

Interactions between invasive herbivores and their long-term impact on New England hemlock forests

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Received: 11 February 2014 / Accepted: 17 July 2014 / Published online: 25 July 2014
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Abstract The introduction of the hemlock woolly adelgid (*Adelges tsugae*) in the eastern United States has caused extensive damage to eastern hemlock (*Tsuga canadensis*) stands. The presence of other herbivores can affect adelgid density and hemlock health. Here, we report the results of long-term work monitoring hemlock forests in a 7,500 km² latitudinal transect of southern New England. In biannual surveys between 1997 and 2011, we assessed change in hemlock basal area, stand-level hemlock defoliation, the density of four exotic herbivores (*A. tsugae*,

Fiorinia externa, *Nuculaspis tsugae* and an unidentified *Nuculaspis* sp.) and explored relationships between biotic and abiotic variables. Hemlock basal area decreased by approximately 60 % over the 14 years of the study. Hemlock stand defoliation increased locally in some stands but on average stand defoliation did not change throughout the study period/area. Local increases in defoliation were probably driven by the northward expansion by *A. tsugae*, and to a certain extent by the co-occurring presence of *F. externa* and *Nuculaspis* scales. Average *F. externa* density increased during the study and also expanded dramatically northward, although its density did not impact hemlock stand defoliation and only reduced hemlock basal area in some stands. Stand-level variation in *F. externa* densities was most strongly affected by the presence of *Nuculaspis* scales, which were present in about 80 % of the stands. While *A. tsugae* continues to be the primary threat to eastern hemlock, its impact needs to be studied in the context of a broader herbivore community.

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Keywords Armored scales · Biological invasions ·
Elongate hemlock scale · Exotic insects · Hemipteran ·
Hemlock woolly adelgid · Interspecific competition

Introduction

Over 400 exotic insects and pathogens affect forest trees in North America (Niemela and Mattson 1996).

Some of these invaders have virtually extirpated formerly common trees like American elms (*Ulmus americana*) and American chestnuts (*Castanea dentata*), while others are responsible for extensive die-offs of many woody species (Hollingsworth and Hain 1991; Orwig et al. 2002; Poland and McCullough 2006). The functional and structural role of trees within ecosystems, in combination with their importance in many late-successional communities, translates into long-lasting and far-reaching consequences of pest-driven losses.

There are many abiotic and biotic factors that can drive the establishment and spread of an exotic pest (Liebhold and Tobin 2008). These include local environmental factors, host availability, and the absence of natural enemies. Additionally, invaders compete with native herbivores for access to host resources. Non-native herbivores might have the advantage of being enemy-free and the ability of circumventing tree defenses that target native insects (Liebhold et al. 1995; Gandhi and Herms 2010). The ever-increasing number of pest introductions, however, will also increase the chances of a novel species sharing host plants with other non-native herbivores. As a result, it is important that interactions between non-native invaders (and other common native herbivores) are taken into account when monitoring the spread of an invasion and its effects.

Eastern hemlock (*Tsuga canadensis*) is a long-lived, shade-tolerant species native to eastern North America. This foundation species provides critical habitat for a wide array of species (Tingley et al. 2002; Ross et al. 2004; Mathewson 2009; Trotter and Evans 2010). Unfortunately, eastern hemlock forests are severely threatened by the invasive hemlock woolly adelgid (*Adelges tsugae*; HWA), a sessile xylem-feeding hemipteran introduced from Japan and first detected in Virginia in 1951 (Souto et al. 1996; Havill et al. 2006). In its invaded range, *A. tsugae* feeds on eastern hemlock and the less abundant Carolina hemlock, *T. caroliniana*. Both hemlock species are generally susceptible to *A. tsugae* and in New England most trees die between 10 and 15 years after initial infestation (Orwig et al. 2002). Since its introduction, *A. tsugae* has spread through over half of the native range of *T. canadensis* and caused rapid stand-level mortality; hemlock stands in the southern portion of the invaded range have been particularly hard-hit (Krapfl et al. 2011; Ford et al. 2012). The loss of

hemlock alters light availability, temperature, and humidity in the understory (Siderhurst et al. 2010). These abiotic changes alter forest succession (Spaulding and Rieske 2010; Preisser et al. 2011) and affect a number of vertebrate, invertebrate, and microbial organisms (Lewis et al. 2008; Rohr et al. 2009). The *A. tsugae*-mediated loss of hemlock stands also has an economic impact as property values in hemlock-dominated areas decline sharply following the death of these trees (Holmes et al. 2010).

A second exotic herbivore, the elongate hemlock scale (*Fiorinia externa*) is a sessile hemipteran that also feeds preferentially on eastern hemlock. Introduced to New York City in 1908, it is now commonly found throughout the eastern hemlock's range and often co-occurs with *A. tsugae* in hemlock stands (Preisser et al. 2008). Unlike *A. tsugae*, *F. externa* rarely kills eastern hemlocks, although high densities can considerably weaken their host (McClure 1980). Experimental assessments of *A. tsugae*–*F. externa* competition reveal that co-occurrence of the two species reduces the densities of both species by ~30 %; intriguingly, *F. externa* appears to reduce the negative impact on *A. tsugae* on plant growth and physiology (Preisser and Elkinton 2008; Gómez et al. 2012). When both herbivores coexist in a stand, *F. externa* densities tend to increase and *A. tsugae* densities tend to decrease over time (Preisser et al. 2008). Moreover, *F. externa* reduces the densities of *Nuculaspis tsugae*, another exotic armored scale that feeds on hemlock, by 74 % and can even result in this species' competitive exclusion (McClure 1981). This example illustrates that invasions can lead to unpredicted interactions with other herbivores and result in impacts that are unpredictable based on single-species evidence.

To date, studies of *A. tsugae*-related hemlock decline have investigated *A. tsugae* range expansion and tree mortality using models that incorporate an array of abiotic factors (McClure 1989a; Evans and Gregoire 2007; Fitzpatrick et al. 2010; Paradis 2011; Orwig et al. 2002, 2012). While these models provide very important information, they do not include other hemlock-feeding herbivores whose presence might substantially alter the outcome of the *A. tsugae*-hemlock interaction. The impact of *F. externa* may be particularly important in this regard, especially given the rapid and recent range expansion of *F. externa* into *A. tsugae*-infested forests in New England (Preisser

et al. 2008). Here, we conducted landscape-level surveys of >120 hemlock stands over multiple years across a latitudinal transect through Connecticut (1997–2011) and Massachusetts (2002–2011). In addition to assessing stand defoliation, these surveys also quantified the densities of four invasive hemipterans on eastern hemlock: *A. tsugae*, *F. externa*, and two *Nuculaspis* sp. scales. One of the *Nuculaspis* scales was conclusively identified as *N. tsugae*, which was accidentally introduced from Japan to New Jersey in 1910 and feeds on several conifer hosts (McClure and Fergione 1977). The goal of our study was to explore exotic herbivore interactions and their range expansion in order to better understand the impact of herbivore communities on hemlock mortality.

Materials and methods

Between 1997 and 2011 we conducted five summer surveys of over 120 hemlock stands in a 7,500 km² latitudinal transect of southern New England, USA, ranging from Long Island Sound in Connecticut to northwestern Massachusetts abutting the Vermont border. Detailed methods for stand selection, along with detailed information about this region's geology and climate, are provided in Orwig et al. (2002). Briefly, each stand was intensively sampled and characterized during the initial visit in order to determine which stand-level factors were associated with hemlock decline and pest invasion. Although subsets of these data have been analyzed elsewhere (see Orwig et al. 2002, 2012 for stand characterization in CT and MA, respectively; Preisser et al. 2008 for changes in insect density between 1997 and 2005; Preisser et al. 2011 for changes in *T. canadensis* regeneration between 1997 and 2009), this paper addresses changes over the 14-year course of the surveys and provides a detailed analysis of the previously unpublished 2011 data. We also provide the first information on the occupancy and stand-level density of invasive *Nuculaspis* scales and their impact on *A. tsugae* and *F. externa*.

Initial stand characterization (1997 for CT, 2002–2004 for MA)

Data on vegetation and site characteristics were collected by sampling one 20 m × 20 m fixed-area

plot as well as five to ten variable-radius plots spaced 30–50 m apart, on a transect that bisected the long dimension of each stand (Orwig et al. 2002). Within each fixed-area plot, all woody stems ≥8 cm diameter at breast height (dbh) were tallied by species and their dbh recorded. We conducted variable-radius plot surveys following the completion of the fixed-area plot survey; in each variable-radius survey, we assessed slope, aspect, topographic position, elevation, and humus depth. We also used the Bitterlich method (Grosenbaugh 1952) to estimate the basal area (m²/ha) of *T. canadensis* and other tree species in each stand. After both the fixed-area plot and variable-radius plot surveys had been completed, mean *T. canadensis* foliar loss ('defoliation') in each stand as a measure of stand health was assessed on the basis of the amount of retained foliage (1 = 0–25 % loss; 2 = 26–50 % loss; 3 = 51–75 % loss; 4 = 76–100 % loss).

Following the vegetation surveys, we haphazardly selected 50 *T. canadensis* (≥2 m in height and ≥8 cm dbh) located along the variable-radius plot transect to assess *A. tsugae* and *F. externa* density. We sampled each tree by examining two one-meter branches located on opposite sides of the tree. Branches with equivalent amounts of new growth were selected whenever possible. After examining the two branches, we rated the *A. tsugae* and *F. externa* density of each tree on a 0–3 scale (0 = none; 1 = 1–10 individuals/m branch; 2 = 11–100 individuals/m branch; 3 = >100 individuals/m branch). Data from the 50 surveyed trees were pooled to produce a mean *A. tsugae* and *F. externa* density rating for each stand. While we would have preferred to mark each tree for subsequent resampling, most of the hemlock stands were on privately-owned land where we were not given permission to establish permanent markers. In order to minimize variation arising from sampling different trees over time, we used GPS coordinates to enter the stands at approximately similar locations during each survey.

Subsequent stand surveys (2005–2011)

We carried out follow-up surveys of each of the initially sampled hemlock stands in summer 2005, 2007, 2009, and 2011. Because our 2005, 2007, and 2009 surveys were aimed at tracking *A. tsugae* and *F. externa* spread and the accompanying changes in hemlock health, we used the above-mentioned

methods to collect data on hemlock defoliation and the densities of *A. tsugae* and *F. externa*. In the 2011 survey, we added two elements to the survey protocol. First, we conducted three variable-radius plot surveys in which we used the Bitterlich method (Grosenbaugh 1952) to estimate the basal area (m^2/ha) of both living and dead *T. canadensis* in each stand. We averaged the three basal area estimates to come up with a mean *T. canadensis* basal area per stand in 2011. This was done to create an equivalent metric to the initial surveys estimates of *T. canadensis* basal area, which included both living and dead hemlocks. Second, we also took information on the densities of two additional scale morphospecies, because several pre-survey scouting trips found some plots where they were present at high densities. These two morphospecies were identified as *Nuculaspis tsugae* and an unidentified *Nuculaspis* sp. scale, respectively, by D. Miller of the USDA-ARS Systematic Entomology Laboratory. The specialist who identified these scales indicated that the unidentified *Nuculaspis* scale is likely also *N. tsugae*, since the appearance and coloration of *N. tsugae* crawlers and second-instar individuals differs substantially from that of adults. Because we cannot be sure they belong to the same *Nuculaspis* species, however, we have kept them separate for all analyses and refer to them as *N. tsugae* and *Nuculaspis* sp., respectively. Densities of both *Nuculaspis* scales were scored as described above and used to explain hemlock defoliation and densities of the two major insects and focus of the survey (*A. tsugae* and *F. externa*) in 2011.

Statistical analysis

We used repeated-measures ANOVA to test for the effects of stand characteristics on stand defoliation and density of the two main hemlock herbivores over time. For *A. tsugae* density, *F. externa* density, and hemlock defoliation the mean stand response was calculated for each sampling date (initial sampling, 2005, 2007, 2009, 2011). Time was used as the repeated factor and the fixed (between subjects) factors were latitude, longitude, aspect, average slope, elevation, humus depth, stand area mean live hemlock stems (all trees ≥ 8 cm dbh) per plot and mean live non-hemlock stems (all trees ≥ 8 cm dbh) per plot. In order to have a more robust model, all non-significant factors that had non-significant interactions were removed for each analysis, and the repeated-measures ANOVA was re-

run. Changes in *T. canadensis* basal area during the study period were analyzed using a paired *t* test comparing 2011 stand values to those scored in the initial surveys. A step-forward model was used to test for effects on the percent change in basal area (m^2/ha) per stand over the study period. The following array of initial predictor variables were included in the model: initial *A. tsugae* density, initial *F. externa* density, latitude, longitude, aspect, average slope, elevation, humus depth, stand area, and all two-way interactions. We followed recommended procedures (Johnson and Omland 2004) and employed model selection to identify the best fit model. Specifically, we used the small sample unbiased Akaike information criterion approach (AICc), a modification of the standard AIC approach recommended when the number of free parameters exceeds the value of the sample size divided by 40 (Hurvich and Tsai 1989). We tested the resulting model using ANOVA; all analyses were performed using JMP v. 9.0.0.

We conducted an in-depth analysis of the 2011 survey data using recursive tree analysis (RTA; decision tree analysis; JMP v.10.0.0) to model the relationship between hemlock defoliation at the stand level and both abiotic variables (latitude, longitude, aspect, area, slope, elevation, which remain constant over time) and biotic variables (insect densities). Additionally, we explored the effects of potential competing herbivores (both *Nuculaspis* scales) on *A. tsugae* and *F. externa*, the primary herbivores impacting *T. canadensis* health. RTA is useful to detect complex patterns among variables in ecological data that might not be detected with other classical statistical techniques (e.g. De'ath and Fabricius 2000); in our case, RTA provides a comprehensive overview of the predictor variables that contributed most to hemlock stand health. The first split in the RTA analyses separates the data into two groups with maximum homogeneity; the two groups are further split until the resulting groups are also strongly homogenous. We conducted K-Fold Cross-validation (splitting the original data into $K = 5$ subsets) to determine the optimum number of splits in each decision tree. We re-ran each analysis five times, calculated the mean optimal number of splits, and then used this value to create our final decision tree. This technique allows for the selection of a tree with the lowest estimated prediction error (Breiman et al. 1984) while eliminating the need for subsequent pruning.

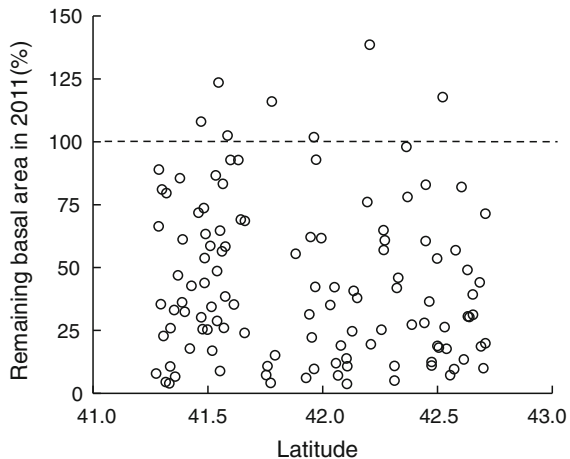


Fig. 1 Percentage of hemlock basal area remaining in 2011 compared to individual stand values scored during the initial surveys (Connecticut: 1997; Massachusetts: 2002–2004). The dashed line indicates 100 % of the original basal area is present in 2011 (i.e. no change) while values above and below represent increases and decreases respectively compared to initial values. Each circle represent a stand along the latitudinal transect. Basal area included both live and dead hemlock trees at the time of sampling. Latitude 42°N separates Connecticut (below) and Massachusetts stands (above)

Results

Change in hemlock basal area between 1997 and 2011

Hemlock basal area (combined dead and living trees) decreased dramatically over the 14 years of the survey, going from an average of 48.3 ± 0.9 m²/ha in 1997 to 19.8 ± 1.3 m²/ha in 2011 ($t = -17.67$ $p < 0.001$). The vast majority of stands suffered a decline ranging losses from 2 to 96 % of the original basal area (Fig. 1). The AICc model-selection algorithm used to analyze percent change in *T. canadensis* basal area per stand over the course of the survey identified four main effects: aspect, latitude, initial *A. tsugae* density, and initial *F. externa* density (Table 1). There was a greater decrease in basal area in the northern portion of the study area (latitude: $p = 0.024$; Fig. 1). Massachusetts stands lost on average 62 % of the original basal area while this loss was only 52 % in Connecticut stands. Hemlock basal area decrease was slightly higher in areas with higher initial *A. tsugae* densities ($p = 0.041$). Stands with initial *A. tsugae* densities between 0 and 10

Table 1 ANOVA on the percent change in *T. canadensis* basal area between 1997 and 2011

Effect	df	F	p
Aspect	1, 114	1.76	0.19
Latitude	1, 114	5.27	0.02
Initial <i>A. tsugae</i> density	1, 114	4.29	0.04
Initial <i>F. externa</i> density	1, 114	0.09	0.76
Aspect \times initial <i>F. externa</i> density	1, 114	8.36	0.01
Latitude \times initial <i>A. tsugae</i> density	1, 114	0.24	0.63

Significant effects ($p < 0.05$) are highlighted in bold

insects per meter branch loss an average of 54 % of the original stand basal area compared to a 60 % loss in stands with moderate to high *A. tsugae* densities. While there was no main effect of *F. externa* initial density ($p = 0.764$) on basal area decline, there was a significant interaction between stand aspect and initial *F. externa* density ($p = 0.005$). This reflects the fact that *F. externa* densities influenced basal area only in west-facing stands.

Hemlock defoliation and insect density over all five survey dates

Stand defoliation was not homogenous across the study area (Latitude: $p < 0.001$; Table 2). Hemlock stand defoliation changed locally over time (Time \times latitude: $p < 0.001$; Table 2). Substantial stand defoliation of previously healthy stands occurred in higher latitudes while stands in lower latitudes remained in poorer health throughout the study. Local differences in stand defoliation might have cancelled each other out over time and explain the observed unchanged average hemlock stand health over the course of the study (Time $p = 0.37$; Table 2), rating an average of 1.96 ± 0.08 in 2011 (Table 3; a value of 2 indicates 26–50 % foliage loss). Stands with higher numbers of *T. canadensis* ≥ 8 cm dbh had lower *A. tsugae* densities and suffered lower defoliation (Live hemlock stems ≥ 8 cm dbh/ha; $p < 0.001$; Table 2). The high *A. tsugae* densities present in some years were mostly in stands with fewer hemlocks ≥ 8 cm dbh (Live hemlock stems ≥ 8 cm dbh/ha \times time; $p < 0.033$; Table 2). Stands with *A. tsugae* had on average ~ 36 % of their trees infested (Table 3). The percentage of infested trees increased proportionally with stand adelgid density. Stands with

Table 2 Results of repeated measures ANOVA assessing the relationship over time (1997–2011) between changes in (1) *T. canadensis* defoliation; (2) stand-level *A. tsugae* densities; (3) stand-level *F. externa* densities; and site-level predictive factors

Effect	<i>T. canadensis</i> defoliation			<i>A. tsugae</i> density			<i>F. externa</i> density		
	df	F	p	df	F	p	df	F	p
Latitude	1, 120	48.68	<0.001	1, 121	79.50	<0.001	1, 120	32.53	<0.001
Longitude	1, 120	7.48	0.007						
Elevation							1, 120	23.57	<0.001
Humus depth							1, 120	2.29	0.130
Live hemlock stems ≥ 8 cm dbh/ha	1, 120	23.64	<0.001	1, 121	12.86	<0.001			
Time	4, 117	1.07	0.37	4, 118	18.16	<0.001	4, 117	3.88	0.005
Time \times latitude	4, 117	6.66	<0.001	4, 118	17.03	<0.001	4, 117	3.53	0.009
Time \times longitude	4, 117	0.94	0.45						
Time \times elevation							4, 117	1.95	0.106
Time \times humus depth							4, 117	2.46	0.049
Time \times live hemlock stems ≥ 8 cm dbh/ha	4, 117	1.75	0.14	4, 118	2.71	0.033			

In order to have a more robust model, non-significant factors and their non-significant interactions were removed for given models (empty cells). Significant effects ($p \leq 0.05$) are highlighted in bold

low to moderate densities (rating 1.5) had on average 80 % of trees within a stand infested.

Insect densities were not homogenous across the study area (Latitude: $p = < 0.001$ for both insects; Table 2) and changed locally over time (Latitude \times time: $p < 0.01$ for both insects; Table 2), suggesting a northward range expansion over the study period for both *A. tsugae* and *F. externa* (Figs. 2, 3) mirroring the increased stand defoliation in higher latitudes. Average *A. tsugae* density in the study area fluctuated from year to year but showed an overall decrease over the survey period (Time: $p < 0.001$ Table 2; Fig. 2), going from 1.45 ± 0.11 (SE) density rating in 1997 to 0.62 ± 0.06 in 2011; In contrast, average *F. externa* density experienced a steady increase (Time: $p < 0.001$ Table 2; Fig. 3) going from 0.37 ± 0.07 density rating in 1997 to 1.81 ± 0.09 in 2011. Stand elevation (range 15–378 m) had a significant effect on *F. externa* density (Elevation: $p < 0.001$ Table 2), being densities higher at lower elevations. Initial humus depth also had a significant effect on *F. externa* density (Humus depth $p < 0.049$ Table 2). Stands with a deeper humus layer supported lower *F. externa* densities.

Hemlock defoliation and insect densities in 2011

In 2011, 37 % of the stands had no to low defoliation (< 25 % foliar loss), 37 % presented moderate defoliation (26–50 %) and 26 % of the stands suffered

severe (51–75 %) to very severe defoliation (> 75 %) (Fig. 4). Defoliation was primarily associated with densities of *A. tsugae* and *Nuculaspis* sp ($R^2 = 0.265$; Fig. 4). 59 % of the surveyed stands had *A. tsugae* densities rating ≥ 0.32 (in a scale from 0 to 3, where 0 = no insect; 1 = 1–10 insects/m branch; 2 = 11–100 insect/m branch; 3 ≥ 100 insects/m branch). Stands with *A. tsugae* density rating ≥ 0.32 suffered higher defoliation levels, resulting in 40 % of those stands having severe or very severe defoliation, while only 6 % of stands with lower *A. tsugae* density (< 0.32) had severe or very severe defoliation (Fig. 4). Stands with higher *A. tsugae* density (≥ 0.32) were further separated by *Nuculaspis* sp. density; within these stands, those with *Nuculaspis* sp. density > 0.33 had higher defoliation, resulting in 57 % of these stands presenting severe to very severe defoliation compared to 33 % of stands with *Nuculaspis* sp density < 0.33 suffering severe defoliation (and no stand with severe defoliation; Fig. 4). *F. externa* density and longitude had smaller impacts and *N. tsugae* density had no impact on hemlock defoliation (Fig. 4).

Fiorinia externa was the only insect explaining some of the variation in *A. tsugae* density ($R^2 = 0.121$; Fig. 5a). *F. externa* was present at densities rating ≥ 0.2 in 84 % of the stands; in those stands *A. tsugae* density rated higher (0.71) than in stands with *F. externa* density < 0.2 (0.15). Stands with very low *F. externa* density (< 0.08) also had very low *A. tsugae* density. In contrast, variation in *F. externa*

Table 3 Stand biotic characteristics in 2011

Variable	Score in 2011
Sampled stands	124
Hemlock defoliation (1–4) ^a	1.96 ± 0.08 (SE)
A. tsugae	
A. tsugae density (0–3) ^b	0.62 ± 0.06
Stands with no (0) A. tsugae	7.3 % (n = 9)
Stands with low (0.01–1) A. tsugae density	70.2 % (n = 87)
Stands with moderate (1.01–2) A. tsugae density	18.5 % (n = 23)
Stands with high (2.01–3) A. tsugae density	4 % (n = 5)
Percentage of A. tsugae infested trees in a stand	35.7 % ± 2.5
F. externa	
F. externa density (0–3) ^b	1.81 ± 0.09
Stands with no (0) F. externa	4 % (n = 5)
Stands with low (0.01–1) F. externa density	22.6 % (n = 28)
Stands with moderate (1.01–2) F. externa density	14.5 % (n = 18)
Stands with high (2.01–3) F. externa density	58.9 % (n = 73)
Percentage of F. externa infested trees in a stand	76.7 % ± 3.3
N. tsugae	
N. tsugae density (0–3) ^b	0.48 ± 0.06
Stands with no (0) N. tsugae	19.4 % (n = 24)
Stands with low (0–1) N. tsugae density	58.9 % (n = 73)
Stands with moderate (1.01–2) N. tsugae density	20.2 % (n = 25)
Stands with high (2.01–3) N. tsugae density	1.6 % (n = 2)
Percentage of N. tsugae infested trees in a stand	28.1 % ± 2.8
Nuculaspis sp.	
Nuculaspis sp. density (0–3) ^b	0.38 ± 0.05
Stands with no (0) Nuculaspis sp.	11.3 % (n = 14)
Stands with low (0.01–1) Nuculaspis sp. density	75 % (n = 93)
Stands with moderate (1.01–2) Nuculaspis sp. density	12.1 % (n = 15)
Stands with high (2.01–3) Nuculaspis sp. density	1.6 % (n = 2)
Percentage of Nuculaspis sp. infested trees in a stand	22.2 % ± 2.2

SE standard error

^a Hemlock defoliation rating: “1”, 0–25 % needle loss; “2”, 26–50 %; “3”, 51–75 %; “4”, 76–100 %

^b Insect density ratings: “0”, no insects detected; “1”, 1–10 organisms/m branch; “2”, 11–100 organisms/m branch; “3”, >100 organisms/m branch

density was largely explained by the densities of both *Nuculaspis* scales, but was not influenced by the density of *A. tsugae* ($R^2 = 0.601$; Fig. 5b). Stands with *N. tsugae* density ≥ 0.33 had higher densities of *F. externa*, however, this seemed to reach a threshold and at a *N. tsugae* density ≥ 1.91 , where *F. externa* densities (1.19) were lower than when *N. tsugae* densities were < 1.91 (*F. externa* = 2.52; Fig. 5b).

Both *Nuculaspis* scales were present across the study area but their densities were not homogeneous across the landscape. Lower latitudes were characterized by having moderate or high density ratings while stand density ratings in Massachusetts were always below 0.5 (< 1 –10 individuals per m branch). Like *A. tsugae* and *F. externa*, *N. tsugae* also expanded

northward since 1989. In our 2011 study we found *N. tsugae* all over Connecticut and Massachusetts, while in 1989 this scale was only present in parts of Connecticut (McClure 1989a, b; Fig. 6). We only have 2011 data for the unidentified *Nuculaspis* sp., therefore nothing can be said regarding the range expansion.

Discussion

Our multi-year landscape surveys showed that hemlock forests continue to decline throughout southern New England. In 14 years, total hemlock basal area was reduced by approximately 60 % in the studied area. A recent study by Trotter et al. (2013) showed a

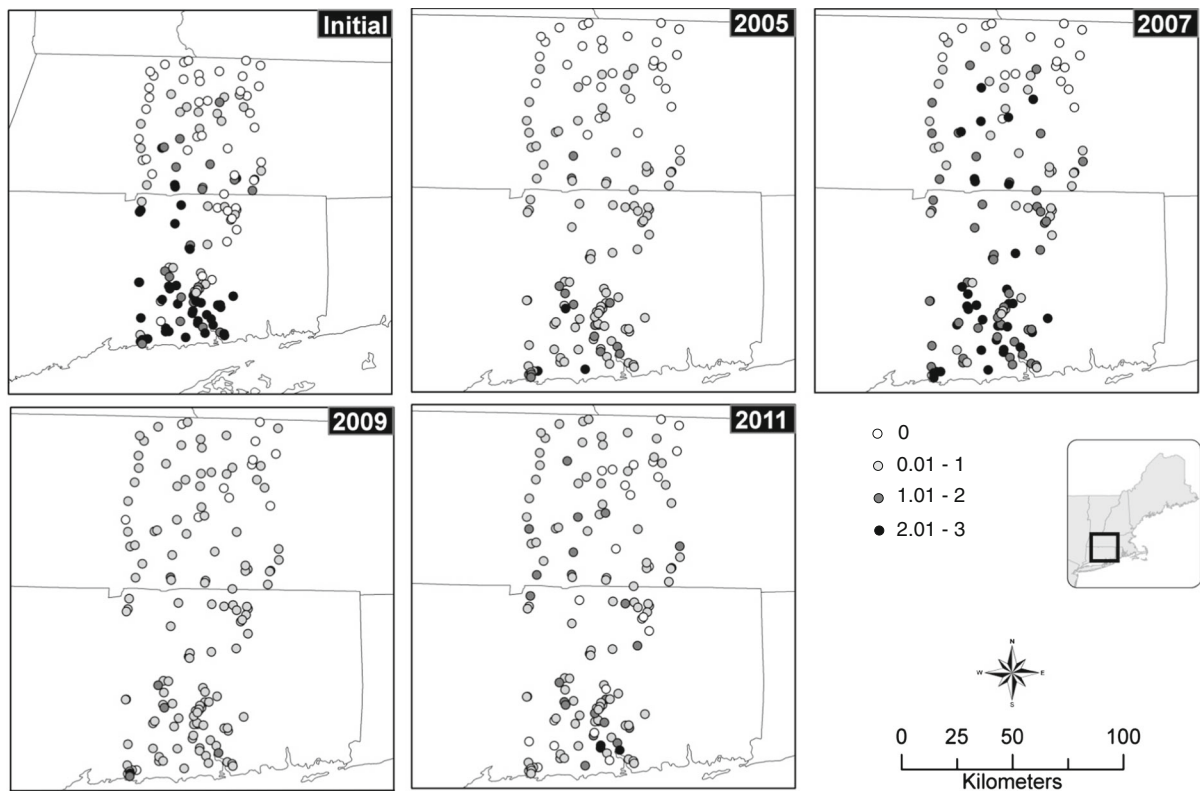


Fig. 2 *A. tsugae* density over time. Each circle represents a sampled stand along a longitudinal transect across Massachusetts and Connecticut. Different colors represent the average stand-level insect density ratings as indicated in the legend. Density ratings were scored from 0 to 3, where 0 is no insect

present, 1 is 1–10 insects/m branch, 2 is 11–100 insects/m branch and 3 is >100 insects/m branch. Average densities are based on 50 sampled trees per stand. The initial time was 1997 and 2002–2004 for the Connecticut and Massachusetts stands, respectively

similar state-level trend in areas that have been long- and widely-infested, such as Connecticut and Massachusetts, where the accumulation of hemlock volume has decreased or stabilized, respectively, in the last decades. This however, was in contrast with their regional data comprising 21 states, which showed an overall increase in median live and dead hemlock basal area in adelgid-infested and uninfested counties over the last two decades. The authors suggest that at such regional scale, the negative effects of the adelgid might be masked by extensive succession and reforestation patterns associated with historical changes in land use.

Despite the decrease in basal area observed in our study, average hemlock stand defoliation did not change across our sampling period, maintaining on average moderate stand defoliation (25–50 % needle loss) across the study area. While there was not an overall increase in defoliation, it is important to note

that there were local changes in stand defoliation and insect densities in addition to local changes in basal area decline. These local changes are consistent with an expansion of both *A. tsugae* and *F. externa* (and *N. tsugae* to a lower extent) into previously healthier stands in northern Massachusetts. Stands in lower latitudes remained in poor health throughout the study and as a result northern stands suffered relative higher losses in basal area. Local increases in insect densities might explain the overall decline in basal area despite the overall decrease in *A. tsugae* density across the study area. Although *F. externa* dramatically increased its average density in the study area and also expanded northward during the course of our survey, it was a minor direct contributor to hemlock stand defoliation and only reduced hemlock basal area in west-facing slopes. However, *F. externa* did also impact hemlock health indirectly by altering *A. tsugae*'s density. In 2011, *N. tsugae* was present

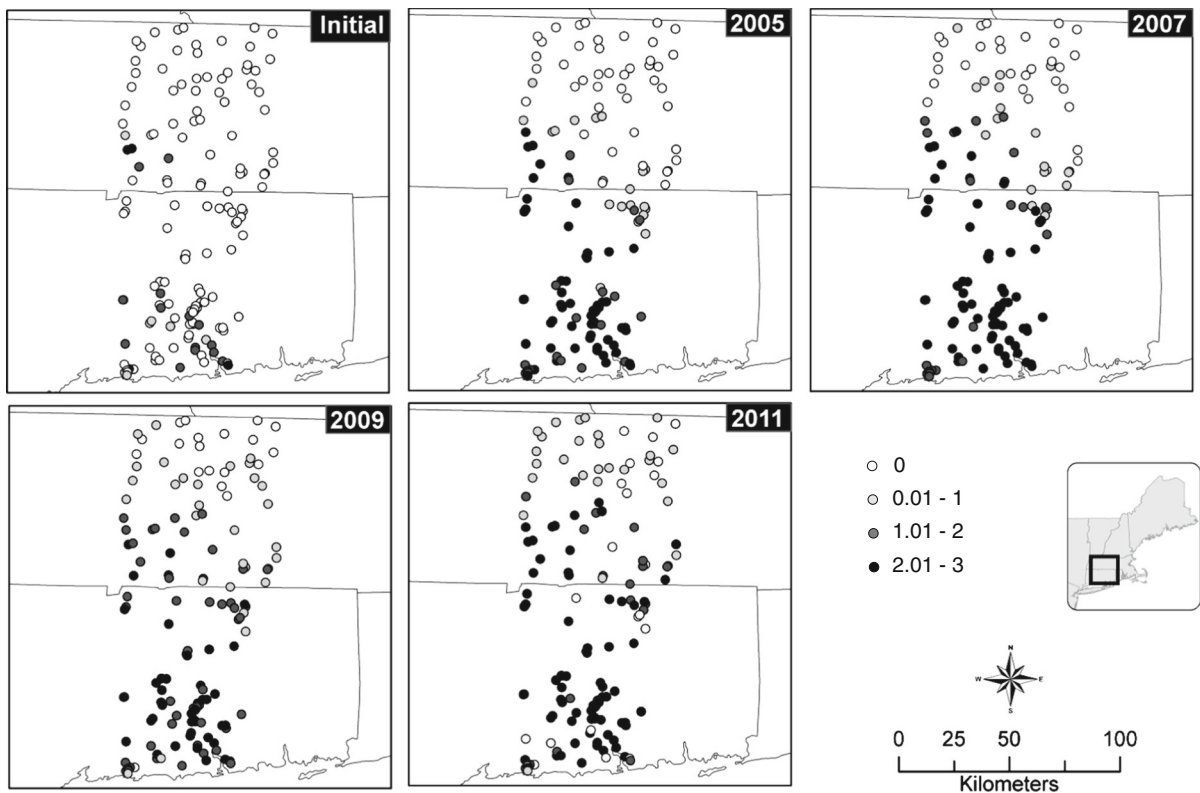


Fig. 3 *F. externa* density over time. Each circle represents a sampled stand along a longitudinal transect across Massachusetts and Connecticut. Different colors represent the average stand-level insect density ratings as indicated in the legend. Density ratings were scored from 0 to 3, where 0 is no insect

present, 1 is 1–10 insects/m branch, 2 is 11–100 insects/m branch and 3 is >100 insects/m branch. Average densities are based on 50 sampled trees per stand. The initial time was 1997 and 2002–2004 for the Connecticut and Massachusetts stands, respectively

throughout the studied area, also indicating a substantial northward expansion into Massachusetts compared to 1989 when this scale was absent in latitudes above 42°N (McClure 1989b). Our results suggest that although *A. tsugae* continues to be the primary threat to eastern hemlock health, species such *F. externa* and *Nuculaspis* scales, affecting *A. tsugae* densities through direct or host-mediated interactions, also warrant increased attention.

Minimum winter temperatures are responsible for substantial *A. tsugae* mortality (Skinner et al. 2003) and help limit the northward expansion of *A. tsugae* (Fitzpatrick et al. 2012; Orwig et al. 2012). The predicted increases in winter temperature caused by global warming may alter the impact of abiotic constraints on the adelgid's range expansion (Dukes et al. 2009) as it is the case for many other herbivores and pathogens (reviewed in Weed et al. 2013).

Although *F. externa* preferentially feeds on eastern hemlock, it can feed on conifer species from genera such as *Abies*, *Cedrus*, *Picea* and *Pinus* (McClure and Fergione 1977). Decline in eastern hemlock abundance and intense competition for the remaining trees might favor colonization and increased abundance of *F. externa* (and *N. tsugae*) in less preferred conifers. The negative physiological impact of low/moderate *F. externa* densities on healthy eastern hemlocks is not large, but the consequences of feeding on other hosts at the species and ecosystem level are unknown.

Biological invasions by exotic herbivores can have profound effects on community composition due to direct and indirect effects on the host's associated herbivore community. For example, the presence of the exotic aphid *Uroleucon nigrotuberculatum* on the introduced tall goldenrod (*Solidago altissima*) in

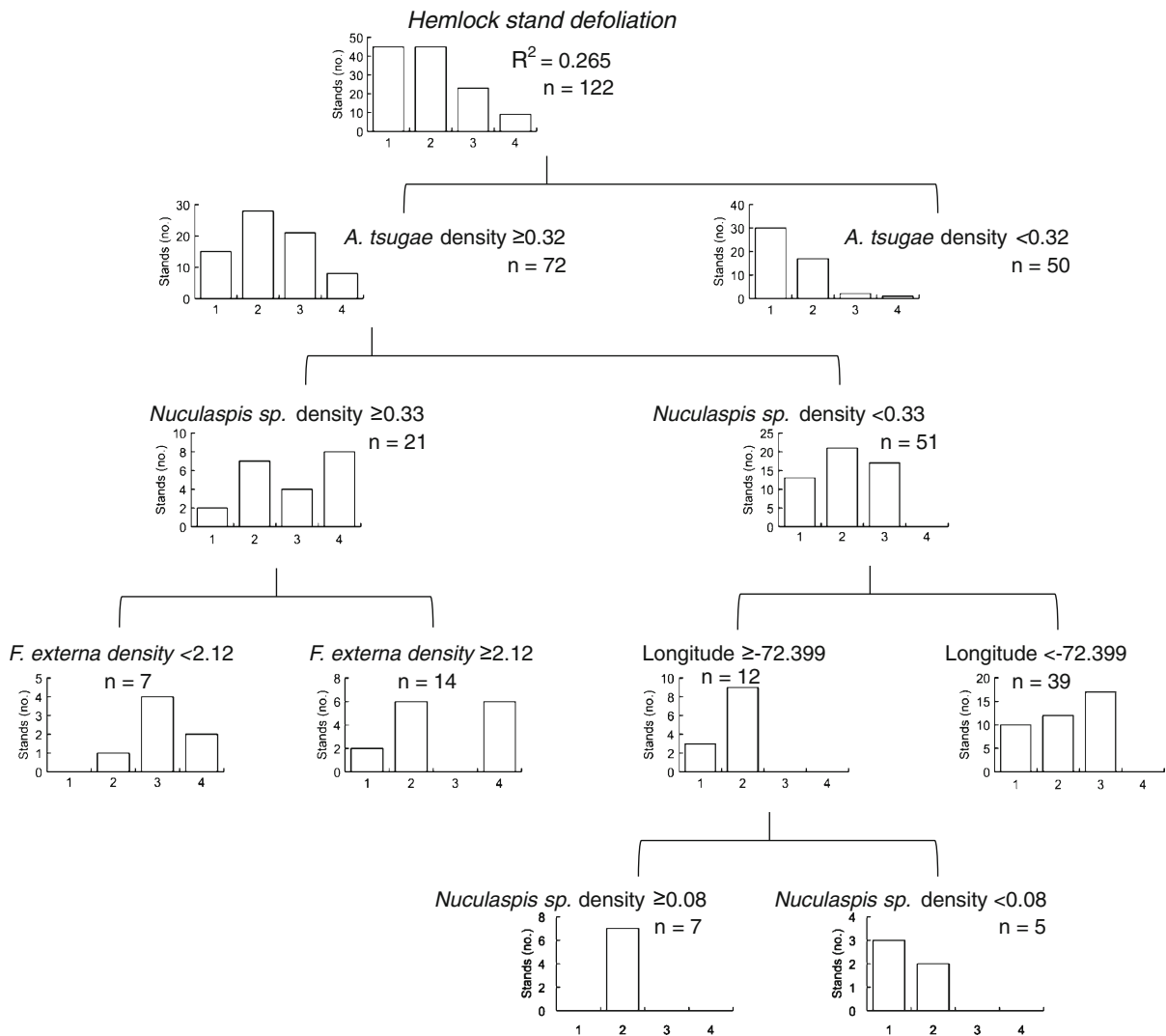


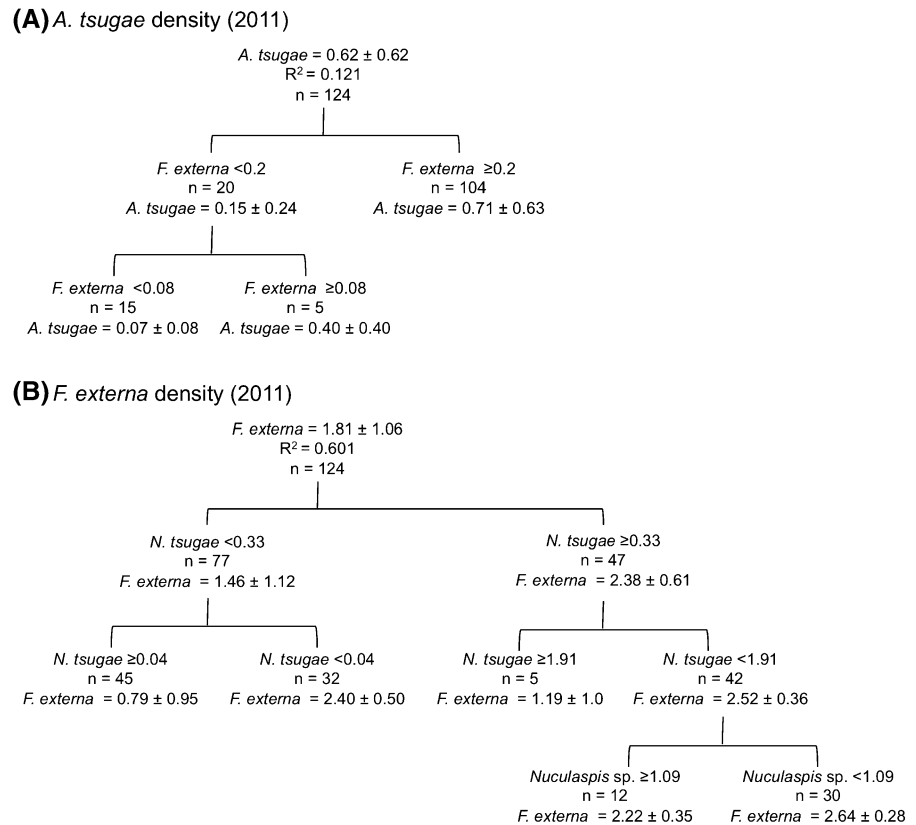
Fig. 4 Recursive tree analysis of hemlock defoliation at the stand level in 2011. Each node is split based on a value of a response variable and the bar figures represent the numbers of stands in each of four categories based on mean *T. canadensis* foliar loss ('defoliation') in each stand (1 = 0–25 % loss;

2 = 26–50 %; 3 = 51–75 % loss; 4 = 76–100 % loss). Insect density ratings: 0, no insects detected; 1, 1–10 organisms/m branch; 2, 11–100 organisms/m branch; 3, >100 organisms/m branch

Japan changed arthropod densities and composition through plant- and ant-mediated interactions (Ando et al. 2011). An increasing number of studies are recognizing the importance of herbivore community composition as a selective force on herbivore traits. In the leaf beetle *Plagioderma versicolora*, for instance, interspecific competition selects for beetles willing to consume a wide variety of leaf ages; in the absence of such competition, the beetles exclusively consume

new leaves (Utsumi et al. 2013). In our own study system, *A. tsugae* has been shown to avoid settling on foliage colonized by *F. externa* (Gómez et al. 2014). Prior colonization by *F. externa* may also ameliorate the negative impact of *A. tsugae* on host growth (Preisser and Elkinton 2008), likely due to asymmetric priority effects that result in large reductions in *A. tsugae* abundance on *F. externa*-infested hosts (Miller-Pierce and Preisser 2012). Because the

Fig. 5 Recursive tree analysis of **a** *A. tsugae* density and **b** *F. externa* density in 2011. The first node of the trees gives an overall mean \pm standard deviation of the response variable followed by the amount of variation explained by the model and the number of stands (n) included. At each following split, a mean splitting value associated with the splitting variable is given, followed by the number of stands and the mean \pm SD of the response variable respectively in that given split. See “Materials and methods” for details. Insect density ratings: 0, no insects detected; 1, 1–10 organisms/m branch; 2, 11–100 organisms/m branch; 3, >100 organisms/m branch



presence of *F. externa* may play a crucial role on the final outcome of *A. tsugae* impact on eastern hemlock, it is important to take into account other common herbivores that can have an impact on *F. externa* densities. Our results suggest that the presence of *Nuculaspis* scales explains a substantial amount of variation in *F. externa* density at the stand level. *Nuculaspis* scales were present, often at low to moderate densities, in over 80 % of the surveyed stands. Heavy infestations of *N. tsugae* on eastern hemlock can cause premature needle drop and tree death (McClure and Fergione 1977). At low *N. tsugae* densities, there was a positive relationship between *F. externa* and *N. tsugae*, however this was inverted at moderate-high *N. tsugae* densities. Previous studies have shown a negative relationship between *F. externa* and *N. tsugae* showing the superior competitive ability of *F. externa* compared to *N. tsugae* when they co-exist on eastern hemlock (McClure 1981). This competitive advantage is explained by earlier colonization by *F. externa* and poor synchrony with a

parasitoid shared by the two scales. It is possible the observed increase in abundance and range expansion of *F. externa* might have contributed to the expansion the *Nuculaspis* scales by debilitating their shared host. To our knowledge, no experimental studies have investigated competition effects between *A. tsugae* and *N. tsugae* and the impact on hemlock health. Because *N. tsugae* has roughly doubled its invaded range in the last 20 years, monitoring its expansion, density and interaction with *A. tsugae* and *F. externa* might be important to predict future impacts on eastern hemlock’s health.

Herbivore interactions are complex, interrelated and often unpredictable. Our results highlight the importance of taking into account multiple herbivores in local communities when assessing the impacts of biological invasions. We suggest this aspect should be included in future field survey studies and theoretical models in order to increase prediction accuracy when assessing the impact of exotic invaders.

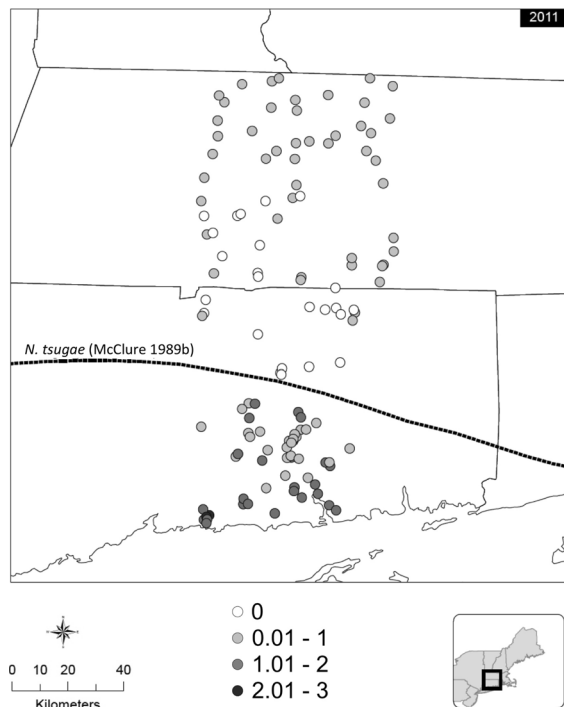


Fig. 6 *N. tsugae* density in 2011. Each circle represents a sampled stand along a longitudinal transect across Massachusetts and Connecticut. Different colors represent the average stand-level insect density ratings as indicated in the legend. Density ratings were scored from 0 to 3, where 0 is no insect present, 1 is 1–10 insects/m branch, 2 is 11–100 insects/m branch and 3 is >100 insects/m branch. Average densities are based on 50 sampled trees per stand. The range occupied by *N. tsugae* in 1989 is indicated below the dashed line and has been adapted from McClure (1989b)

Acknowledgments The authors thank property owners for allowing survey teams in their plots. B. Peixoto for her help during fieldwork and P. August for the landscape figures in the manuscript. This project was funded by the following grants: NSF DEB-0715504, NSF DEB-1256769, NIFA 2011-67013-30142 and is a contribution of the Harvard Forest Long-Term Ecological Research Program (DEB 06-20443).

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