–1998. Hemlock mortality was much more strongly related to HWA density than to EHS density, and many stands remain relatively healthy despite an overall increase in hemlock mortality. There was a positive correlation between HWA and EHS densities in stands with low mean HWA densities, suggesting the potential for host-plant-mediated facilitation of EHS by HWA. Our findings underline the importance of research explicitly addressing interactions between competing invasive species, and of determining the potential consequences of these interactions for the invaded ecosystem.

Keywords *Tsuga canadensis* · *Adelges tsugae* · *Fiorinia externa* · Plant–herbivore interactions · Competition · Facilitation

Introduction

A range of studies have shown that exploitative competition between herbivores is common and can strongly influence community composition (Denno et al. 1995). Such competition is especially important among sessile haustellate (i.e., possessing sucking

E. L. Preisser (✉)
Department of Biological Sciences, University of Rhode Island, 100 Flagg Rd., Kingston, RI 02881, USA
e-mail: preisser@uri.edu

E. L. Preisser · J. S. Elkinton
Department of Plant, Soil, and Insect Sciences, University of Massachusetts at Amherst, Amherst, MA 01003, USA

A. G. Lodge
Kenyon College, Gambier, OH 43022, USA

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

mouthparts) herbivores, whose immobility and feeding mode make them particularly susceptible to changes in resource quality. The outcome of such interactions are often asymmetric, with early-arriving species inducing changes in plant chemistry that negatively impact later-arriving species (Denno et al. 2000; Faeth 1986; Inbar et al. 1999; van Zandt and Agrawal 2004). Facilitative interactions between herbivores via reduced plant defenses or the spatial re-allocation of resources within host plants are less common but have also been documented (Arsenault and Owen-Smith 2002; Masters et al. 1993; Nakamura et al. 2003).

Despite ecologists' steadily increasing concern about biological invasions, the consequences of interactions between invasive herbivores for their shared native host plants have received little attention. This is surprising since invasive species are often largely free of natural enemies and other regulatory forces present in their native range (Mooney and Cleland 2001; Sakai et al. 2001) and can thus reach extremely high densities, increasing the likelihood and potential importance of interspecific interactions. Across a variety of studies, competition was more common in interactions involving invasive herbivores than in interactions between native species (Denno et al. 1995). Alternately, invasive herbivores may facilitate other exotics in a process termed ''invasional meltdown'' (Parker et al. 2006; Simberloff and Von Holle 1999).

In the New England region of the United States, the eastern hemlock *Tsuga canadensis* is the host plant for two invasive herbivores, the hemlock woolly adelgid *Adelges tsugae* ('HWA') and the elongate hemlock scale *Fiorinia externa* ('EHS'). HWA is an especially severe threat, having decimated hemlock stands throughout the northeast (McClure 2002; McClure and Cheah 1999). Both species are largely sessile phloem-feeding homopterans whose rapid population growth rates and tendency to occur in dense aggregations may increase the potential for interspecific competition (see ''natural history of the system,'' below). McClure (1980) found that EHS competitively excluded the non-native scale *Nuculaspis tsugae* on hemlock. By settling on foliage approximately one month before *N. tsugae*, EHS occupies prime feeding sites while its subsequent feeding decreases foliar nitrogen and host plant quality. A similar situation occurs between HWA and EHS, with HWA settling approximately one month earlier than EHS. HWA is also bivoltine, while EHS is univoltine in New England (McClure 1978). It has been suggested that these advantages should lead to the competitive exclusion of EHS by HWA (McClure 1997).

Although the effects of both HWA and EHS on hemlocks have been studied, their interactions and the effect of their combined presence on hemlocks remain essentially unknown (McClure 2002, but see Danoff-Burg and Bird 2002). The latter issue is especially important since the loss of eastern hemlock will significantly alter ecosystem structure and function (Ellison et al. 2005; Kizlinski et al. 2002; Yorks et al. 2000). While such questions are most often addressed in small-scale manipulative experiments, both interspecific interactions and host plant effects may vary as a function of the spatial scale over which they are examined. In grasslands, for instance, the correlation between plant species diversity and community-level vulnerability to biological invasions switches from negative to positive as the sampled unit increases from meters to hectares (Naeem et al. 2004). Such findings highlight the importance of replicated large-scale surveys in assessing the effects of invasive species at the landscape level.

We report the results of a 2005 re-survey of 142 hemlock stands in southern New England that had previously been assessed for HWA density, EHS density, and hemlock health. We compare our data with that of the initial surveys to explore the landscape-level spread of HWA and EHS, their interactions, and their impact(s) on *T. canadensis*. Our findings assess the importance and nature (competitive versus facilitative) of interspecific interactions between these two invasive herbivores, information critically important for predicting the speed and severity of hemlock loss in the face of one or both species.

Methods

Natural history of the system

The hemlock woolly adelgid *Adelges tsugae* ('HWA') is a native of Japan and China that was introduced near Richmond, Virginia in the 1950s; it had spread to southern New England by 1985

(McClure and Cheah 1999). HWA is bivoltine and obligately parthenogenetic in its invaded range, and feeds exclusively on eastern hemlock and Carolina hemlock (*Tsuga caroliniana*). The early-instar 'crawler' phase can move along branches under its own power and/or be passively dispersed between trees by wind or biotic agents (McClure 1990b). The sessile adults feed at the base of hemlock needles on ray parenchyma tissue (Young et al. 1995); a high-density HWA infestation can kill even mature trees in four years (McClure 1991) and most trees usually die within 10–15 years (Orwig et al. 2002).

The elongate hemlock scale *Fiorinia externa* ('EHS') was introduced into New York City from Asia in 1908 and has now been reported in at least 14 eastern states (Lambdin et al. 2005). It is found almost exclusively on eastern hemlock in the northeastern US (McClure and Fergione 1977). Although EHS is univoltine and reproduces sexually, its life cycle is otherwise very similar to that of HWA: overwintering adults lay eggs that hatch in late spring to produce 'crawlers' that can both move actively and be dispersed passively. The crawlers settle on the underside of hemlock needles and mature into sessile adults that feed on the mesophyll (McClure 2002). While EHS is not as harmful to hemlocks as HWA, high-density infestations can weaken or kill already-stressed trees (McClure 1980).

Survey methods

Our surveys were carried out in a 7500 km^2 region of southern New England stretching from Long Island Sound in southern Connecticut to near the Vermont border in Massachusetts (Fig. 1). Elevations along this north-south transect range from 10 to 350 m a.s.l and details of climate and geology are contained in Orwig et al. (2002). The region is characterized by cold winters and warm summers, with the coastal areas being lower in elevation and experiencing milder winters than the northern portion of the transect.

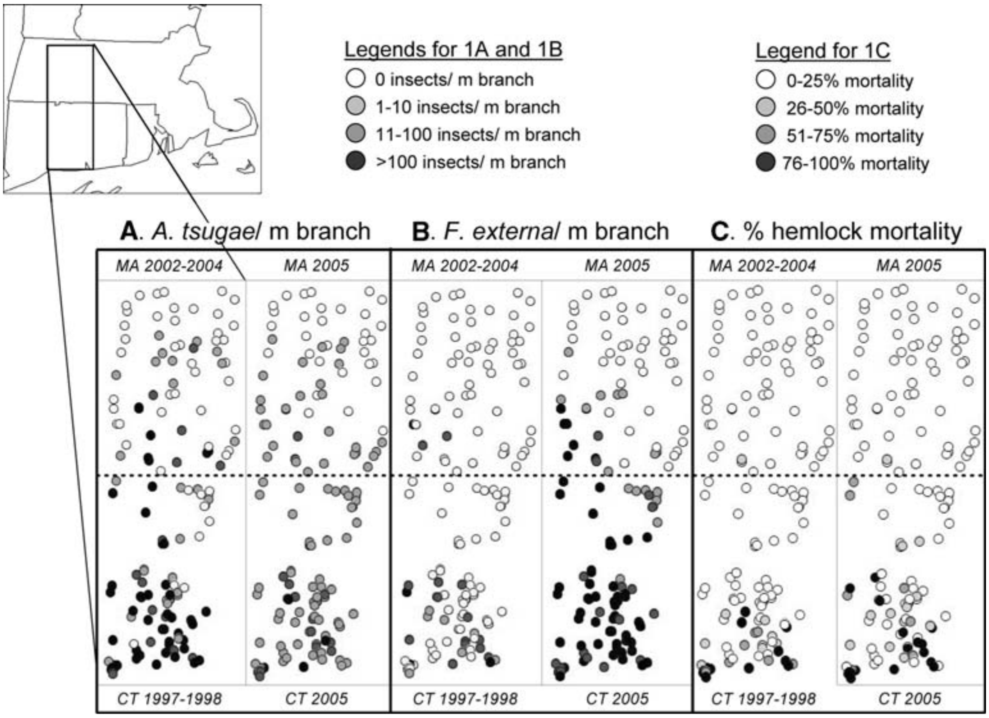

Fig. 1 Results of two transect surveys of 142 *T. canadensis* stands. Circles represent surveyed stands, 50 sampled trees per stand. In Fig. 1A–C, the left panel presents initial survey data (CT: 1997/1998, MA: 2002–2004), and the right panel presents 2005 survey data. Dashed line indicates MA/CT border. **(A and B)** *Adelges tsugae* and *Fiorinia externa* stand density ratings. Open circles: 0 insects/ m branch; light gray: 1–10/m branch; dark gray: 11–100/m branch; black: >100/m branch. **(C)** % *T. canadensis* mortality. Open circles: 0–25% mortality; light gray: 26–50% mortality; dark gray: 51–75% mortality; black: 76–100% mortality

Details of how the stands were initially located are given elsewhere (Orwig et al. 2002); briefly, aerial photographs were used to identify likely sites (n = 237) that were visited in 1997–1998 (CT) or 2002–2004 (MA). Hemlock importance values (HEMIV) were calculated by summing the relative basal area from variable radius plots and relative density from fixed area plots. Values included both live and recently dead trees to represent ''pre-HWA'' importance. Each stand was also characterized according to slope, aspect, topographic position, and elevation. To ensure that the survey covered a diverse region, the target regions of MA and CT were divided into 30 and 24 north-south rectangular USGS quadrants, respectively.

We revisited 63 hemlock stands in Massachusetts and 79 stands in Connecticut (142 total) during the summer of 2005. Our sampling scheme was designed to ensure that, whenever possible, at least one site was visited in both the northern and southern portions of each quadrant. A maximum of 10 stands were visited per quadrant. The stands ranged in size from seven to 305 ha, with a mean of 45 ha, and all had been previously sampled for HWA and EHS density as well as hemlock mortality (CT sampling data from Orwig et al. 2002; MA sampling data from Orwig et al. in preparation).

In the 2005 survey, stands were again sampled for HWA and EHS infestation and hemlock mortality. We sampled 50 haphazardly selected hemlock trees (>2 m in height) in each stand by examining the undersides of two meter-long branches on approximately opposite sides of each tree and classifying HWA and EHS density per m branch for each tree from 0 to 3 (0=none; 1 = 1–10 organisms/m branch; 2 = 11–100 organisms/m branch; 3 $\geq$ 100 organisms/m branch). The percent of dead standing hemlocks in each stand (mortality) was estimated to the nearest 10% based on a walk-through of the sampled portion of the stand. All procedures were explicitly designed to replicate those of the previous survey as far as was practically possible.

Statistical analysis

Between-stand analysis

For the 2005 survey, we determined the mean HWA and EHS density rating per tree in each stand, based on 50 surveyed trees per stand ('HWAavg' and 'EHSavg') as well as percent hemlock mortality ('MORT') for each of the 142 sampled stands. We also analyzed the change in these three variables, ΔHWAavg, ΔEHSavg, and ΔMORT, calculated as (2005 survey data—initial survey data). Because the 63 MA stands were initially sampled much later (2002–2004) than were the 79 CT stands (1997/98), we used only the CT data to calculate ΔHWAavg, ΔEHSavg, and ΔMORT. Since the three variables were non-normally distributed, we used Wilcoxon signed-rank tests in JMP-IN 5.1 (SAS 2004) to test whether their means differed significantly from zero.

GIS overlays and digital elevation models (1:250,000 scale DEM; USGS, unpubl. data) were analyzed in ArcView 3.2 (ESRI 1999) to determine stand size, patch characteristics, and spatial distribution. We transformed aspect values from circular variables into a measure relevant to vegetational dynamics: aspect = cosine (45−azimuth degrees) + 1 (Beers et al. 1966). The resulting values ranged from 0 (sunny southwestern slopes) to 2 (the least exposed northeastern slopes). Stand geographic coordinates (i.e., Universal Trans-Mercator $x-y$ coordinates, in meters) were also converted to distance matrices using the euclidean distance between sampling pairs.

We used Mantel tests to assess the significance of environmental and stand variables in determining herbivore density and hemlock mortality; this technique includes space (i.e., geographic location) as a predictor variable in the analysis. Mantel tests perform a linear regression on distance matrices generated from dependent variables (HWAavg, EHSavg, and MORT, as well as changes in each of these variables) and predictor variables (space, latitude, stand size, etc.). Positive Mantel coefficients indicate that spatially clustered points tend to have similar values, negative Mantel coefficients indicate that they tend to have dissimilar values, and Mantel coefficients statistically indistinguishable from zero imply no relationship. Mantel r coefficients are typically much smaller in magnitude than conventional correlation coefficients, even when highly statistically significant (Dutilleul et al. 2000). Partial Mantel coefficients were also calculated (e.g., MORT vs. elevation while controlling for location) to assess the relative contribution of each predictor variable for its partial effect on the dependent variable (Urban et al. 2002). Mantel test coefficients and significance levels were calculated with Manly's RT randomization program (Manly 1997), with 1000 randomizations for each test. The dependent variables were also used as predictor variables in a Mantel analysis of the relationship among HWAavg, EHSavg, and MORT for all 142 stands, and in an analysis of the relationship among ΔHWAavg, ΔEHSavg, and ΔMORT for the 79 CT stands.

Within-stand analysis of 2005 survey data

We examined the correlation between HWA and EHS density at the within-stand level using a subset of the 2005 data. Because stands in which one or both species are rare or absent provide little information about their interactions, we restricted our analysis to stands with at least 10 trees containing HWA and at least 10 trees containing EHS (65 of 142 stands).We then used data on individual trees within each stand to calculate the Spearman's rank correlation coefficient, ρ,(for each of the 65 stands. ρ describes the correlation between the HWA and EHS density ratings on trees within a stand and ranges from -1 (inverse correlation) to 1 (positive correlation); its use was necessary to account for the non-normal distribution of density ratings (a typical characteristic of data taken on an ordinal scale). After a preliminary Mantel analysis revealed that the data was not spatially autocorrelated, we used a stepwise model selection algorithm to select the best-fit model from an array of initial predictor variables (HWAavg, EHSavg, MORT, latitude, longitude, and all 2- and 3-way interactions). We tested the best-fit model using ANOVA in JMP-IN 5.1 (SAS 2004) and removed any terms with a VIF $\geq$10; the resulting model's residuals were normally distributed.

Results

Between-stand analysis of 2005 survey data

HWA and EHS were most abundant in the southern portion of the study area (Fig. 1A and B), and their densities were most strongly related to latitude (HWAavg all and EHSavg all; $r = 0.278$ and 0.325, respectively) (Digital appendix A.1). The density of both HWA and EHS were positively related to stand elevation ($r = 0.120$ and 0.194, respectively). While EHS density was negatively correlated with longitude (abundance declined from W to E), HWA density was positively correlated with longitude. Unlike HWA, EHS density was also positively correlated with stem density, stand basal area, and hemlock importance value (Digital appendix A.2). Neither HWA density nor EHS density were correlated with hemlock dbh or stand size (data not shown). HWA and EHS densities between stands were strongly correlated (Digital appendix A.3).

Hemlock mortality was more strongly related to HWA density ($r = 0.601$) than to EHS density ($r = 0.155$) (Digital appendix A.3). It was strongly correlated with latitude and weakly correlated with longitude, due to higher mortality occurring in the southwest part of the study area (Fig. 1C). The average % hemlock mortality of the 63 MA stands was 11.7 ± 0.45% (SE), while the average mortality of the 79 CT stands was 37.2 ± 3.41%. Mortality was spatially autocorrelated ($r = 0.207$) and most strongly related to latitude ($r = 0.317$) (Digital appendix A.1). Mortality was not related to basal area, stand density, or hemlock importance value (Digital appendix A.2).

Stand-level changes in CT

HWA was present in 68 of 79 CT stands during 1997–1998; it had spread to all 79 stands by 2005 (Fig. 1A; Fig. 2A, solid line). Although the number of stands with HWA increased, HWA density did not; the mean stand density rating declined 85% from 1997/98 to 2005 (Fig. 2A, filled bars; Wilcoxon sign-rank test with 78 df = -1428, $P < 0.001$). ΔHWAavg was spatially autocorrelated, meaning that stands with similar locations experienced similar changes in HWA abundance (Digital appendix A.1; $r = 0.143$). Although ΔHWAavg was most strongly related to stand location, it was also negatively related to longitude (e.g., ΔHWAavg all in Digital appendix A.1; $r = -0.156$) and positively related to hemlock importance value (Digital appendix A.2; $r = 0.123$). ΔHWAavg was not correlated with ΔEHSavg or ΔMORT (Digital appendix A.3).

EHS dramatically expanded its range in CT over our survey period, increasing from 22/79 stands in 1997/98 to 79/79 stands in 2005 (Fig. 1B; Fig. 2B, solid line). In contrast to HWA, this rapid range expansion was correlated with a mean increase in EHS density ratings from 0.56 to 2.17 (Wilcoxon

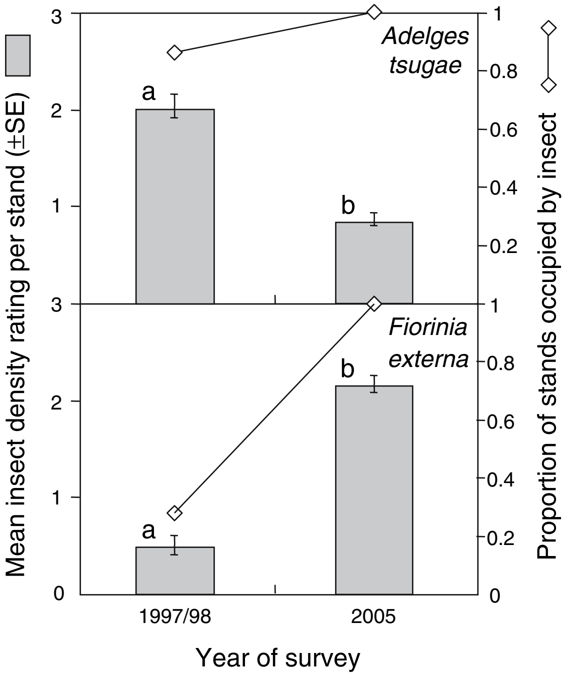

Fig. 2 Mean stand density rating ±SE (left axis, filled columns) and proportion of 79 CT stands occupied (right axis, open diamonds connected by lines) in 1997/1998 and 2005 by *A. tsugae* (**A**, top panel) and *F. externa* (**B**, bottom panel)

with 78 df = 1520, $P < 0.001$; Fig. 2B, filled bars). Changes in EHS abundance were spatially autocorrelated (Digital appendix A.1; $r = 0.099$), and this 'location effect' was the term most strongly related to ΔEHSavg (ΔEHSavg all; $r = 0.392$ in Digital appendix A.1, $r = 0.415$ in Digital appendix A.2). ΔEHSavg was not correlated with either ΔHWAavg or ΔMORT.

Hemlock mortality in CT increased 40% between 1997/98 and 2005, from 26.7 ± 3.52% to 37.2 ± 3.41% (Fig. 1C; Fig. 3; Wilcoxon with 78 df = 737, $P < 0.001$). Since our estimate of % hemlock mortality does not reflect trees that have died and fallen since the 1997/98 census, our estimates are conservative and likely underestimate the 'true' increase in hemlock mortality over this period. Changes in % hemlock mortality were negatively related to stand slope (Digital appendix A.1; $r = -0.155$), as lowland stands experienced greater increases in hemlock mortality than did stands in more hilly locations. ΔMORT was also weakly related to stand aspect, i.e., % hemlock mortality began to increase in stands growing on relatively protected northern and northeastern aspects (Digital appendix A.1; $r = 0.084$). Changes in % hemlock mortality were not related to any other predictor variables and were not spatially autocorrelated.

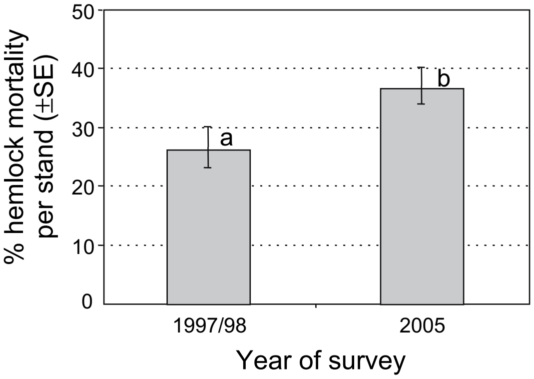

Fig. 3 Mean % *Tsuga canadensis* mortality per stand ±SE for 79 CT stands sampled in both 1997/98 and 2005

Within-stand correlation of HWA and EHS density ratings

ρ, the correlation between HWA and EHS densities on individual trees within a single stand, was inversely correlated with HWAavg (Digital appendix A.4; $F_{1,49} = 4.06$, $P = 0.049$). When corrected for the other terms in the model, ρ went from significantly positive (0.11, 95% CI: 0.024, 0.196) in stands with low mean HWA densities to marginally negative (−0.21, 95% CI: −0.470, 0.050) in stands with high mean HWA densities. The fact that there was no significant effect of EHS density on ρ ($P = 0.764$) suggests that the implied switch between commensalism and antagonism in the HWA-EHS interaction is largely mediated by the adelgid's effect on its host.

ρ was positively correlated with % hemlock mortality per stand (Digital appendix A.4; $F_{1,49} = 4.91$, $P = 0.031$). ρ went from marginally negative (−0.036, 95% CI: −0.104, 0.032) in the healthiest hemlock stands to significantly positive (0.137, 95% CI: 0.011, 0.263) in the stands with the greatest hemlock mortality. Although latitude was weakly significant ($P = 0.061$), the main effect of longitude was not. There was a significant latitude × longitude interaction ($F_{1,49} = 4.37$, $P = 0.042$), explained by the fact that ρ was lower in southwest versus northeast stands.

Discussion

Adelgid, scale, and hemlock health

Our work corroborates previous research documenting the rapid northward spread of HWA following its 1950s introduction into Virginia (Fig. 4A and sources cited therein). HWA crawlers can be passively dispersed via wind or bird/animal vectors (McClure 1990b), and a single disperser can eventually infest an entire forest. The adelgid's combination of rapid dispersal and asexual reproduction is the most likely explanation for the patchy 1997–1998 distribution of HWA behind the rapidly moving invasion front (Fig. 1A). The proportion of HWA-occupied hemlock stands in CT increased significantly in 2005, likely because crawlers from infested stands colonized nearby areas (Fig. 2A). While HWA remained absent from much of northern MA, the proportion of infested stands in the southern portion of the state increased as HWA dispersal 'filled in' previously uninfested stands (Figs. 1A, 4A).

Although HWA was initially predicted to competitively exclude EHS (McClure 1997), our research documents the rapid northern range expansion of EHS into an adelgid-dominated landscape (Figs. 1B, 4B).

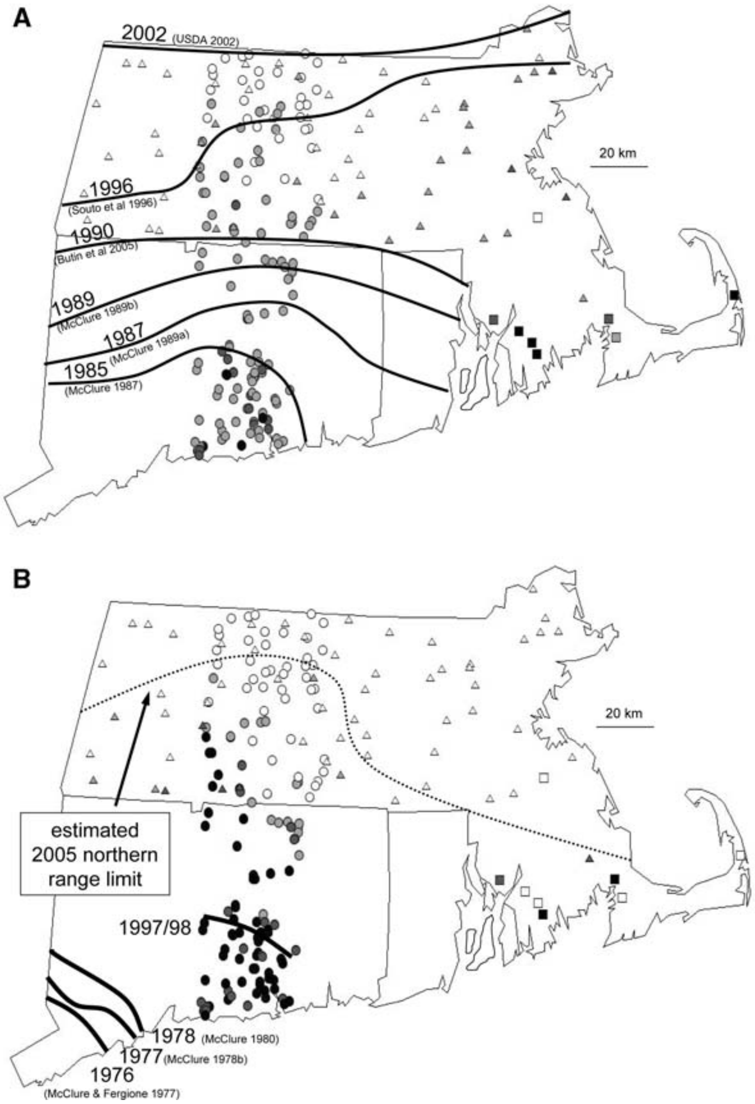

Fig. 4 Range expansion of *Adelges tsugae* (**A**) and *Fiorinia externa* (**B**) into New England, 1976–2005. Bold lines indicate ranges reported in published literature (Butin et al. 2005; McClure 1978, 1980; McClure 1987; McClure 1989a, 1989b; McClure and Fergione 1977; Souto et al. 1996; USDA 2002). ○ = 2005 density estimates from current research. Δ = density estimates taken between 10/2004 and 04/2005 from naturally occurring hemlock stands throughout Massachusetts (data from Preisser *et al* in preparation). ☐ = density estimates taken between 10/2004 and 04/2005 from planted hemlock stands that had not been treated with insecticide (data from Preisser *et al* in preparation). Open symbols denote stands with no HWA (**A**) or EHS (**B**), light gray indicates low density (1–10/m branch), dark gray indicates medium density (10–100/m branch), and black indicates high density (>100/m branch) of HWA or EHS

Between 1997/98 and 2005, the number of EHS-occupied hemlock stands in CT increased >350% (Fig. 2B). This expansion is especially striking in light of the fact that EHS remained largely restricted to the area surrounding New York City for ~70 years following its 1908 introduction (Sasscer 1912). This delay may be partially due to the fact that sexually reproducing species like EHS require multiple colonists to start a new population, an interpretation consistent with the high degree of spatial autocorrelation exhibited by EHSavg ($r = 0.487$; Digital appendix A.1) and the fact that EHS range expansion appears to be occurring along a discrete 'wave front' (Figs. 1B, 4B). It may also explain why EHS, unlike HWA, was more abundant in stands with a higher stem density, basal area, and hemlock importance value (Digital appendix A.2); stands with more or larger hemlocks may more easily reach the number of minimum number of individuals necessary for rapid population growth. The sharp increase in EHS-occupied stands and per-stand EHS density (Figs. 1B and 2B) suggests that EHS has not yet reached the northern limit of its invaded range.

Hemlock mortality in the 2005 survey was much more strongly related to HWA versus EHS abundance ($r = 0.601$ and 0.155, respectively; Digital appendix A.3), providing evidence that EHS is not a major source of hemlock mortality. Our conclusion contrasts with previous work finding that EHS, rather than HWA, was the primary cause of hemlock decline (Danoff-Burg and Bird 2002). Our contrasting findings are likely a function of the varied scale of the two studies: while we examined 50 trees in each of 142 stands (7,100 trees total), Danoff-Burg and Bird (2002) performed a more intensive survey of 153 trees in a single stand. Given that the within-stand correlation between HWA and EHS varies widely as a function of overstory mortality and stand-level adelgid density (Fig. 4), our results caution against relying heavily on data from a single survey site.

Hemlock mortality was also strongly related to latitude and higher in the southern portion of the study transect (Fig. 1C). Hemlock mortality in CT increased 40% between 1997/98 and 2005 (Fig. 3) and was in fact probably higher than our estimate; since we had no way of knowing whether fallen trees had died before or after the initial survey, our estimates included only dead standing trees. While we were concerned that unavoidable methodological differences (i.e., different people were responsible for the estimates in the two surveys) might confound the results, there was a strong positive correlation between the initial and 2005 stand-level mortality estimates for both MA ($F_{1,49} = 30.8$, $P < 0.0001$; $r^2 = 0.386$) and CT ($F_{1,77} = 37.2$, $P < 0.0001$; $r^2 = 0.326$). Stands with high (>75%) hemlock loss are concentrated in southern CT, while stands in MA and northern CT appear relatively healthy (Fig. 1C). Although the situation remains dire, initial fears of the rapid and complete loss of hemlocks throughout southern New England have not yet been realized (Orwig and Foster 1998).

Relationships between adelgid and scale abundance

The correlation between HWA and EHS densities on individual trees within a stand was a function of stand-level adelgid, but not scale, density (Digital appendix A.4). This implies an asymmetric relationship between HWA and EHS, with HWA affecting EHS more than the reverse. Such asymmetric interactions appear particularly common and influential in interactions between sessile herbivores (Denno et al. 1995; Denno et al. 2000). In this case, the bivoltine nature of HWA in conjunction with its ability to colonize and begin feeding on hemlock foliage before the late-spring arrival of EHS is likely a major factor in its dominance. The fact that HWA is far more lethal to hemlock than EHS may accentuate its dominance; left unchecked, it can quickly kill the resource on which both depend.

The positive correlation between HWA and EHS at low adelgid densities suggests that HWA may facilitate the invasion of this invasive herbivore. Since both insects are sessile sap-feeders, this facilitation (if it truly exists) likely occurs via the adelgid's effect on their shared host. HWA-weakened hosts may be more vulnerable to colonization by EHS crawlers, increasing the rate of scale population growth. Similar preferences for weakened hosts occur in a range of systems; bark beetles, for instance, target hosts weakened by injury or previous herbivory (Raffa and Berryman 1987) . This interpretation is supported by the fact that HWA and EHS become more positively correlated as stand health decreases, suggesting that facilitation increases in heavily impacted stands (Digital appendix A.4). It is also consistent with a shifting balance between facilitation and antagonism: while low adelgid densities weaken the host hemlock's defenses and facilitate scale invasion, higher HWA densities magnify the severity of resource competition and the relationship becomes increasingly antagonistic.

The decrease in per-patch HWA density between 1997/98 and 2005 (Fig. 2, filled bars) has several potential explanations. Cold winter temperatures decrease HWA survival (Parker et al. 1998; Skinner et al. 2003), and a wide-ranging field survey found that HWA overwintering survival was inversely correlated with latitude (Shields and Cheah 2005). The winters of 2003–2004 were the second and third coldest in the past 20 years in MA (NOAA 2006), and HWA overwintering survival was much lower than in previous years (A. Paradis, personal communication). It is also possible that the declining health of hemlock stands has made them less suitable for high-density adelgid populations. This explanation is supported by the fact that hemlock mortality increased significantly between 1997/98 and 2005 (Fig. 3), and previous research has shown that adelgids perform poorly on low-quality foliage (McClure 1991).

While climate and host quality are likely responsible for the majority of HWA decline, a third intriguing possibility involves the potential for hemlock-mediated negative feedback from EHS to HWA. McClure (1991) suggests that the HWA-hemlock interaction involves two discrete 'waves' of HWA colonization. Rapid HWA population growth on initially healthy hemlocks leads to declining hemlock health and a subsequent crash in adelgid numbers. After the temporarily HWA-free hemlock recovers and invests in new foliage, HWA recolonizes and kills the weakened tree (McClure 1991). EHS might affect this process in a manner similar to that seen on red pine, where the pine scale *Matsucoccus resinosa* competitively excludes the pine adelgid *Pineus boerneri* (McClure 1990a). Although both are capable of colonizing healthy trees and both decline dramatically as the tree weakens, *M. resinosa* can survive on lower-quality resources than the adelgid and thus continues to reproduce on even poor-quality trees. The continued presence of the pine scale keeps tree health low and precludes *P. boerneri* colonization and population growth in a manner consistent with the R* model of resource competition (Tilman 1990). It is possible that similar interactions may be occurring between HWA and EHS. For instance, the temporal advantage that HWA crawlers derive by settling 1–2 months earlier than EHS crawlers may be offset by the fact that the crawlers of both species often settle on hemlock branches on which adult HWA and EHS have overwintered. The nearly year-round occupancy of hemlock foliage could mean that exploitative competition between these species occurs on both a between- and within-year basis. This would allow high-density scale populations (at densities similar to those currently found throughout CT) to keep resource levels low throughout the year, precluding the hemlock's investment in the high-quality foliage essential for adelgid colonization (McClure 1991). If so, the invasion of EHS may provide some indirect benefit to hemlocks in New England.

Conclusion

Despite widespread agreement on the importance of exploitative competition in structuring herbivore assemblages, there has been surprisingly little research documenting the outcome and importance of interactions between invasive herbivore species. Work in this area is especially important since (A) the frequency of invasive-invasive interactions should increase as the number of invasive species continues to rise; and (B) the relative absence of regulatory forces often allows invasive species to achieve high population densities. In the adelgid-scale interaction, the dual advantages of earlier settlement and bivoltine reproduction should allow HWA to competitively exclude EHS in New England. Our research documents that this 'predictable' outcome has not occurred; on the contrary, HWA abundance has decreased during the same period that EHS density has exploded. Landscape-level surveys like ours assess correlative rather than causative relationships, and it is possible that these patterns and the slower-than-expected rate of hemlock decline will prove transitory. Even so, however, our results highlight the need for experimental work addressing the interaction between these two invasive species. In a broader sense, the distinctive population dynamics characteristic of invasive species may mean that interactions between invasive species may not have outcomes similar to those interactions occurring between native-native or invasive-native species pairs.

Acknowledgements A. Ellison made many helpful comments on this manuscript, and ELP benefited from discussing these ideas with M. McClure. AGL received financial support from NSF REU award DBI #04–52254. DAO received financial support from NSF award #DEB-0236897. ELP and JSE received financial support from USDA award #04-CA-11244225–275.

Appendix

Digital appendix A.1 Between-stand correlation of location, HWA density per m branch (50 tree avg. per stand; HWAavg), EHS density per m branch (50 tree avg. per stand; EHSavg), and % hemlock mortality (MORT) in 142 Connecticut and Massachusetts hemlock stands sampled in 2005 with the predictor variables geographic location, longitude, latitude, aspect, slope, and elevation

Dependent variable	Location		Longitude		Latitude		Aspect		Slope		Elevation	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Location	–	–	0.662	0.001	0.656	0.001	NS		−0.063	0.039	0.469	0.001
HWAavg	0.146	0.001	NS		0.269	0.001	NS		NS		0.225	0.001
HWAavg| location	–	–	−0.286	0.001	0.313	0.001	NS		NS		0.198	0.001
HWAavg| all	−0.110	0.001	0.019	0.001	0.278	0.001	NS		NS		0.120	0.027
EHSavg	0.487	0.001	0.094	0.001	0.652	0.001	NS		NS		0.503	0.001
EHSavg|location	–	–	−0.551	0.001	0.565	0.001	−0.021	0.036	−0.041	0.002	0.331	0.001
EHSavg|all	0.299	0.001	−0.172	0.001	0.325	0.001	−0.019	0.015	0.044	0.001	0.194	0.001
MORT	0.207	0.001	NS		0.299	0.001	NS		NS		0.181	0.002
MORT | location	–	–	−0.254	0.001	0.283	0.001	NS		NS		NS	
MORT | all	−0.043	0.001	0.044	0.001	0.317	0.001	NS		NS		NS	
ΔHWAavg	0.143	0.001	0.083	0.014	0.153	.001	NS		NS		0.066	0.047
ΔHWAavg|location	–	–	−0.096	0.022	NS		NS		NS		NS	
ΔHWAavg|all	0.288	0.001	−0.156	0.022	NS		NS		NS		NS	
ΔEHSavg	0.099	0.005	0.077	0.016	0.072	0.031	NS		NS		NS	
ΔEHSavg |location	–	–	NS		NS		NS		NS		NS	
ΔEHSavg |all	0.392	0.005	NS		−0.247	0.014	NS		NS		NS	
ΔMORT	NS		NS		NS		0.088	0.038	−0.151	0.032	NS	
ΔMORT |location	–	–	NS		NS		0.087	0.040	−0.149	0.038	NS	
ΔMORT |all	NS		NS		NS		0.084	0.041	−0.155	0.038	NS	

Change in HWA density (ΔHWAavg), change in EHS density (ΔEHSavg), and change in % hemlock mortality (ΔMORT) were calculated using data from 79 CT stands sampled in both 1997/98 and 2005.*r* is the Mantel coefficient and *P* is the significance after 1000 randomizations; NS indicates values of *r* where $P > 0.05$

* | Location indicates a partial correlation controlling for location

** | all indicates a partial correlation controlling for the other five predictor variables

Digital appendix A.2 Between-stand correlation of HWA and EHS density (HWAavg and EHSavg) and % hemlock mortality (MORT) in 142 Connecticut and Massachusetts hemlock stands sampled in 2005 with the predictor variables geographic location, basal area (m^2 ha^{-1}), density (stems ha^{-1}), and overstory hemlock importance value (IV)

Dependent Variable	Location		Basal area		Stand density		Hemlock IV	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Location	–		NS		NS		NS	
HWAavg	0.124	0.001	NS		NS		NS	
HWAavg| location*	–		NS		NS		NS	
HWAavg| all**	0.132	0.001	NS		NS		NS	
EHSavg	0.439	0.001	0.040	0.009	0.050	0.003	NS	
EHSavg|location	–		0.026	0.027	0.029	0.012	0.030	0.011
EHSavg|all	0.439	0.001	0.024	0.032	0.035	0.019	0.030	0.017
MORT	0.207	0.001	NS		NS		NS	
MORT| location	–		NS		NS		NS	
MORT| all	0.211	0.001	NS		NS		NS	
ΔHWAavg	0.143	0.001	NS		NS		0.115	0.005
ΔHWAavg| location*	–	–	NS		NS		0.124	0.002
ΔHWAavg| all**	0.267	0.001	NS		NS		0.123	0.002
ΔEHSavg	0.099	0.005	NS		NS		NS	
ΔEHSavg|location	–	–	NS		NS		NS	
ΔEHSavg|all	0.415	0.005	NS		NS		NS	
ΔMORT	NS		NS		NS		NS	
ΔMORT| location	–	–	NS		NS		NS	
ΔMORT| all	NS		NS		NS		NS	

Change in HWA density (ΔHWAavg), change in EHS density (ΔEHSavg), and change in % hemlock mortality (ΔMORT) were calculated using data from 79 CT stands sampled in both 1997/98 and 2005 *r* is the Mantel coefficient and *P* is the significance after 1000 randomizations; NS indicates values of *r* where $P > 0.05$

*| Location indicates a partial correlation controlling for location

** | All indicates a partial correlation controlling for all the other predictor variables

Digital appendix A.3 Significant (*P* < 0.001) simple between-stand Mantel correlation coefficients (*r*) after 1000 randomizations among HWAavg, EHSavg, and MORT in 142 Connecticut and Massachusetts hemlock stands sampled in 2005

Predictor variables			
Dependent variable	HWAavg	EHSavg	MORT
HWAavg	—	0.209	0.516
EHSavg	0.162	–	0.103
MORT	0.601	0.155	–

ΔHWAavg, ΔEHSavg, and ΔMORT for the 79 Connecticut stands sampled in 1997/8 and 2005 were similarly analyzed; however, there were no significant correlations between any of the three variables

Digital appendix A.4 MANOVA of stand-level factors affecting Spearman's rank correlation coefficient, ρ, of HWA and EHS density ratings at the within-stand level (2005 survey data on 50 trees/stand, 65 total stands)

EFFECT	SS	df	*F*	*P*
Latitude	0.062	1	3.681	0.061
Longitude	0.009	1	0.518	0.475
MORT	0.082	1	4.914	**0.031**
HWAavg	0.068	1	4.060	**0.049**
EHSavg	0.002	1	0.091	0.764
Latitude × Longitude	0.073	1	4.365	**0.042**
Latitude × MORT	0.001	1	0.030	0.862
Latitude × HWAavg	0.008	1	0.503	0.481
Longitude × HWAavg	<0.001	1	0.019	0.890
MORT × HWAavg	0.007	1	0.446	0.508
MORT × EHSavg	0.058	1	3.478	0.068
HWAavg × EHSavg	0.005	1	0.284	0.597
Latitude × Long. × HWAavg	0.058	1	3.480	0.068
Latitude × MORT × HWAavg	0.051	1	3.063	0.086
MORT × HWAavg × EHSavg	0.123	1	7.343	**0.009**
Error	0.820	49		

Bold values indicate $P < 0.05$

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