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ORIGINAL PAPER

Changes in the regional abundance of hemlock associated with the invasion of hemlock woolly adelgid (*Adelges tsugae* Annand)

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Abstract Since its introduction, the non-native hemlock woolly adelgid (*Adelges tsugae*) has spread to infest hemlock (*Tsuga* spp.) in at least 18 states in the eastern USA. Previous studies have documented highly variable rates of hemlock mortality among infested stands making it difficult to estimate regional impacts. Here data from the US Forest Service Forest Inventory and Analysis program collected from 432 eastern U.S. counties reveals several surprising and conflicting regional patterns. First, median live and dead hemlock basal area has generally increased over the last two decades across the eastern U.S. This has generally been the case in both infested and uninfested counties. Second, the median percentage of hemlock which is alive has decreased over the past ~20 years, again in both infested and uninfested counties. Third, the ages of infestations are negatively correlated with the percentage of live hemlock, as might be expected given the known impact adelgids can have on a stand through time; however this relationship depends on the exclusion of uninfested counties, as counties infested >12 years and uninfested counties have similar percentages of live hemlock. Combined, these data suggest increasing tree density associated with the past century of reforestation and succession in the eastern U.S. may currently be overwhelming the negative impacts of the adelgid at the regional scale, however, the long-term stability of this situation is not known, and data from long-infested counties suggest the landscape may be at a "tipping point".

Keywords Invasive species · Forest insects · Forest Inventory and Analysis · Succession

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Introduction

Invasive species represent a major threat to the economic (Holmes et al. 2009; Pimentel et al. 2000, 2005) and ecological (Liebhold et al. 1995; Vitousek et al. 1996) stability and sustainability of forested systems globally. As invasive species increase their geographic distribution, they can reduce or eliminate dominant forest species (Loo 2009). Some long-established invaders such as chestnut blight (*Cryphonectria parasitica* Murr. Barr) and Dutch elm disease (*Ophiostoma ulmi* Nannf. and *O. novo-ulmi* Brasier) have greatly altered species distributions and abundances (Keever 1953; Loo 2009; McCormick and Platt 1980), while some invasive species such as beech bark disease have predominantly altered stand structure (Garnas et al. 2011; Morin et al. 2007). Other, more recent arrivals such as the hemlock woolly adelgid (*Adelges tsugae* Annand), sudden oak death [*Phytophthora ramorum* (Werres, de Cock and Man in't Veld)], the Asian longhorned beetle [*Anoplophora glabripennis* (Motschulsky)], the emerald ash borer (*Agrilus planipennis* Fairmaire), and laurel wilt disease [*Raffaelea lauricola* (T.C. Harr Fraedrich and Aghayeva)] threaten to further alter forested stands in the eastern United States.

One of the challenges land managers, conservation ecologists, foresters, and invasive species biologists face when dealing with new or ongoing threats to forested systems is a lack of data quantifying the severity of both the actual and the potential damage caused by an invading species over large geographic scales (Loo 2009). Past work on changes in forest structure or tree species abundance has largely focused on stand-scale data (Davidson et al. 1999; Kuhlman 1971), while only a few studies have quantified the impacts of an invasive insect or disease at the landscape scale (Gansner and Herrick 1987; Morin et al. 2007).

The hemlock woolly adelgid offers an opportunity to evaluate the evolving impacts of an invasive herbivore on a widely distributed tree species. First documented in eastern North America in Richmond, Virginia in 1951 (Gouger 1971), *A. tsugae* has expanded its range to include at least 18 states in the eastern United States. In Japan, [the source of the populations now distributed through the eastern United States (Havill and Foottit 2007 Havill et al. 2006)], this herbivore feeds on both its primary host *Picea torano* Koehne (syn. *Picea polita*) as well as secondary hosts in the genus *Tsuga* (Inouye 1953), and populations appear to be kept in check through a combination of host resistance, host tolerance, and a complex of generalist and specialist predators (Havill and Foottit 2007; Kohler et al. 2008; Montgomery and Lyon 1996; Wallace and Hain 2000). In eastern North America, suitable spruce species are unavailable, restricting populations to parthenogenetic reproduction on eastern (*Tsuga canadensis* (L.) Carrière) and Carolina (*T. caroliniana* Engelm.) hemlock, neither of which has shown significant resistance to the adelgid, though Ingwell and Preisser (2011) have provided evidence that rare resistant individuals may occur on the landscape. Coupled with a lack of control by native predators, adelgid population densities can quickly increase following infestation. Left untreated, adelgid infestations can lead to needle loss, the cessation of new growth, and ultimately, hemlock mortality (Orwig and Foster 1998, 2000).

Although the adelgid was first documented in the eastern United States in 1951 in Richmond, VA, it initially received little attention. However in the late 1970s and early 1980s the species began to rapidly expand its range, moving into forested settings in New Jersey, New York, and Connecticut where extensive hemlock decline and mortality were reported (Orwig and Foster 1998). The adelgid has continued to spread anisotropically through the eastern U.S. at a rate of 7.6–20.4 km year^{-1}, based on infestation records from 1951 to 2006 (Evans and Gregoire 2007; Morin et al. 2009). Currently, HWA attacks hemlock trees from southern Maine to northern Georgia, and as of 2003 HWA had spread to include approximately 45 % of the range of hemlock in the eastern U.S. (Morin et al. 2011).

Within this invaded range the impact of the adelgid has varied, with observed rates of hemlock loss within individual infested stands ranging from near 0 to more than 95 % (Orwig and Foster 1998; Paradis et al. 2008). To date, studies evaluating the impact of *A. tsugae* on forest structure have focused on individual stands (Eschtruth et al. 2006; Krapfl et al. 2011; Orwig and Foster 1998) or regions within a state (Orwig et al. 2002). Here we seek to expand on these studies by using data from the USDA Forest Service Forest Inventory and Analysis (FIA) database to address three key questions. First, has the abundance (basal area) of hemlock and other commonly associated tree species changed in the eastern United States over the past two decades? Second, are changes in live or dead hemlock basal area in the eastern U.S. associated with infestation by the hemlock woolly adelgid? Third, is there a detectable relationship between changes in hemlock abundance, and the age of infestations at the county level? The combination of regional stand data available through the FIA program and the documented stand level impacts of the hemlock woolly adelgid make this system well suited to evaluating the current impacts of an invasive forest insect at a landscape scale.

Methods

The FIA program of the U.S. Department of Agriculture (USDA) Forest Service conducts a three-phase nationwide inventory of forest attributes (Woudenberg et al. 2010). The current FIA sampling design is based on a tessellation of the United States into hexagons approximately 2,428 ha in size with at least one permanent plot established in each hexagon. In phase 1, the population of interest is stratified and plots are assigned to strata to increase the precision of estimates. In phase 2, tree and site attributes are measured for forested plots established in each hexagon. Phase-2 plots (on which this study is based) consist of four 7.32-m fixed-radius subplots on which standing trees and various other environmental characteristics are inventoried. Phase-3 plots, which are a subset of phase-2 plots, focus on specific forest health variables such as coarse woody material, ozone damage, and soil characteristics. We did not analyze the phase-3 data because of the relatively few plots (only 1 phase-3 plot is measured for every 16 phase-2 plots) falling within the range of HWA.

This study's 21-state study area includes: Alabama, Connecticut, Delaware, Georgia, Kentucky, Maine, Maryland, Massachusetts, Michigan, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Vermont, Virginia, West Virginia, and Wisconsin. County level estimates of live and dead basal area (ft^2) of both hemlock and other species of interest were generated from FIA plots in the 21 included states surveyed between 1985 and 2008 (Woudenberg et al. 2010). Species codes for hemlock varied among counties, with some counties reporting the incidence of *T. canadensis* and *T. caroliniana* separately, while some simply reported "hemlock" as a general category. Because the eastern U.S. hosts only two species of hemlocks in forested settings, and because Carolina hemlock has a limited distribution and shares a high susceptibility to hemlock woolly adelgid infestation with eastern hemlock, we pooled all hemlock into a single species group. Basal areas of red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*) were also summarized, as these species are commonly associated with hemlock in eastern N. America.

Prior to 1995, the FIA program collected data regionally using a periodic measurement system with sample designs that varied slightly by region and decade. Generally, inventories were conducted in each state every 6–18 years, depending on the state and region (Bechtold and Patterson 2005). More recently, FIA data collection has been restructured such that some plots are surveyed in each state every year. As a result of these changes in survey schedules, inventory intervals varied among counties over the three inventory periods included in the study (Table 1). To accommodate this variation, county inventory data were categorized into three time periods corresponding to the three most recent available inventories. The mean number of years between inventories 1 (earliest) and 3 (most recent) was 19.26 ($\pm$0.222 years). Counties missing data for a given parameter (e.g., hemlock basal area), or counties which had fewer than 5 FIA plots reporting a species in any of the included time periods were excluded from the analysis of that species. Limiting analyses to counties with a minimum of 5 FIA plots was done to avoid the over-weighting of stands in counties with fewer FIA plots while maintaining adequate sample sizes (numbers of counties). A post hoc sensitivity analysis of the effect of filter size by re-running the analyses using filters ranging from 1 to 15 plots including hemlock/county. These analyses produced patterns consistent with the initially selected filter (5 plots) suggesting the analyses are robust to variation in minimum number of plots within a county required for inclusion.

The rate of change in basal area for both live and dead trees in each of five species groups (all species pooled, hemlock, red maple, sugar maple, and American beech) was estimated by subtracting basal area ha^{-1} in inventory 1 from the corresponding basal area ha^{-1} in inventory 3, then dividing the result by the number of years between inventories 1 and 3. A Wilcoxon sign rank test was used to determine whether the median value for each species group deviated significantly from the hypothetical median of 0 (indicating no annual change) (Remington and Schork 1985). Pair-wise comparisons among species groups were tested using a Mann–Whitney *U* test. Statistical analyses were conducted using MatLab™ 7.1.

Table 1 Number of counties inventoried by year for each of the three inventory periods used in the analyses

Inventory 1		Inventory 2		Inventory 3	
Inventory year	Counties inventoried	Inventory year	Counties inventoried	Inventory year	Counties inventoried
1980	56	1992	32	2006	270
1983	52	1993	59	2007	117
1984	32	1996	29	2008	45
1985	22	1997	32		
1986	9	1998	22		
1987	5	1999	40		
1988	25	2000	37		
1989	125	2002	23		
1990	27	2003	16		
1991	10	2004	89		
1993	53	2005	53		
1995	16				
Total	432		432		432

The rate of change in the percent of the total standing basal area for each species group made up of live trees was estimated by subtracting the percentage of the standing (live) basal area in inventory 1 from the total basal area of inventory 3, and dividing by the number of years between inventories. Median values for each county were compared with the hypothetical median of 0 (indicating no change), and pair-wise comparisons among species groups were conducted using the methods described above. To determine whether a relationship exists between the percent live hemlock within in counties and the age of the infestation, we use a generalized mixed models (GLIMMIX) approach with a Beta response distribution and a Logit link function in the statistical software SAS (SAS Institute 1999).

Infested counties were defined as counties with documented populations of *A. tsugae* prior to 2007. The age of an infestation for a given county was defined as the number of years between 2007 and the first year of documented infestation. County-level records of the year of initial adelgid establishment were provided by the USDA Forest Service, Northeastern Area State and Private Forestry in Morgantown, WV, and are available online (http://na.fs.fed.us/fhp/hwa/infestations/infestations.shtm). Because these data were not based upon systematic surveys, slight inconsistencies may exist among years and regions in how adelgid populations were detected. The hemlock woolly adelgid is passively dispersed, and its distribution within counties is assumed to be random.

Results

Forest Inventory and Analysis data indicate substantial changes in forest structure over the last 20 years across the 432 surveyed U.S. counties (Fig. 1a, b). During this time period, the basal area of live trees in the all species group increased (Wilcoxon SRT $p < 0.0001$). The live basal areas of hemlock, red maple, and sugar maple all increased (Wilcoxon SRT $p < 0.0001$ for each), though the basal area of American beech remained constant (SRT $p = 0.3538$). Dead tree basal areas also increased over this time period for the all species group, hemlock, red maple, sugar maple, and American beech (SRT $p < 0.0001$). To determine whether the hemlock woolly adelgid is associated with a change in live or dead hemlock basal area, counties with hemlock were separated into infested and uninfested categories, based on the presence of HWA prior to the most recent inventory (2007). Comparison of these categories of counties shows that both infested and uninfested counties have experienced an increase in the basal area of both live and dead hemlock, indicated by a net positive change in median basal area per acre, per year (Wilcoxon SRT $p < 0.0001$), however the rate of accumulation of both live and dead hemlock basal area

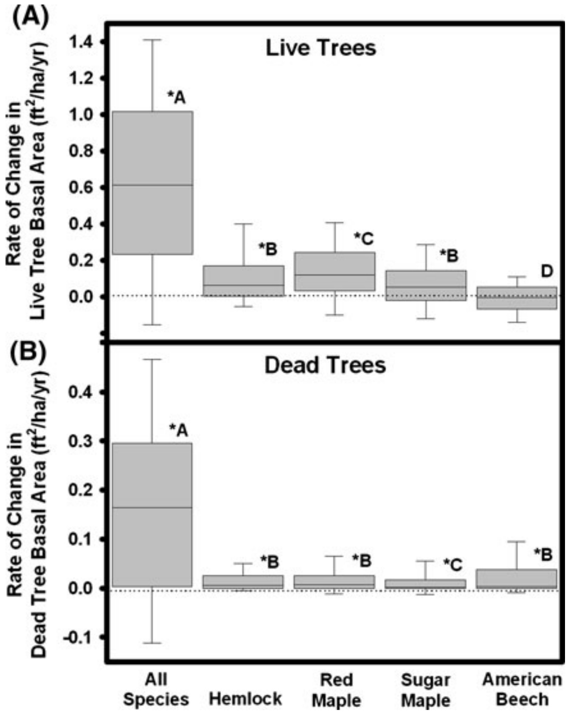


Fig. 1 Median changes in live (**a**) and dead (**b**) tree basal areas among species groups, *letters* indicate pair-wise differences. Median values above 0 (statistically denoted with *) indicates a trend of increasing basal area

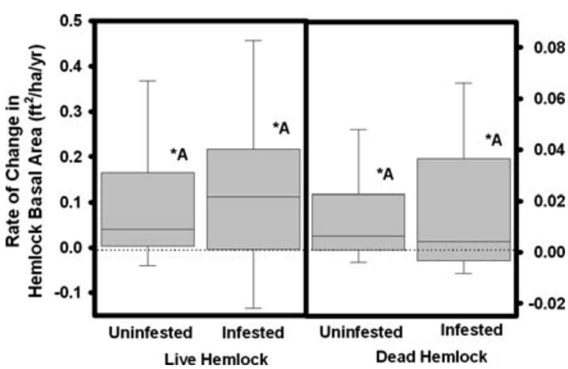


Fig. 2 Change in median dead hemlock basal area and median live hemlock basal area in counties that were infested and uninfested with HWA. *Letters* indicate differences between infested and uninfested groups. Median values higher than 0 (statistically denoted with *) indicates a trend of increasing basal area

did not differ between infested and uninfested counties (Mann–Whitney U $p < 0.2795$ and $p < 0.5120$, live and dead tree basal area, respectively) Fig. 2.

Although the median change in basal area was positive for hemlock, red maple, and sugar maple (as

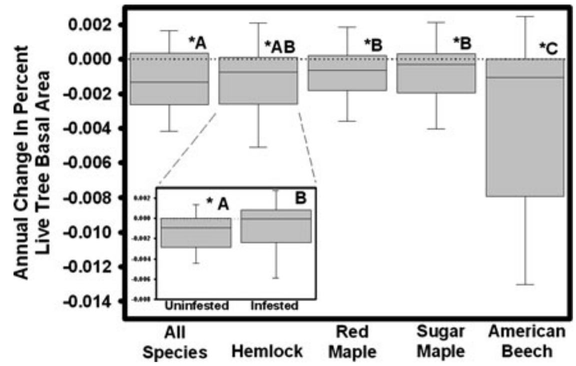


Fig. 3 **a** Changes in the percentage of basal area made up of live trees for each of the species groups. Values below 0 (statistically denoted with *) indicates a trend in which increasing percentages of the trees are dead. **b** (Nested) separates the hemlock group by infestation status

well as all species pooled) across the distribution of hemlock in the eastern United States, the median percentage of basal area that is alive (live tree basal area/total tree basal area) decreased over the last ~20 years (interval between inventories 1 and 3, Wilcoxon RST $p < 0.0001$) for each of the five species groups (Fig. 3). Rates of decrease (change in percent of trees which are alive year^{-1}) were similar among hemlock, red maple, and sugar maple. American beech, however, showed a significantly higher rate of decrease relative to hemlock, red, and sugar maple (Mann–Whitney $p = 0.0145$, $p < 0.0003$, $p < 0.0001$, respectively). Separation of counties into infested and uninfested categories shows that the annual rate of change in the percentage of hemlock which are alive in infested counties has not changed (Wilcoxon SRT $p = 0.0923$), while it has decreased among uninfested stands (Wilcoxon SRT $p = 0.0001$).

While infested counties as a whole have not shown a decrease in live hemlock basal area, or a decrease in the percent of hemlock basal area that is alive, regression of percent live basal area against time indicates that there is a weak but statistically significant positive relationship between the percent of the hemlock population which is currently alive (as of 2007), and the newness of the adelgid infestation (Type III tests for fixed effects $F = 6.83$, $p < 0.012$) (Fig. 4). A time-series perspective of the infestation of counties in the eastern U.S. suggests the adelgid has moved in two waves, pre-1996, and 1996–2007 (Fig. 4, bar chart). As such, infested counties can be placed in two groups, those infested for more than

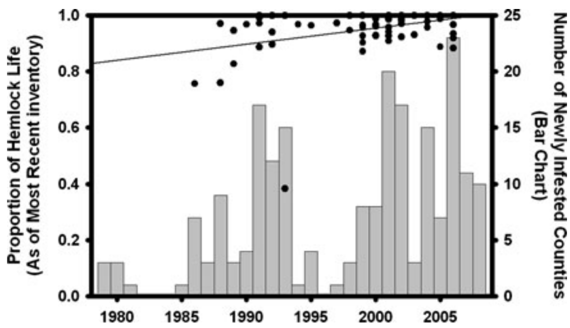


Fig. 4 Scatter plot and regression line show the relationship between year of infestation and the percent live hemlock basal area in the most recent inventory in relation to the number of years that the county has been infested. *Bars* indicate the number of counties reporting new infestations by year

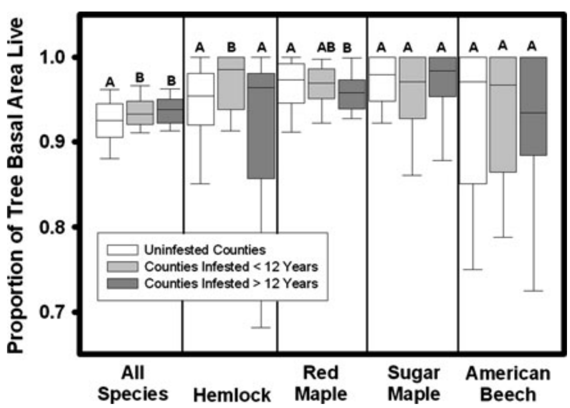


Fig. 5 Median percent of live basal area in most recent FIA inventory (2007) among uninfested counties, counties infested for more than 12 years, and those infested 12 years or less. *Letters* indicate pair-wise comparisons within species groups, *different letters* indicate $p < 0.05$ based on Mann–Whitney U

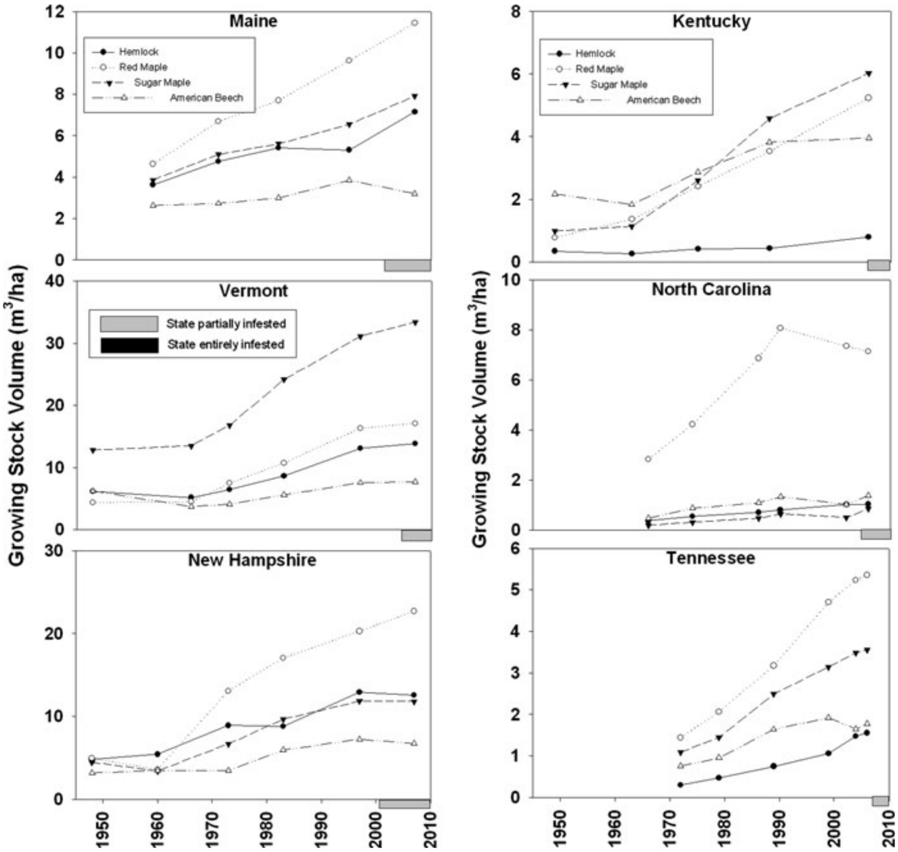
12 years, and those infested more recently (note $T_0 = 2007$). Based on these data, it is logical to compare the percentage of live hemlock basal area among three groups, those infested for more than 12 years, those infested more recently, and those which were uninfested as of 2007 (Fig. 5). Surprisingly, this assessment suggests that although the relationship shown in Fig. 4 is consistent among infested counties, there is no difference between counties which have been infested for more than 12 years and those which have not been infested (Fig. 5). Thus the statistical significance of the regression shown in Fig. 4 is based on the difference between recently and long-infested stands in the absence of uninfested stands. The inclusion of uninfested stands (age of infestation = 0) results in the loss of statistical significance ($F = 1.319$, $p > 0.24$).

Evaluating changes in the basal area of hemlock and other tree species over a longer time frame may provide a useful context to understand more recent species dynamics. Though long-term records of basal area are not available, historical data summaries of volume by species groups are available at the state level in published FIA inventory summaries starting in the 1940s ("Appendix"). Shown in Figs. 6, 7 and 8, the patterns of change in volume agree with the above analyses, suggesting changes in hemlock basal area generally vary among states infested for more than 12 years, recently infested, and uninfested states. Overall, it is clear that the general trend in the eastern U.S. over the last 50 years has been one of increasing hemlock volume, though the state-level data for Connecticut and Massachusetts (states which are completely infested, and which have been infested for an extended period) suggest the rate of accumulation may be slowing, and in Connecticut, hemlock volume may be decreasing.

Discussion

Although previous studies have clearly shown that infestation by the hemlock woolly adelgid can have substantial negative impacts on the density of hemlock within stands (Eschtruth et al. 2006; Orwig and Foster 1998; Orwig et al. 2002), analysis of the FIA data suggests the impacts of the adelgid are not evident at a regional scale as of the 2007 FIA surveys. This lack of the expected pattern of generally reduced hemlock in the eastern U.S. begs the question; why? The history of forest succession in the eastern United States and the history and biology of the hemlock woolly adelgid suggest several possible scenarios.

First, it is possible that the impacts of the adelgid are relatively insignificant at a regional scale, in contrast to the damage documented within individual stands. This conflict between patterns at these scales might be expected if two conditions are met; (1) impact varies substantially among stands and (2) impacted stands are relatively rare. Previous work (Orwig and Foster 1998; Orwig et al. 2002) has shown variable hemlock mortality among stands, and Paradis et al. (2008) noted that while some stands suffered high rates of hemlock mortality, others experienced very little, and

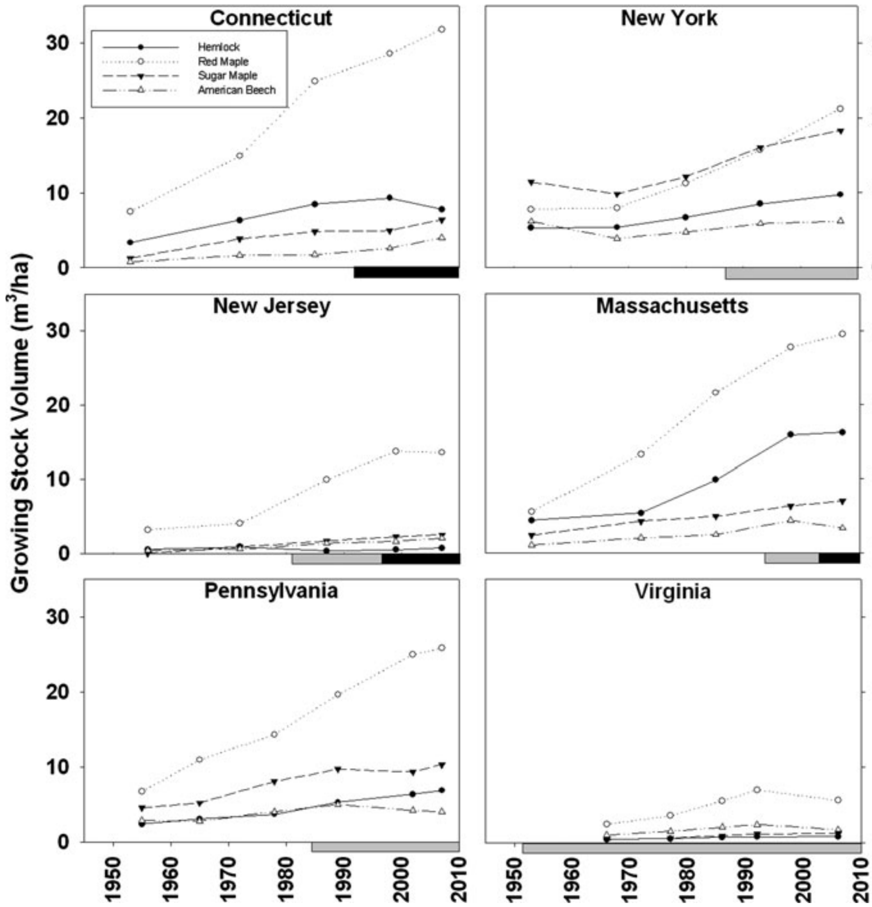


Figs. 6–8 State-level records of basal area, *grey* sections along the X axis indicate periods when infestations were documented for some counties within the state. The *black sections* indicate the time period in which all counties were infested. **6** States infested <12 years (as of 2007). **7** Uninfested states (as of 2007). **8** States infested >12 years (as of 2007)

so the first condition may be met. However, there is little evidence that the second condition (rarity of impacted stands) is met, for example, Orwig et al. (2002) found that 90 % of the 114 stands they surveyed in Connecticut were infested, and that two thirds of the stands surveyed had adelgid-driven hemlock mortality. In the southern Appalachian Mountains, Krapfl et al. (2011) found the adelgid in all 34 of the stands surveyed. They also found that between 2003 and 2008/2009 (pre- and post-hemlock woolly adelgid infestation, respectively), the density of hemlock (stems ha^{-1}) decreased, though the total hemlock basal area (m^2 ha^{-1}) did not change. Thus, while the impact of the adelgid varies among stands, infested stands are not rare on the landscape.

The impact of the adelgid must also be evaluated in the context of historic patterns of stand dynamics, structure, and disturbance, particularly long-term trends in reforestation and forest succession. Though hemlock represented a major component of many mature eastern forests at the time of European colonization, most of these forests were removed for purposes of timber utilization or land conversion for agricultural purposes (Foster 1992). Over the last 150 years, many of these formerly forested areas have been abandoned and once again support developing forests, a process demonstrated by the increases in red maple and sugar maple found in Fig. 1. Although much of the early successional secondary forests initially contained little hemlock, with time, shade tolerant species such as hemlock have increased in the understory (Foster 1992), a pattern shown both in the last half century (Figs. 6, 7 and 8), and in the period covered by the 3 most recent FIA inventories (Fig. 1). Over the last half century these young trees have continued to grow into size classes included in the FIA inventories. This regional trend of increasing hemlock basal area may be large enough to overwhelm the current impacts of the hemlock woolly adelgid, obscuring its effects, and state-level FIA reports have consistently shown gross growth exceeding mortality and removals of hemlock (Alerich 1993; Frieswyk and Widmann 2000a, b; Griffith and Widmann 2003 in "Appendix").

Figs. 6–8 continued



Though hemlock has generally increased in abundance over the past half-century, the stability of the balance between the addition of hemlock through succession and reforestation, and the removal of hemlock by the adelgid is not known. The FIA data suggest that with time the percentage of hemlock which is alive in a stand has decreased (Fig. 2) indicating stands may be accumulating dead standing material, and the balance between hemlock accumulation and loss may be shifting. Further, the changes in the volume of hemlock in long-infested states such as Connecticut (Fig. 8) suggest hemlock densities may be at a turning point. Work by Preisser et al. (2011) has shown that infestation by the adelgid is negatively correlated with seedling density, suggesting reductions in hemlock that do occur may be enduring.

Currently, the data are inconsistent with regards to the extent to which adelgids have played a role in the accumulation of dead trees at the landscape scale. A strict comparison of the rate of change in the percent of hemlock which are alive between infested and uninfested counties (Fig. 3) does not indicate infestation status has been associated with an annual decrease in the percentage of live hemlock. To the contrary, rates of decrease have been higher among uninfested counties, however, this stands in contrast to the pattern shown in the scatter plot of Fig. 4. Regression of the percent live hemlock in counties against the age of the infestation suggests a negative relationship, with the percent live hemlock decreasing as the age of an infestation increases. The analysis shown in Fig. 4 is consistent with stand and forest-scale studies by Eschtruth et al. (2006) and Orwig et al. (2002) who found positive relationships between infestation age and hemlock mortality. Data presented by Eschtruth et al. (2006) also suggest that several years may pass between the detection of the adelgid within stands, and declines in hemlock health. Accordingly, the lack of an apparent response among counties may be partially due to the recency of invasion. Other external factors may also play critical roles in determining the timing and severity of impact by the adelgid. For example, a more recent and expanded version of the Orwig et al. (2002) study, conducted by Preisser et al. (2008) found that hemlock mortality in New England has proceeded at a slower rate than was predicted by earlier studies, and that these unexpected results may be the result of interactions between multiple invading herbivores.

Further complicating the interpretation of these data are the differences in percent live hemlock basal area among recently infested, long-infested, and uninfested counties. Uninfested counties have current (as of 2007) percentages of live hemlock similar to those of long-infested counties. Partitioning the data this way raises the question as to whether the recently infested counties are perhaps the exception to a general landscape pattern of basal area accumulation, and that perhaps the recently infested counties are responsible for the apparent lack of an annual decrease in percent live hemlock among infested counties shown in Fig. 3. Further work is needed to determine whether there are fundamental structural differences between recently invaded and long-infested hemlock stands, and whether these differences are related to invasion or other yet-unidentified factors.

Some of the conflicting and inconsistent patterns found in our analyses may have arisen from the complex pattern of adelgid spread since its introduction, and the moderating influence of climate on adelgid population dynamics. Initially, the adelgid spread primarily to the north and east from Richmond, VA, moving into New Jersey, New York (notably Long Island), and southern Connecticut. Orwig et al. (2002) found that hemlock mortality in Connecticut was inversely correlated with latitude such that stands to the south generally exhibited higher rates of hemlock mortality than those to the north, a pattern which they note agrees with the chronosequence of adelgid movement through the state. This pattern also correlates with minimum winter temperatures which have been shown to limit adelgid winter survival (Paradis et al. 2008; Parker et al. 1998, 1999; Skinner et al. 2003; Trotter III and Shields 2009). As a consequence, the north–south gradient of hemlock mortality in Connecticut may be driven by two factors, climate and age of infestation, with both working in parallel. Regionally however, these factors are operating in opposing directions.

In the eastern U.S., hemlock woolly adelgid populations south of about the Mason Dixon line may not be limited by temperatures (Trotter III and Shields 2009) and hemlock mortality rates are expected to be high, however these more southern infestations tend to be more recent (http://na.fs.fed.us/fhp/hwa/maps/distribution.shtm). Simultaneously, northern populations (which have been in place for decades in some areas), are found in areas where winter mortality may play a significant role in moderating population density and concomitantly, hemlock mortality. Consequently, long-infested (northern) hemlock stands may have been buffered against high rates of hemlock mortality by high rates of adelgid winter mortality, while more southern adelgid infestations may be too recent for impacts to be manifest.

In addition, there are attributes of the FIA data which may make it difficult to detect the regional impacts of the hemlock woolly adelgid. Most critically, Phase-2 FIA inventories classify trees as either "dead" or "alive" but do not provide information about tree condition. Because of this, stands may be heavily impacted by the adelgid and experience dramatic increases in needle loss, canopy transparency, and bud die-back; however if the trees remain alive (i.e. still have some green foliage at the time of the survey) phase-2 FIA surveys will not document these impacts. Consequently, FIA data are well suited for detecting the impact of the adelgid on the mortality of trees at a landscape scale, while providing little information regarding sub-lethal or stand-health effects.

Changes in dead tree basal area may have particularly limited sensitivity to changes associated with adelgid infestation. Phase-2 surveys include only those dead trees which are standing. Once a dead tree falls, it is no longer included in the FIA survey data (except as coarse woody debris). If numerous trees have fallen between inventories, their contribution to increases in dead tree basal area would not be included in the dead tree category. However it is reasonable to expect that the increase in tree mortality (even if those trees fall and are not included in the dead tree basal area) would result in a detectable decrease in live-tree basal area, a pattern not evident in the FIA data. Though measuring tree mortality rates directly would be a preferable approach, FIA plot designs have changed over the span of several decades analyzed here, thus precluding comparison of the status of the same individual trees among successive surveys.

Overall, stand-scale studies have shown that infestation by the hemlock woolly adelgid increases hemlock mortality rates, yet, analyses of regional patterns of hemlock basal area and volume show inconsistent patterns of change related to the adelgid. Recent work by Krapfl et al. (2011) found similar conflicting patterns in which stands of hemlock in the southern Appalachian Mountains had shown reductions in stem density since infestation, though basal area had not changed. Regional trends in forest succession coupled with the interaction between the timing of invasion and the climate of the invaded area may be responsible for the apparent lack of an effect of the adelgid on regional hemlock abundance as of the inventories of 2007, and this possible lag in effect may offer a window of opportunity for management and conservation efforts. However, these scenarios do not preclude the possibility that the hemlock of eastern forests may be approaching a tipping point, beyond which the effects of the adelgid transition from negligible to significant.

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