



Invasions by two non-native insects alter regional forest species composition and successional trajectories



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ABSTRACT

While invasions of individual non-native phytophagous insect species are known to affect growth and mortality of host trees, little is known about how multiple invasions combine to alter forest dynamics over large regions. In this study we integrate geographical data describing historical invasion spread of the hemlock woolly adelgid, *Adelges tsugae*, and beech scale, *Cryptococcus fagisuga*, with regional forest inventory data collected by the US Forest Service's Forest Inventory and Analysis program to quantify the individual and combined impacts of these pest species. This analysis indicates that regional impacts of these insects on their hosts occur surprisingly slow but act to change regional forest succession pathways. Because beech and hemlock commonly co-occur in eastern North American forests, invasions by the two pest species are altering the current and future composition of large forest regions through their impacts on these two late-successional species. Such results demonstrate how forest insect invasions can profoundly modify forest dynamic processes, resulting in long-term changes in forest ecosystems.

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1. Introduction

Invasions by non-native insects and pathogens are major causes of disturbance, affecting the stability, productivity, and economic value of forest ecosystems worldwide (Liebhold et al., 1995; Holmes et al., 2009; Aukema et al., 2011). Most invading forest insects and diseases are not particularly abundant and consequently have negligible effects, but a few have altered forest ecosystems in profound ways (Niemela and Mattson, 1996; Aukema et al., 2010). Over the last century, a large number of invasive species have become established in forests of eastern North America (Liebhold et al., 2013) and some of these organisms, such as chestnut blight, emerald ash borer, and beech bark disease have caused extensive tree mortality.

Forest insect and pathogen invasions can affect forest communities in a multitude of ways, acting both directly and indirectly (Lovett et al., 2006; Loo, 2009). Such effects include changes in tree species composition (Fajvan and Wood, 1996; Jedlicka et al., 2004), tree age structure (Garnas et al., 2011), nutrient cycling (Townsend et al., 2004; Lovett et al., 2006), carbon sequestration (Peltzer et al., 2010), and the abundance of organisms such as aquatic invertebrates (Smock and MacGregor, 1988), large mammals (Kendall

and Arno, 1990) and birds (Showalter and Whitmore, 2002; Tomback and Achuff, 2010).

While there is an extensive body of literature on the ecological impacts of invasive species in forest ecosystems, most studies have been limited to sampling from individual stands. The critical importance of evaluating impacts of invaders across their entire range has been recognized (Parker et al., 1999), but only a handful of studies have taken a regional perspective to measuring impacts. Here we use the concept of regional evaluation to quantify individual and combined impacts across the entire range of two invading species. Given trends of continued accumulation of non-native insects and diseases in forest ecosystems worldwide, there is a serious need to assess the impacts of these species at the regional level. The implementation of quarantine measures to exclude future invasions can only be justified based on economic assessments of area-wide impacts of past invasions (Holmes et al., 2009; Aukema et al., 2011), thus highlighting the need for regional estimation of pest impacts over their entire range.

Of particular importance is the need to understand how invading species alter regional trends in forest species composition and thereby alter long-term forest dynamics. Given the extraordinarily large number of damaging forest insect and pathogens species that are accumulating worldwide, an immediate question is what is the cumulative impact of these species on forest dynamics? Many of these invading organisms are capable of causing extensive

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mortality but little is known about how they may interact to alter long-term trends in forest dynamics and consequently modify long-term forest ecosystem processes.

To address this problem, we explore the individual and combined effects of two major pest species invading the northeastern US: the hemlock woolly adelgid (HWA), *Adelges tsugae*; and beech scale (BS), *Cryptococcus fagisuga*, which is the causal agent of beech bark disease (BBD). Their hosts, eastern hemlock (*Tsuga canadensis* (L.) Carr.), Carolina hemlock (*Tsuga caroliniana* Englem.), and American beech (*Fagus grandifolia* Ehrh.) were known to have dominated large portions of presettlement northern forests (Bürgi et al., 2000; Thompson et al., 2013).

Current forests in the northeastern US differ vastly from those that existed prior to the time of European settlement (Irland, 1999; Bürgi et al., 2000; Thompson et al., 2013). Humans have greatly altered forest composition via harvesting and conversion to agricultural land use, followed by extensive agricultural abandonment. Other factors, such as alteration of presettlement fire regimes and elevated deer populations have also greatly influenced current forest composition (Nowacki and Abrams, 2008; Horsley et al., 2003). Forests in the northeastern US are in flux and it is in this context of a changing forest that the regional impacts of forest insect and disease invasions should be considered. Specifically, dominance by shade-tolerant hemlock and beech is increasing as a result of successional processes (Flinn and Vellend, 2005; Thompson et al., 2013) but it is not clear how this trend is altered by insect and disease invasions.

Therefore, in the analysis presented here we focus on how HWA and BS invasions combine to alter regional succession trajectories. While this analysis is specific to the eastern United States, it provides insight into understanding the more general problem of how alien forest pests affect forested ecosystems, a phenomenon that is affecting forests worldwide.

1.1. Species backgrounds

Beech and hemlock dominate a large fraction of the late-successional forests of the eastern United States (Fig. 1A), and they both fill distinctive roles in forest ecosystems. Mast produced by American beech is a critical source of food for various forest wildlife species. Eastern hemlock is particularly common in riparian areas where it plays a unique role in modifying microclimates, soil chemistry, and stream temperatures. Both species are long-lived, shade tolerant and compose a substantial proportion of the species composition in late-successional forests in the maple/beech/birch type (online Supplement 1).

BBD is an insect-fungus complex involving the non-native BS which feeds on bark fluids from stems of American beech, providing an opportunity for the native canker fungi *Neonectria coccinea* var. *faginata* and *Neonectria ditissima* to invade the inner living bark and cambium leading to dieback and mortality (Mize and Lea, 1979; Houston, 1994). While some trees survive infections for several decades, one effect of the accumulation of cankers is reduced growth (Gavin and Peart, 1993; Gove and Houston, 1996).

The BS was accidentally introduced with live plants imported to Halifax, Nova Scotia from Europe, in the 1890s (Houston, 1994). The scale insect has since slowly spread (~15 km/yr) into the New England states, New York, Pennsylvania, and West Virginia and several discontinuous “jumps” have transported it into North Carolina, Tennessee, and Michigan (Fig. 1B) (Morin et al., 2007; Wiefelich et al., 2013). In 2004 the range of BBD comprised about 30% of the range of beech in the USA, but that area included about 50% of the total beech basal area (Morin et al., 2005).

Three phases of BBD are generally recognized: (1) the “advancing front”, which corresponds to areas recently invaded by scale populations; (2) the “killing front”, which represents areas where

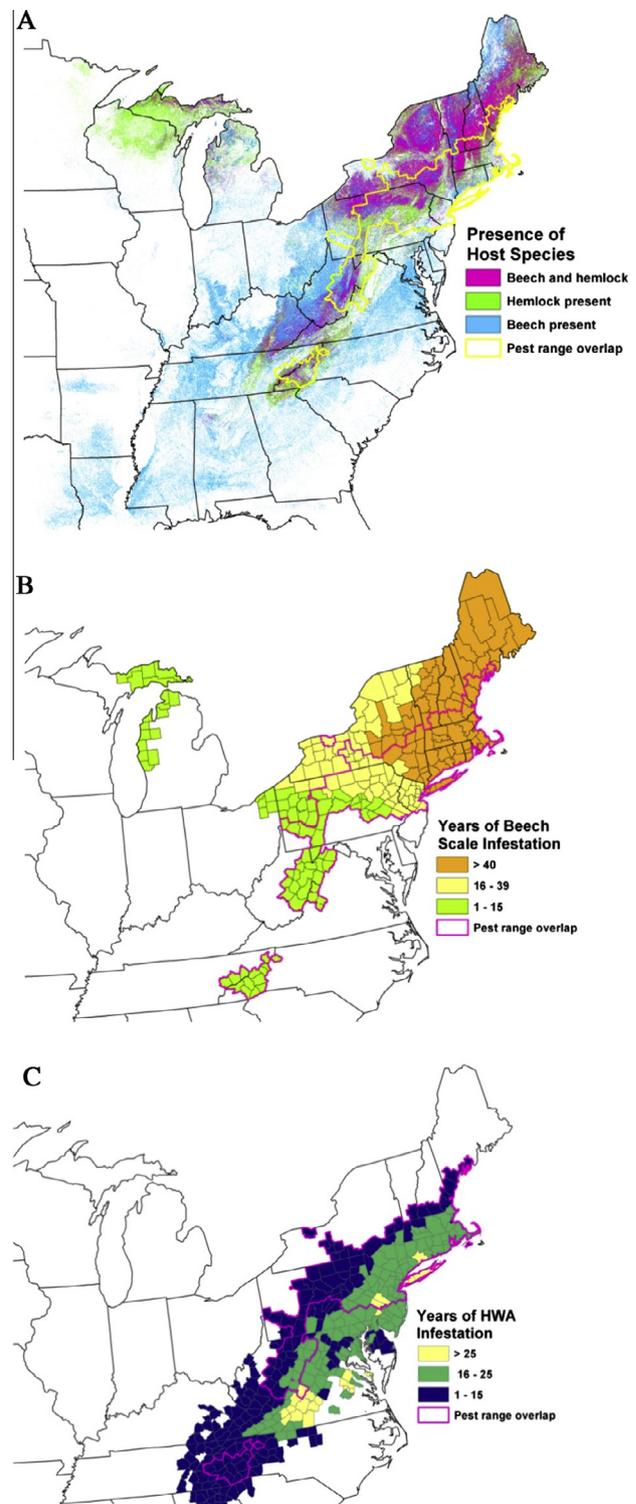


Fig. 1. Maps of species distributions in the eastern United States. (A) Distribution of American beech, *Fagus grandifolia*, and hemlock, *Tsuga* spp. derived from interpolated maps of species volume density from FIA plots (Wilson et al., 2012); (B) historical spread of the beech scale (2006); and (C) historical spread of hemlock woolly adelgid (2006).

fungal invasion has occurred (typically 3–5 years after the scale insects appear, but sometimes as long as 20 years) and tree mortality begins; and (3) the “aftermath forest”, which are areas where the disease is endemic (Shigo, 1972; Houston, 1994).

The hemlock woolly adelgid, native to East Asia, may have been introduced to the eastern US as early as 1911; however, the first

report of its presence was in Richmond, VA in 1951 (Havill and Montgomery, 2008). Since then, it has slowly expanded its range at 8–30 km/yr (Fig. 1C) (Evans and Gregoire, 2007; Morin et al., 2009). Further spread of the adelgid into northern New England is unlikely under current climates because of its inability to tolerate cold winter temperatures (Trotter and Shields, 2009). In areas where the species has established, populations often reach high densities, causing widespread defoliation and sometimes mortality of hemlock (McClure et al., 2001; Orwig et al., 2002).

Limited information exists about the long-term effects of BBD and HWA on forest composition. It appears that in some stands, the advent of BBD results in significant decreases in the proportion of beech, but in other stands, beech is able to persist because of its often prolific regeneration through sprouts and seedlings (Houston, 1994; Twery and Patterson, 1984; Runkle, 1990; Houston, 2001). Despite regional increases in beech mortality following invasion, considerable amounts of live beech remain in invaded areas. Additionally, the volume of beech is still increasing in most areas, although this increase is generally smaller than for associated tree species (Morin et al., 2007).

Impacts of HWA vary within the range of the infestation. Observed rates of hemlock loss within individual infested stands have ranged from near 0 to more than 95% (Orwig and Foster, 1998; Paradis et al., 2008). To date, studies evaluating the impact of HWA on forest structure have focused on individual stands (Eschtruth et al., 2006; Orwig and Foster, 1998) or regions within a state (Orwig et al., 2002). Despite the mortality induced by HWA, hemlock volume is still generally increasing across the range of the infestation (Morin et al., 2011; Trotter et al., 2013).

Since seedlings are an important indicator of future overstory species composition, impacts on the species distribution of seedlings are also important for the trajectory of stands into the future. Mortality of overstory beech results in a proliferation of basal sprouts from surviving stumps (Shigo, 1972; Houston, 1994) creating dense “beech brush” conditions (Horsley and Bjorkbom, 1983) that can interfere with regeneration of other hardwood species such as sugar maple (Hane, 2003).

2. Methods

The Forest Inventory and Analysis (FIA) program of the US Department of Agriculture (USDA) Forest Service conducts an inventory of forest attributes nationwide (Bechtold and Patterson, 2005). The current FIA sampling design is based on a tessellation of the United States into hexagons approximately 2,458 hectares in size with at least one permanent plot established in each hexagon. The population of interest is stratified and plots are assigned to strata to increase the precision of estimates. Tree and site attributes are measured for forested plots established in each hexagon. Plots consist of four 7.2-m fixed-radius subplots on which standing trees and various other environmental characteristics are inventoried.

Prior to 1999, FIA collected data regionally using a periodic measurement system with sample designs that varied slightly through time and by region. Generally, inventories were conducted in each state every 6–18 years, depending on the state and region. Since 1999, FIA has adopted an annual inventory system, where some plots are surveyed using a consistent plot design in each state every year, across the ranges of BBD and HWA. This system provides a statistically robust sampling program for estimation of mortality and net growth rates (Bechtold and Patterson, 2005). Prior to the availability of the remeasured annualized FIA plot system, it was not possible to directly estimate mortality and growth across large areas. As a result, previous studies that used FIA data to quantify regional impacts of HWA and BBD (Morin et al., 2007, 2011; Trotter et al., 2013) relied on estimates of standing dead tree

volume to quantify impacts rather than directly quantifying mortality rates.

We used these historical FIA surveys to examine changes in host tree species density over time. Since FIA plot data collected prior to the 2000s were not collected annually, we were unable to examine growth and mortality rates over time for the entire study region. Therefore, we used periodic and annual inventory data to estimate host species basal area over time in two states that are partially infested by BBD and HWA, West Virginia and Pennsylvania. By extracting basal areas from successive surveys and standardizing basal area relative to the first estimate, we were able to characterize temporal trends in host species density. Therefore, the first estimate is scaled to one and subsequent estimates represent proportional change. To elucidate the potential impact of BBD and HWA on these trends, we also estimated the time series in two categories of BBD and HWA historical presence: infested greater than 15 years (i.e., infested prior to 1999) and uninfested or infested less than or equal to 15 years.

This study represents the first analysis of annualized FIA data for regional estimation of mortality and growth rates in relation to BBD and HWA invasion. The study utilized FIA plot data from 22 states where the ranges of American beech and eastern hemlock overlap: Alabama, Connecticut, Delaware, Georgia, Kentucky, Maine, Maryland, Massachusetts, Michigan, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, South Carolina, Tennessee, Vermont, Virginia, West Virginia, and Wisconsin.

Remeasured plots (originally surveyed 2001–2005 and remeasured 2006–2010) were used to compute annual net growth and mortality rates as proportions of live volume at the time of the initial survey (i.e., annual mortality volume/live volume at time 1). Annualized net growth and mortality rates for trees 12.7-cm in diameter and greater were calculated for eastern hemlock and American beech, as well as for commonly associated species, sugar maple (*Acer saccharum* Marsh.) and red maple (*Acer rubrum* L.) based upon changes measured between successive forest inventories. A detailed description of methods for computing mortality and net growth are provided in Bechtold and Patterson (2005).

Numbers of seedlings per hectare were calculated for eastern hemlock, American beech, sugar maple, red maple, and birch species (*Betula* spp.). Only data from large-diameter stands in the FIA maple/beech/birch forest-type group (measured 2006–2010) were included in order to avoid data from young, regenerating stands overwhelming the estimates. It is important to note that FIA only counts hardwood seedlings that are at least 30.5 cm tall and conifer seedlings that are at least 15.2 cm tall. Seedlings must also be less than 2.5 cm in root collar diameter. To be classified as large-diameter stands, FIA protocols require that the predominant (based on stocking) diameter class of live trees is at least 27.9 cm for hardwoods and at least 22.9 cm for conifers.

Historical county-level records of the year of initial BS insect and HWA establishment through 2006 were compiled by the US Forest Service, Northeastern Area State and Private Forestry, Morgantown, WV, and are available online (BS – <http://na.fs.fed.us/fhp/bbd/infestations/infestations.shtm>; HWA – <http://na.fs.fed.us/fhp/hwa/infestations/infestations.shtm>). These data were not based upon systematic surveys and therefore slight inconsistencies may exist among years and regions in how adelgid and BS populations were detected. Detection surveys were spatially crude and variation can exist within counties, but these represent the best available spatial distribution data available for the present of these two invaders. Although these records are based on establishment of the BS insect, we generally refer to BBD throughout the remainder of the paper.

Annual net growth rates, annual mortality rates, and numbers of seedlings per hectare for each species were estimated from

inventory data as described above. These were estimated for specific ranges of pest invasion duration based on inventory plots that fell within counties grouped according to specific invasion duration classes. The classes used for length of BBD establishment were 0, 1–15, 16–40 and greater than 40 years and for HWA classes were 0, 1–15, 16–25, and greater than 25 years. Note that the two highest HWA classes were combined for the seedling analysis due to low sample sizes in the individual classes. The BBD classes were selected to correspond to the recognized phases of beech bark disease invasion: (1) the advancing front, (2) the killing front, and (3) the aftermath forest (Houston, 1994). Invasion by HWA does not appear to occur in discrete phases like BBD so the use of such terminology does not seem appropriate. However, we chose similar classes for HWA to determine if mortality progression would be comparable to BBD, but the largest class is a shorter duration due to HWA's more recent invasion (i.e., HWA has not been present in many areas for more than 40 years).

Additionally, in order to ascertain the potential combined BBD and HWA impacts, estimates are presented for the counties where the ranges of infestations of both pests overlap for comparison with the counties that are only infested by one pest (Fig. 1B and C). We tested the statistical significance of the difference between net growth rate, mortality rate, and seedlings per hectare estimates within each species by pest duration categories with two-tailed *t*-tests ($\alpha = 0.05$). The false detection rate adjustment (FDR) was employed to control experiment-wide error levels within each family of comparisons (Benjamini and Hochberg, 1995). This resulted in a reduced critical threshold for determining significance between estimates in each multiple comparison family. All associated statistics are listed in online Supplement 2.

Finally, linear regression analyses were employed to model the relationship of county level estimates of net growth and mortality as a function of duration of HWA and BBD invasions and the interaction between them to account for spatial overlap. The durations were not divided into classes for the regression analyses. Plots of residuals versus predicted values were examined to ensure that the assumptions of linearity and homoscedasticity were met, and normal probability plots of residuals were inspected to test for normally distributed errors. The intent of the regression analyses is to examine the significance and direction of the relationships, not to predict mortality or growth from duration of infestation.

3. Results

Eastern hemlock and American beech co-occur across large forested regions (Fig. 1A). More than half of the volume of eastern hemlock and beech occurs in the FIA maple/beech/birch forest-type group, with the majority of the remaining hemlock occurring in FIA pine groups and beech in the FIA oak/hickory group (online Supplement 1). Within the maple/beech/birch group, both hemlock and beech comprise substantial proportions of volume across all diameter classes though hemlock is particularly dominant in large diameters (online Supplement 3).

Live basal area of both hemlock and beech has generally been increasing over the last three decades in areas uninfested and in areas infested less than 15 years by BBD or HWA in West Virginia and Pennsylvania. By contrast, basal area of beech has begun to decrease in areas that have been infested by BBD for more than 15 years in West Virginia and Pennsylvania, and basal area of hemlock has begun to decrease in areas of West Virginia that have been infested by HWA for more than 15 years. Although hemlock basal area has not started to decrease in areas of Pennsylvania that have been infested by HWA for more than 15 years, basal area increase is much less than in areas where the insect has been present for a shorter period or is absent (Fig. 2).

Evaluation of the remeasured annual inventories indicates that annual beech mortality rates increase with increasing duration of BBD infestation but this pattern is not seen for associated species (Fig. 3A). Beech mortality rates appear to increase markedly after 15 years, but from the 16–39 to >40 year BBD infestation durations mortality rates did not increase significantly (online Supplement 2). It is important to recognize that these are not increases in cumulative mortality, but in annual rates. This means that beech mortality rates increase following BBD establishment (Fig. 3A), but then settle in to sustained, constant annual mortality rates after 15 years of BBD presence (online Supplement 2). Additionally, linear regression analyses indicated that the annual mortality rate of American beech was positively associated with duration of BBD infestation ($p < 0.0001$) and negatively associated with the interaction between BBD and HWA establishment duration ($p = 0.0259$) (online Supplement 4).

Mortality can be compensated for by growth of surviving trees and ingrowth of young trees into the minimum (12.7 cm and greater) diameter class. The combined effect of growth and ingrowth with mortality is described by net growth. Although the means indicate that the annual net growth rate of American beech generally decreases with increasing BBD duration (Fig. 3B), statistical comparisons of the means did not reveal significant differences between the duration categories (online Supplement 2). However, county-level linear regression analyses indicated that the annual net growth rate of American beech was inversely related with duration of BBD ($p < 0.0001$) and positively associated with the interaction between BBD and HWA duration ($p = 0.0529$) (online Supplement 4). Nevertheless, uninfested areas have net growth rates that are nearly four times higher than regions infested for more than 40 years but even in areas where BBD has been present the longest (and mortality is greatest), net beech volume continues to increase (i.e., net growth > 0).

Evaluation of the remeasured annual inventories indicate that annual mortality of eastern hemlock increased strongly with increasing numbers of years of HWA presence (Fig. 4A). Annual mortality rates of hemlock appear to increase most markedly after 15 years, but beyond 25 years mortality rates did not increase significantly relative to the 16–24 year class (online Supplement 2). Additionally, annual mortality of eastern hemlock was positively correlated with duration of HWA infestation ($p < 0.0001$) and negatively correlated with the interaction between BBD and HWA duration ($p = 0.0007$) (online Supplement 4).

Similarly, hemlock net growth rates decrease as duration of HWA invasion increases (Fig. 4B). Means indicate a lag in these declines; net growth rates in regions with recent infestations are similar to those in uninfested counties but once invasion duration surpasses 15 years, net growth rates drop significantly and actually become negative when HWA is present for more than 25 years. Although statistical comparisons of the means do not indicate a significant difference between the 16–25 and >25 year classes (online Supplement 2), linear regression analysis indicated that annual net growth of eastern hemlock was negatively correlated with duration of HWA infestation ($p < 0.0001$) (online Supplement 4).

Interestingly, beech appears to benefit from hemlock mortality associated with HWA and hemlock benefits from beech mortality related to BBD. This compensatory growth and offsetting mortality is illustrated by examining the region where the ranges of HWA and BBD overlap. American beech and hemlock mortality rates are lower and net growths are higher when the other species' pest duration is greater than 15 (Fig. 5A and B).

Seedling densities were at least partially associated with the duration of BBD and HWA invasions. Beech seedlings densities are much higher in BBD infested areas while the opposite trend occurs for sugar maple (Fig. 6A). Densities of eastern hemlock

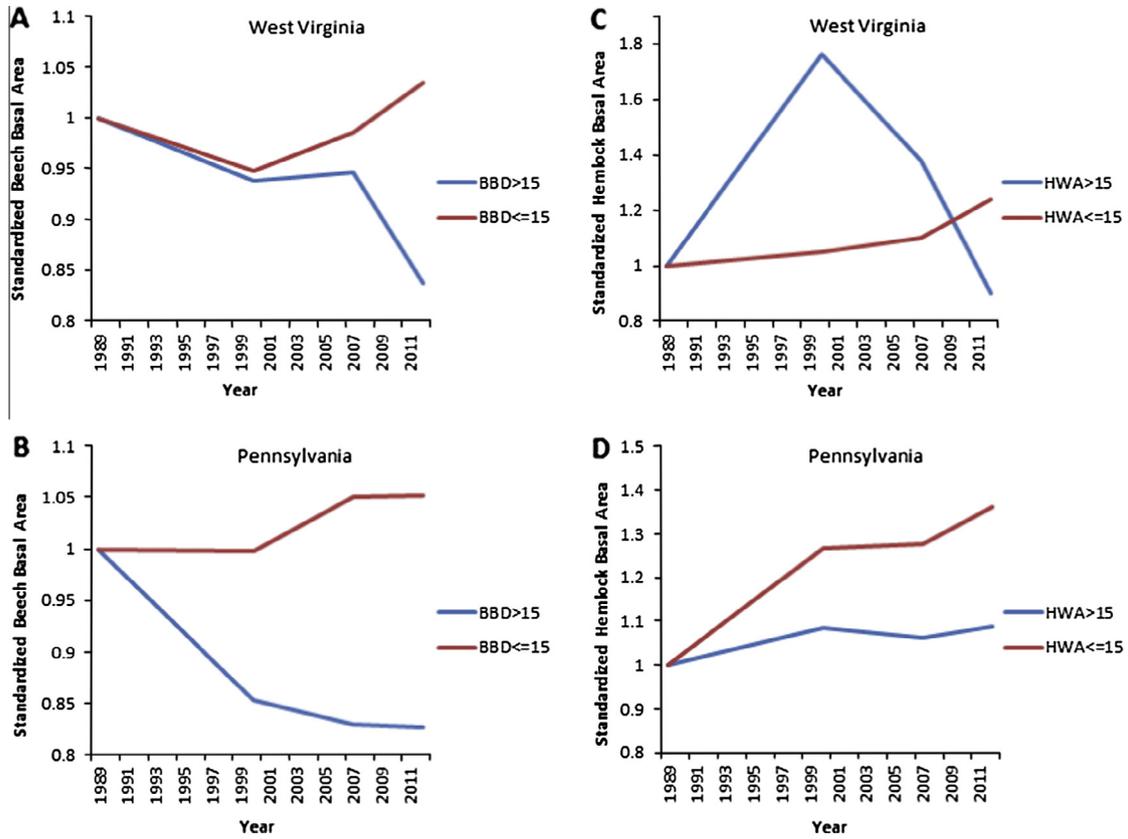


Fig. 2. Standardized host species basal area by species, state, and pest infestation duration category: (A) beech basal area in West Virginia; (B) beech basal area in Pennsylvania; (C) hemlock basal area in West Virginia; and (D) hemlock basal area in Pennsylvania.

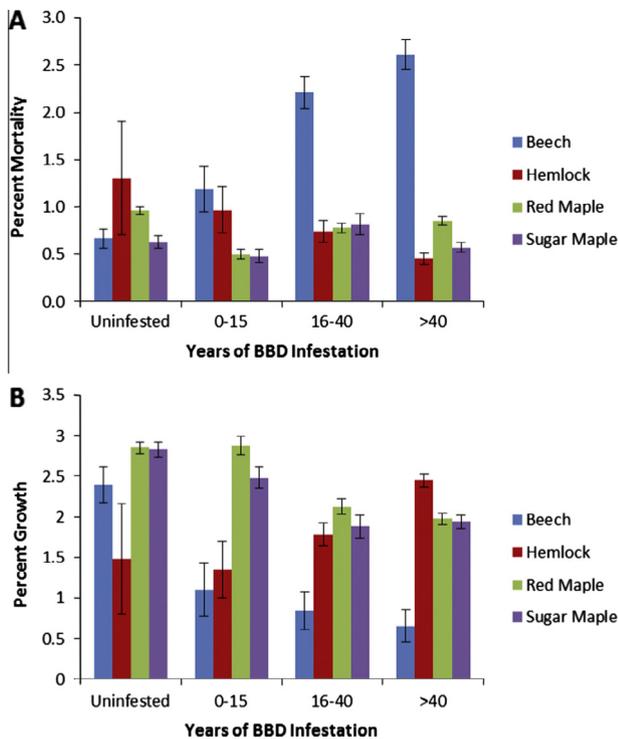


Fig. 3. Annual percent mortality (A) and net growth (B) of American beech, hemlock, red maple, and sugar maple by years of BBD infestation (error bars represent 68% confidence intervals. Remeasured plots (originally surveyed 2001–2005 and remeasured 2006–2010) were used to compute annual net growth and mortality as proportions of live volume at the time of the initial survey (i.e., annual mortality volume/live volume at time 1).

seedlings are similar across all HWA infestation classes (Fig. 6B). Densities of seedlings of both maple species decrease with years of HWA infestation, and the number of birch and beech seedlings are similar across categories. Densities of beech seedlings are much higher in counties that have been infested by BBD for more than 15 years regardless of whether HWA is also present (Fig. 7).

4. Discussion

The impacts of these two invaders on growth and mortality of host species have previously been studied at specific sites (BBD – Mize and Lea, 1979; Jones and Raynal, 1987; Gavin and Peart, 1993; Gove and Houston, 1996; Kasson and Livingston, 2011; HWA – Orwig and Foster, 1998; Orwig et al., 2002; Eschtruth et al., 2006; Rentch et al., 2009). These studies documented very high levels of mortality associated with infestations as well as declines in the dominance of host species in affected stands. However, such studies generally have not captured the range of impacts seen as these invasive insects persist for many years (Fitzpatrick et al., 2012). While it is not surprising that we found mortality and decreases in net growth associated with invasions, it is noteworthy that mortality rates increase and net growth rates decrease in both hemlock and beech over several decades following initial invasions by these insects. There may be several explanations for these protracted increases in damage. One reason may be that an area (e.g., county) may be designated as “infested” but it may take several years before all stands in the area become infested and the severity of infestations may be quite variable. Another factor is that populations of both HWA and BS may fluctuate following establishment (McClure, 1991; Garnas et al., 2012). Such recurring outbreak episodes may have cumulative adverse impacts on trees and

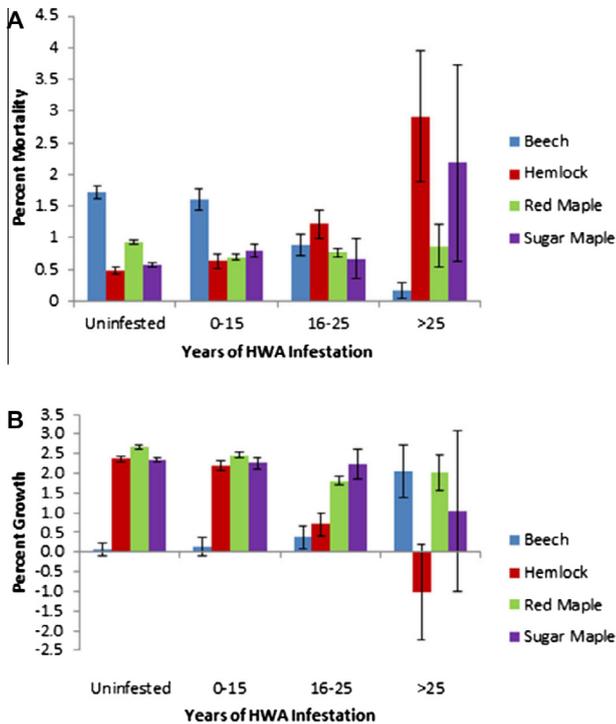


Fig. 4. Annual percent mortality (A) and net growth (B) of American beech, hemlock, red maple, and sugar maple years of HWA infestation (error bars represent 68% confidence intervals). Remeasured plots (originally surveyed 2001–2005 and remeasured 2006–2010) were used to compute annual net growth and mortality as proportions of live volume at the time of the initial survey (i.e., annual mortality volume/live volume at time 1).

result in tree mortality that increases over many years. Other environmental factors such as climate, soils and land use also likely affect growth, mortality, and seedling density and the duration of infestation only explains a fraction of the variation in these properties (e.g., [online Supplement 4](#)). Furthermore, geographical variation in these other environmental factors may be confounded with the duration of pest invasion but nevertheless it is still possible to characterize consistent regional impacts of these invasions (Figs. 3 and 4).

In addition to the differences in net growth and mortality observed in beech and hemlock in relation to BBD and HWA infestation history, distinct trends were also seen in densities of seedlings among species in relation to infestation history. Since seedlings are an important indicator of future overstorey species composition, impacts on the species distribution of seedlings are important for the trajectory of stands into the future. Beech seedlings densities are higher in areas where beech scale is present (Fig. 6A), but hemlock seedlings densities did not vary across HWA infestation history classes (Fig. 6B). The trend in beech seedling densities reflects a phenomenon commonly observed in stands heavily affected by BBD; mortality of overstorey beech results in a proliferation of basal sprouts from surviving stumps and roots (Shigo, 1972; Houston, 1994) creating dense “beech brush” conditions (Horsley and Bjorkbom, 1983) that can interfere with regeneration of other hardwood species such as sugar maple (Hane, 2003). Indeed, we found that sugar maple seedling densities decrease as the density of beech seedlings increases (Fig. 6A). These results indicate that prolific beech sprouting may adversely affect sugar maple regeneration even at the regional scale, which may further exacerbate the impacts on long-term successional dynamics given that sugar maple is another shade tolerant species. The lack of an observed impact of HWA presence on hemlock seed-

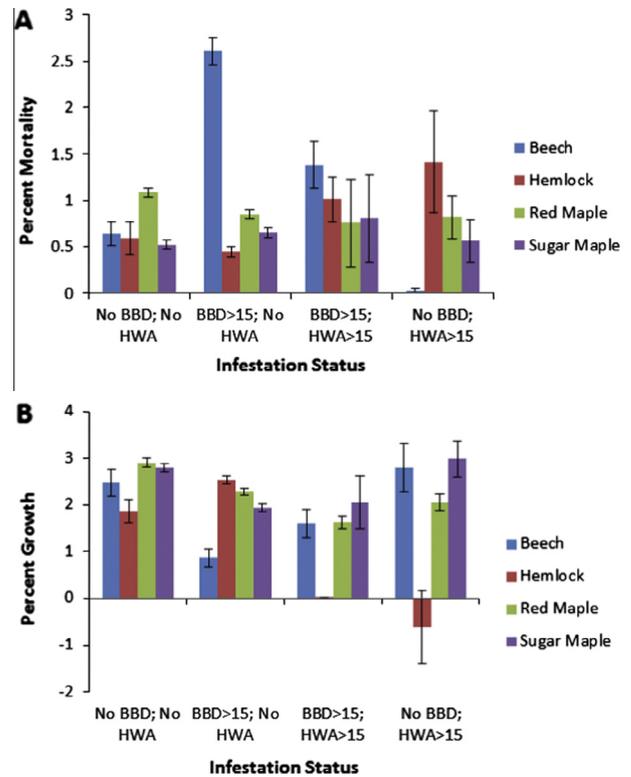


Fig. 5. Annual percent mortality (A) and net growth (B) of American beech, hemlock, red maple, and sugar maple in overlapping and non-overlapping HWA and BBD infested areas (error bars represent 68% confidence intervals). Remeasured plots (originally surveyed 2001–2005 and remeasured 2006–2010) were used to compute annual net growth and mortality as proportions of live volume at the time of the initial survey (i.e., annual mortality volume/live volume at time 1).

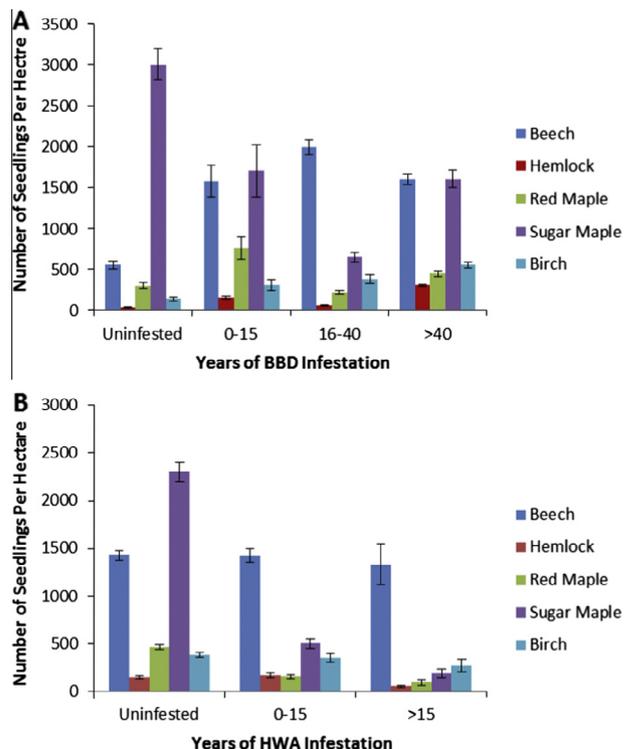


Fig. 6. Number of seedlings per hectare of American beech, hemlock, red maple, sugar maple, and birch by years of (A) BBD infestation and (B) HWA infestation (error bars represent 68% confidence intervals).

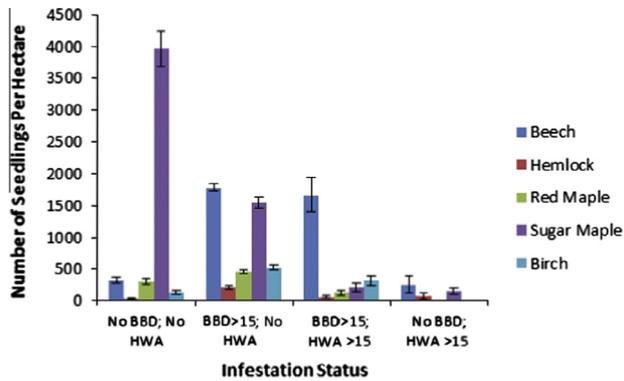


Fig. 7. Number of seedlings per hectare of American beech, hemlock, red maple, sugar maple, and birch in overlapping and non-overlapping HWA and BBD infested areas (error bars represent 68% confidence intervals).

ling densities suggests that hemlock may persist, at least at low levels, in the region over the coming decades.

Another interesting result is the apparent increase in beech net growth in response to HWA induced overstory hemlock mortality. Similarly, hemlock net growth responds favorably to BBD induced beech mortality (Figs. 3B and 4B). Previous studies have identified compensatory growth of small-diameter beech in response to the loss of overstory beech (Gravel et al., 2011) but not growth in other species (Garnas et al., 2011). Since beech and hemlock frequently co-occur in the same stands, it is not surprising that we observed that each compensate for losses of the other species, though such compensation was surprisingly not seen in sugar or red maple. As HWA and BS continue to expand their ranges, the area where both species are present is likely to expand and this may decrease the potential for compensatory growth. Orwig (2002) reported a concurrent increase in maple growth associated with a decrease in hemlock growth in south-central Connecticut. Although this phenomenon may occur in stands that have been severely impacted by HWA, the results of this study do not indicate that compensatory growth has occurred in associated species at the regional scale even though hemlock growth has decreased (Fig. 4B). Several studies have reported that black birch (*Betula lenta* L.) is the species that benefits the most from declines in hemlock based on prolific regeneration and re-establishment (Orwig and Foster, 1998; Orwig, 2002; Stadler et al., 2005; Sullivan and Ellison, 2006), but our results show that the number of birch seedlings is similar across HWA infestation duration categories. Increases in black birch regeneration may be occurring in some areas, but this is not evident at the regional scale (Fig. 6B).

To fully understand the impact of BBD and HWA invasion at the regional scale, it is necessary to consider the observed variation in growth rates, mortality rates and seedling densities with respect to long-term successional trends in the region. Online Supplement 5 illustrates how the most common shade-tolerant species (including beech and hemlock) found in northeastern deciduous forests have been steadily increasing in dominance over the last half century. This trend reflects well-documented successional processes operating in the region; extensive forest clearing prior to 1900, followed by regrowth and agricultural abandonment, and has placed forests in the region in a long-term trend of increasing dominance by shade-tolerant species such as hemlock and beech (Flinn and Vellend, 2005; Thompson et al., 2013).

Results presented here provide some indication of how invasions by two phytophagous insect species may likely modify species composition trends into the future. Because impacts on net growth of their hosts are delayed over several decades, the reversal of trends of increasing beech and hemlock dominance is currently

evident only in stands where BBD and HWA have been the longest (Figs. 3 and 4). The full impact of these invading pests is likely to play out very slowly in the future. Hemlock volume is continuing to increase in many areas that are already infested with HWA despite the adverse effects of this insect (Fig. 2D, Trotter et al., 2013). Forest succession across the region is favoring increases in hemlock ingrowth from the understory and may be capable of offsetting declines following HWA-caused tree mortality. However, it appears that after 25 years of HWA presence, such ingrowth offsets are not sufficient and total hemlock density begins to decrease at the regional scale (Figs. 4 and 5). These decreases may be reinforced by a trend of decreased hemlock regeneration in areas with long histories of HWA though we did not detect such an effect (Fig. 6B). As HWA persists in areas over many years, we can thus anticipate a slow-motion decline in hemlock density across the entire infested region in the future. It should, however, be pointed out that HWA is not expected to expand its current range substantially to the north due to climatic unsuitability (Trotter and Shields, 2009), and hemlock in these northern portions of its range are likely to escape this future downward trend. Nevertheless, warming due to climate change could make the northern range of hemlock more suitable for HWA in the future.

Long-term trends in beech, however, can be anticipated to be slightly different. The pattern of increased beech regeneration in response to BBD documented here (Fig. 6A) and several other studies (Shigo, 1972; Houston, 1994) means that beech is likely to persist following scale presence over many years. Nevertheless, increases in beech density (Fig. 2) are likely to be dampened over the long-term. The persistence of BBD over future decades is also likely to result in a shift in the distribution of beech volume to lower diameter classes (Garnas et al., 2011).

The loss of hemlock as a result of HWA invasion has already had impacts on ecosystem properties such as stream temperatures and soil chemistry (Stadler et al., 2005; Orwig et al., 2008). Similarly, beech is an important source of mast and losses of large beech have been implicated in declines of certain wildlife species (Storer et al., 2005). The future regional trends in hemlock and beech volume are likely to translate into changes in other regional properties, such as water chemistry (Eshleman et al., 1998), hydrologic budgets (Ford and Vose, 2007), and wildlife densities (Storer et al., 2005).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.12.018>.

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