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Review

Hemlock woolly adelgid in the southern Appalachians: Control strategies, ecological impacts, and potential management responses

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ABSTRACT

Hemlock woolly adelgid (*Adelges tsugae* Annad; or HWA) is a non-native invasive pest that attacks and kills eastern hemlock (*Tsuga canadensis* (L.) Carrière) and Carolina hemlock (*Tsuga caroliniana* Engelm.). Hemlock is a "foundation species" due to its strong influence on ecosystem structure and function, especially in riparian areas. HWA management involves the integrated use of multiple approaches including chemical control, biological control, cultural treatments, host resistance, and host gene conservation. Despite extensive control efforts, large areas in the eastern US, but especially in the southern Appalachian region, have experienced extensive hemlock mortality. Most of the short-term impacts of HWA induced mortality on ecosystem structure and function are localized and small; however, long-term impacts such as large pulses of woody debris and changes in species composition that impact structure and function could be significant. Using a decision analysis framework, land managers should begin to strategically implement land management decisions to address observed short-term impacts and plan and manage for projected longer-term impacts. In order to maintain ecosystem services in response to long-term impacts, restoration efforts may require novel approaches, such as the introduction of non-native species, facilitated movement of native species to new habitats (e.g., white pine), and aggressive management of existing species (e.g., *Rhododendron*) with mechanical removal, fire, or chemicals.

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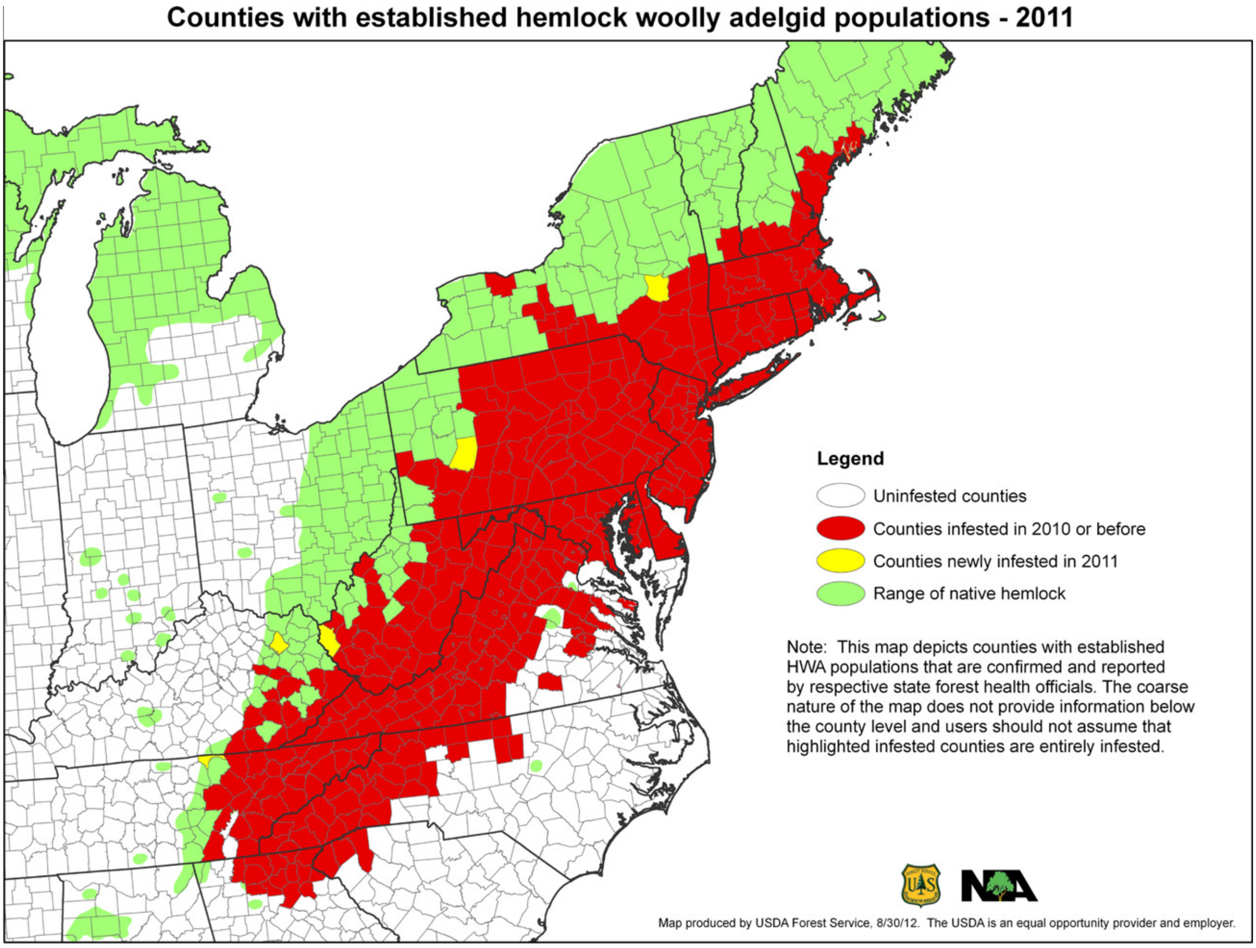

Fig. 1. Current distribution (2011) of hemlock woolly adelgid in the eastern US. Map provided by the US Forest Service, Northeastern Area State and Private Forestry.

1. Introduction

Hemlock woolly adelgid (*Adelges tsugae* Annad; hereafter referred to as HWA) is a non-native invasive pest that attacks and kills eastern hemlock (*Tsuga canadensis* (L.) Carrière) and Carolina hemlock (*Tsuga caroliniana* Engelm.). It was accidently introduced from Asia into the eastern US by the 1950s and has spread into 18 states (Fig. 1). In North America, HWA produces two asexual generations on hemlock each year, including a winter (sistens) and a spring (progrediens) generation (McClure, 1989). The tiny, first-instar nymphs (crawlers) of each generation disperse actively on their natal trees or passively to other trees by wind or attachment to birds and other animals. Crawlers insert their piercing/sucking mouthparts at the bases of hemlock needles and extract nutrients from the xylem ray parenchema cells (Young et al., 1995). The developing, sessile adelgids secrete a woolly, wax-like substance that eventually encompasses the insect and serves as an "ovisac" in which eggs are laid. Occasionally, a winged generation called the sexuparae develops simultaneously with the progrediens generation and migrates away from hemlock to establish a sexual generation on spruce (*Picea* spp.), but successful reproduction of HWA on spruce in North America has not been observed (McClure, 1989).

At present, HWA is severely impacting the health of eastern hemlock trees of all sizes and ages (Elliott and Vose, 2011) throughout the N.E. and mid-Atlantic region of the US, but especially in the southern Appalachian region, where HWA is particularly virulent (Lovett et al., 2006; Roberts et al., 2009; Nuckolls et al., 2009; Elliott and Vose, 2011). Efforts to identify variables that limit the rate of decline in infested trees have proven to be generally unsuccessful (Rentch et al., 2009), although some studies suggest that trees growing in mesic sites survive longer than those on drier or waterlogged sites (Orwig, 2002; Pontius et al., 2002). Once infested and left untreated, trees rarely recover (Pontius et al., 2006; Ford et al., 2012) and for many ecosystem processes, there are no functional differences between declining (i.e., those with significant crown loss) and dead trees (Nuckolls et al., 2009). While scientists and land managers continue to apply new and existing biological and chemical controls, large areas in the eastern US, including the southern Appalachian region, have already experienced extensive mortality.

Efforts to eradicate or control HWA with a combination of biological and chemical controls in the eastern US have expended tens of millions of dollars (Aukema et al., 2011). A driving force behind these control efforts is that hemlock is an iconic tree in the eastern US that serves important ecological roles. Although eastern hemlock comprises a small percentage of (~5% or less) of the total volume of tree species over most of the southern Appalachian region (Elliott and Vose, 2011; and unpublished data from the US Forest Service Forest Inventory and Analysis database), hemlock has been described as a "foundation species" (Ellison et al., 2005) due to its strong influence on ecosystem structure and function. For example, hemlocks are a naturally occurring and important evergreen species in near-stream areas (Narayanaraj et al., 2010) providing year-round critical habitat and cover for birds (Tingley et al., 2002) and other animals, and shading streams to maintain the cool water temperatures (Synder et al., 2002) required by trout and other aquatic organisms (Ross et al., 2003). Year-round hemlock foliage also imparts controls over microclimatic conditions and water, carbon, and nutrient cycling, especially during times of the year when deciduous species are dormant (e.g., late fall, winter, and early spring). Hemlock needles and wood decompose slowly (Elliott et al., 1993; Webster et al., 2012), resulting in a thick litter layer and a stable long-term source of coarse wood to stream habitats (Hedman et al., 1996) for fish and other aquatic species, and to the forest floor (Webster and Jenkins, 2005) habitats for salamanders and other wildlife. Hemlocks are also prized and valued for their visual beauty in both forest and urban settings (Holmes et al., 2010; Aukema et al., 2011).

As a result of the rapid spread and virulence of HWA in the southern Appalachians, land managers are asking important questions, including: (1) how can they optimize current control strategies and rapidly implement new ones? (2) how will the loss of hemlock impact the condition of southern Appalachian forests today and in the future?, (3) what management actions can be implemented to minimize impacts and restore forest health in areas impacted by HWA?, and (4) what is the optimal management framework for negotiating this episodic transition in the southern Appalachians? To begin to answer these questions, we synthesize the current state of the knowledge on HWA control, effects of hemlock mortality on ecosystem structure and function, and restoration challenges for eastern hemlock in the southern Appalachian region of the US Focusing specifically in the southern Appalachians is important because differences in climatic conditions, eastern hemlock phytosociology, and co-occurring vegetation shape HWA virulence, its effects on ecosystem structure and function, and restoration options in different ways than in the northeastern region. Finally, we develop a decision analysis framework for managing HWA that can also serve as a model for dealing with highly virulent pests in other forest ecosystems.

2. HWA monitoring and control

Hemlock woolly adelgid management in the southern Appalachians is part of a coordinated, multi-agency effort to reduce the spread and impact of this pest throughout the range of hemlock in the eastern US. Although management efforts for HWA were underway by the early 1990s, a formal HWA Initiative was developed in 2001 through the cooperation of the USDA Forest Service and Animal Plant Health Inspection Service, the National Association of State Foresters, and the National Plant Board. This multi-ownership coordinated approach is critical to address the diversity of forest ownership in the southern Appalachian region, where about 60% of the eastern hemlock occurs on private lands (unpublished data based on US Forest Service Forest Inventory and Analysis plots containing eastern hemlock).

A key component of HWA management is monitoring and predicting infestation rates. Management of HWA in the southern Appalachians faces unique challenges due to the comparatively rapid rate of HWA spread and hemlock mortality in this region. For example, Evans and Gregoire (2007) estimated a northward expansion rate (from Pennsylvania northward) of 8.1 km yr^{-1} and a southward expansion rate (from PA southward) of 15.6 km yr^{-1}. The primary limit to northward expansion rates is temperature, where extremely cold temperatures constrain HWA populations (Morin et al., 2009). As a result of this rapid southern expansion, HWA now occurs in nearly the entire hemlock range in the southern Appalachians (Fig. 1), and the few remaining un-infested areas (i.e., the extreme southern and western portions of the range in Kentucky, Tennessee, Alabama, and Georgia) are likely to become infested in the next few years.

HWA management in the southern Appalachians is focused on reducing HWA populations rather than complete eradication. Broadly, HWA management involves the integrated use of multiple approaches including chemical control (Cowles et al., 2006), biological control (Onken and Reardon, 2011), cultural treatments (Ward et al., 2004), host resistance (Montgomery, 2009), and host gene conservation (Jetton et al., 2008a,b). The extent to which these tactics are used in a given location depends on a number of factors including the management or ownership context, the degree to which the technology is developed, available funding, relative hemlock health and HWA population levels. To date, chemical and biological control have received the most management attention and funding, although all these tactics will likely play a role in ensuring the long term sustainability of *Tsuga* species in the eastern US.

2.1. Chemical control

Use of insecticides remains an important component of HWA management and control in the southern Appalachians. In many areas heavily impacted by the adelgid, insecticides have been the only way to retain a hemlock component in the forest or landscape. Large numbers of hemlock trees are treated annually in hemlock conservation areas, parks, campgrounds and other locations where high-value hemlocks occur on both public and private land and where trees are accessible. The most commonly used products are systemic insecticides such as imidacloprid and dinotefuran. Imidacloprid is often applied as a soil drench, soil injection, or stem injection, whereas dinotefuran can also be applied as a basal trunk spray. Dinotefuran is highly water soluble and has rapid efficacy, whereas imidacloprid typically has an extended residual effect of three or more years. Both insecticides have use restrictions around water or in areas with a high water table – a substantial limitation in the mesic southern Appalachians. Recent studies suggest that imidacloprid movement in soils in the southern Appalachians is limited (Knoepp et al., 2012) and it has only been detected in rare instances and at low concentrations in streams after soil application (Churchel et al., 2011). In some environmentally sensitive areas, high pressure sprays of insecticidal soaps or horticultural oils can be used instead of systemic insecticides, but these treatments have no extended efficacy and are difficult to apply to very tall trees. In general, insecticide use for hemlock is limited to single-tree applications, is associated with environmental concerns and limitations, and is relatively cost-, time- and labor-intensive. Such control tactics will remain an important component of HWA management in the South, being used on individual or small groups of trees, and across larger areas of forest in national forests and parks. However, due to rapid rates of hemlock mortality, as well as regulatory and budgetary constraints, its use is not practical for long term protection of large numbers of trees on a landscape scale.

2.2. Biological control

Biological control of HWA dates to the early 1990s and has focused on predator species collected from the adelgid's native range in East Asia and the Pacific Northwest of the United States (Onken and Reardon, 2011). The most widely released predator to date has been a lady beetle from Japan, *Sasjiscymnus tsugae* (Sasji and McClure), of which over 2 million have been released since 1995 at more than 400 sites from the southern Appalachians to Maine (Cheah, 2011). Although populations have established and spread at a number of sites, post-release recoveries of *S. tsugae* have been sporadic and usually at low numbers (Onken and Reardon, 2011). Recent recoveries of *S. tsugae* in the Great Smoky Mountains National Park were associated with the oldest release sites, suggesting that this predator may take 5–7 years or more to reach detectable levels in the landscape (Hakeem et al., 2010). If this is true, many hemlock stands in the southern Appalachians may become infested, decline, and die before *S. tsugae* populations could begin to have an impact. As noted in the following sections, this may already be occurring in some areas of the southern Appalachians.

Laricobius nigrinus Fender, an adelgid predator native to the Pacific Northwest, has been released in the southern Appalachians for biological control of HWA since 2003 and is becoming well established at numerous hemlock sites from the southern Appalachians to New England (Mausel et al., 2010, 2011). Establishment and reproduction of *L. nigrinus* at certain release areas in western North Carolina and elsewhere has been so successful that thousands of beetles from subsequent generations have been collected from these sites and redistributed to other hemlock forests in the eastern US. (Onken and Reardon, 2011; R. McDonald, Symbiont Biological Pest Management, pers. comm. 2012). *L. nigrinus* has suppressed HWA populations in field studies in Virginia (Mausel et al., 2008) and research aimed at quantitatively determining the impact of *L. nigrinus* on hemlock health is ongoing. A related species from the native range of HWA in Japan, *Laricobius osakensis* Shiyake and Montgomery, has been approved for use as a biological control agent in the US. (Lamb et al., 2011) and releases of this additional winter predator in the southern Appalachians and elsewhere are expected in the near future. One unexpected result of releasing *L. nigrinus* in the eastern US is that it has subsequently interbred and hybridized with *Laricobius rubidus* LeConte, the only congener endemic to eastern North America and a common predator of pine bark adelgid (*Pineus strobi* (Hartig)) on eastern white pine (*Pinus strobus* L.). The potential non-target effects of this hybridization are still uncertain, but it may result in a mosaic hybrid zone where the relative abundance of, *L. nigrinus*, *L. rubidus*, and their hybrids vary depending on forest habitat conditions (e.g., relative abundance of hemlock and white pine) and the establishment and dispersal patterns of *L. nigrinus* (Havill et al., 2012).

Despite the promise shown by *Laricobius* spp. for control of HWA, the predatory stages of these beetles (adults and larvae) are inactive by late spring and do not feed on adults of the early summer HWA generation (progrediens). Thus, establishment or use of an effective late spring or early summer natural enemy would complement the role of *Laricobius* spp. in reducing HWA populations. Additional species under consideration for biological control of HWA include a lady beetle from the Pacific Northwest (*Scymnus (Pullus) coniferarum* (Crotch)), and silver flies in the family Chamaemyiidae (Montgomery et al., 2011; Ross et al., 2011). Furthermore, aerial spray application of an insect-killing fungus (*Lecanicillium muscarium* R. Zare & W. Gams) combined with a fungal enhancer has recently been pilot tested against HWA at a southern Appalachian site in eastern Tennessee. Preliminary results suggest that this treatment reduces HWA population growth relative to untreated plots (Costa, 2011).

Successful biological control of HWA will likely require a suite of natural enemies whose combined effect is sufficient to regulate HWA populations in a way that no single agent or tactic could do in isolation. With the fast pace of HWA expansion and rapid hemlock mortality in the southern Appalachians, biological control efforts will very quickly need to become more successful over larger areas to prevent further hemlock mortality.

2.3. Host resistance

Carolina and eastern hemlocks lack resistance to HWA (Bentz et al., 2008; Montgomery, 2009), while hemlocks from western North America and Asia exhibit varying levels of resistance. The general consensus suggests that Chinese hemlock (*T. chinensis*, native to mainland China) and northern Japanese hemlock (*T. diversifolia*, native to northern Japan) are most resistant with the other hemlock species being slightly- to moderately-less resistant. However, caveats exist, in that differing HWA strains or environmental factors can affect these results. For example, western hemlock (*T. heterophylla*, native to western North America) and eastern hemlock are typically considered moderately resistant and highly susceptible, respectively, however they can exhibit differential responses to HWA in each other's native environment— western hemlock can support high densities of HWA in eastern North America and eastern hemlock can exhibit more resistance to HWA than western hemlock in western North America (Montgomery and Gottschalk, 2008). Furthermore, the potential for HWA adapting to colder environments, even without a sexual cycle (McClure, 1996), suggests the potential for adaptation to hosts with varying levels of resistance (Butin et al., 2005).

Studies of HWA resistance demonstrate the presence of both antixenosis (reduced host preference) and antibiosis (reduced insect performance) (Montgomery, 2009). Tolerance (a third component of resistance) has not been systematically explored, although some reports suggest southern Japanese hemlock (*T. sieboldii*, native to southern Japan and the same host species that the HWA of eastern North American originates from (Havill et al., 2006)) may exhibit tolerance to HWA (Montgomery, 2009). In addition various anecdotal reports indicate that some infested Carolina and eastern hemlocks in the wild live longer than others, suggesting the possibility of genetic variation within these species for resistance to HWA.

Terpenes and terpenoids are typically associated with pest resistance properties in plants and especially the conifers. Studies of the foliar volatile terpenoids of hemlocks show that the most, least and intermediate resistant species group the same (with the exception of mountain hemlock (*T. mertensiana*, native to western North Americawhich groups alone), suggesting an important role of these compounds in resistance/susceptibility to HWA (Lagalante and Montgomery, 2003). Chemical analyses of 13 clonal cultivars of eastern hemlock indicated that some cultivars vary enough in quantities of some terpenoids to suggest that they may contain a level of resistance (Lagalante et al., 2007). Such a screening of a large and diverse collection of eastern hemlock followed by standardized testing for HWA resistance should provide definitive information on these relationships including the presence and magnitude of genetic variation in resistance. Finally the highly abundant iso-bornyl acetate in eastern hemlock and in the equally susceptible, yet phylogenetically, unrelated Carolina hemlock are likely indicative of susceptibility to piercing/sucking insects such as HWA and resistance to defoliators such as hemlock looper (*Lambdina fiscellaria*) (Lagalante et al., 2007). Apparently the evolution of Carolina and eastern hemlocks in the absence of HWA has led to these foliar chemical profiles that offer a measure of defense against chewing insects and none against the sucking/piercing insects (Lagalante et al., 2007). In addition, temporal and spatial studies of foliar terpenoids suggest that the HWA has evolved a mechanism, diapause, to avoid feeding during foliar growth (early- and mid-summer) when these chemical compounds are in flux (Lagalante et al., 2006).

Studies on the foliar chemical contents of various hemlock species have shown potentially important differences among resistant and susceptible species (Pontius et al., 2006). In particular, resistant species show lower nitrogen (N) and potassium (K) and higher phosphorus (P) and calcium (Ca) compared to susceptible species. In addition, HWA densities (sisten generation) on experimentally colonized plots of hemlocks were higher on trees with lower P and higher K which is consistent with the non-colonized species comparisons. The results along with regional monitoring data of eastern hemlocks suggest that higher N and K enhance hemlock palatability increasing HWA density levels and tree decline, while higher P and Ca levels provide an opposite effect. Whether these foliar macronutrient difference cause HWA density difference or are in response to HWA herbivory is unknown and suggested for further study (Pontius et al., 2002).

Given the lack of resistance in the hemlocks of eastern North America, geneticists have been investigating interspecies hybridization as a means to generate genetic variation for research and breeding purposes (Bentz et al., 2002). Consistent with the phylogenetic analyses based on nuclear ribosomal DNA (rDNA) and chloroplast DNA (cpDNA) sequences (Havill et al., 2008), Chinese hemlock is cross-compatible with Carolina hemlock, but not eastern hemlock, while eastern hemlock was found to be cross-incompatible with all tested hemlocks (Bentz et al., 2002; Pooler et al., 2002). The cross-incompatibility of any species to eastern hemlock significantly limits the potential for inter-species breeding as a tool for developing resistance through backcross breeding as is being conducted with American chestnut (Hebard, 2006). However, the possibility for such a program for Carolina hemlock is promising given its cross-compatibility with Chinese hemlock and the relative ease and accuracy of HWA resistance screening (Bentz et al., 2008; Montgomery, 2009). Resistance levels in the hybrid crosses are intermediate to slightly higher than intermediate suggesting some level of dominance genetic effects (Montgomery, 2009). Interestingly the Carolina hemlock with Chinese hemlock cross can be made in both directions (either species serving as female or male), however the hybrids of the crosses with Chinese hemlock as the female parent showed significantly higher resistance than those with Carolina hemlock as the female parent (Montgomery, 2009). Advanced generation crosses are being made and tested to further study the genetics of resistance as well as the potential for developing a multi-generation backcross breeding program (R.T. Olsen, personal communication). In addition extensive seed collections of Carolina and eastern hemlocks are being made in effort to conserve the genetic diversity in these species for use in ongoing and future breeding programs (Jetton et al., 2008a,b; Potter et al., 2011). Simultaneously analyzing resistance, foliar chemistry and the interacting genomes (e.g., Smith et al., 2010) of these materials should allow for substantial gains in understanding of this host-pest interaction and lead to new insights for developing host resistance for deployment in eastern North America.

3. Effects of hemlock mortality on southern Appalachian forests

With the rapid spread and virulence of HWA in the southern Appalachians, land managers need to understand the impacts of hemlock mortality in order to develop restoration strategies and prioritize control efforts. Investment in HWA control and prevention of widespread infestation has been a priority for land managers. For example in 2011, the US Forest Service invested more than 2 million dollars in direct control and research to improve control strategies in the southern region (Wes Nettleton, personal communication, USDA Forest Service, Forest Health Protection). To our knowledge, no comparable coordinated investments have been undertaken to understand effects or develop and test restoration options. Widespread hemlock mortality across its southern range suggests that research efforts quantifying effects will become even more important for developing management options to deal with those effects in the coming years.

3.1. Local scale rates of HWA spread and hemlock mortality

Most eastern hemlock trees in the southern Appalachians are located in near-stream areas (Roberts et al., 2009; Narayanaraj et al., 2010). As a result, eastern hemlock decline and mortality will disproportionately impact riparian zones and nearby streams more than upland areas where it is less prevalent. Once HWA invades a localized area in the southern Appalachians, the rate of HWA spread within watersheds can be extremely rapid. For example, HWA was first detected at the Coweeta Hydrologic Laboratory, a 1600 ha forested watershed in western NC, in 2003. In response, HWA presence/absence and hemlock canopy condition were intensively monitored on a network of long-term permanent plots within the Coweeta basin (Elliott and Vose, 2011 (neither biological nor chemical control efforts were implemented in this portion of the Coweeta basin). At the initiation of the study, HWA was not present in any of the study plots; however, within two years, HWA was present in all study plots and, within four years, average crown loss exceeded 80% (Elliott and Vose, 2011) (Fig. 2). Hemlock woolly adelgid kills hemlock trees considerably faster in the southern Appalachian region than in the northeastern US. For example, Ford et al. (2012), studying hemlock in North Carolina, found that seven years after initial HWA infestation, >85% of hemlock trees of all size classes were dead. Studies in the northeastern US suggest that comparable levels of mortality (e.g., 50–80%) may not be observed until 15–17 years after infestation (Small et al., 2005; Lewis et al., 2008) Rapid mortality and rates of spread are hypothesized to be related to warm winters that can sustain high HWA populations (Paradis et al., 2008; Morin et al., 2009; Trotter and Shields, 2009), as temperatures required to limit HWA populations (i.e., <−25 °C) are rarely experienced in the southern Appalachians (Laseter et al., 2012; Ford et al., 2012).

3.2. Immediate impacts

The most immediate impacts of HWA include changes in microenvironmental conditions in the understory and streams (e.g., light, temperature), litterfall from declining hemlocks, and growth of hemlock and co-occurring trees and shrubs. These immediate impacts may be transient or sustained, but regardless, they influence additional short and long-term dynamics discussed below. HWA infested trees display progressive needle loss and branch dieback (McClure and Cheah, 1999; Cobb et al., 2006). As a result, the contribution of hemlock leaf and branch litter to the forest floor and streams increases initially (Nuckolls et al., 2009; Knoepp et al., 2011; Siderhurst et al., 2010; Webster et al., 2012) and then declines as foliage production ceases on dead and severely impacted trees. As the decay of standing dead hemlocks proceeds over time, the amount of branch litter and woody debris increases significantly (Siderhurst et al., 2010). This loss of foliage results in an increase in light levels in the lower canopy and forest floor (Ford et al., 2012); however, in areas where dead and declining trees are still standing, light levels increase primarily in the winter months. These light response patterns have important implications in the southern Appalachians, especially with regards to how increased light levels influence the amount and timing of growth responses of co-occurring species.

3.3. Short-term impacts on terrestrial ecosystem structure and function

Short-term (1–5 years) impacts of hemlock mortality on forest ecosystem structure and function appear to be relatively minor in the southern Appalachians, although possible exceptions could be the short-term impacts on streamflow and species composition. Tree-level transpiration measurements scaled to the watershed suggests that annual streamflow may increase by as much as 10% annually and 30% in the spring due to reduced transpiration in dead and declining hemlocks (Ford and Vose, 2007); however, to our knowledge, no studies have documented changes in streamflow at the watershed scale (e.g., Roberts et al., 2009). It is also likely that the loss of evergreen cover may impact birds (Tingley

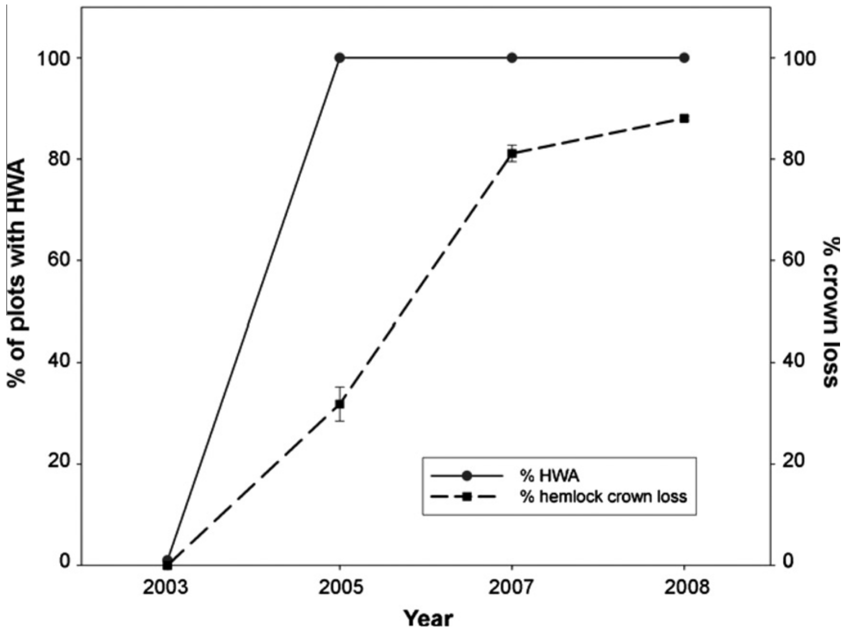

Fig. 2. Progression of hemlock infestation and crown loss within a 1600 ha watershed in the southern Appalachians (see Elliott and Vose, 2011 for description of methods).

et al., 2002) and other terrestrial species that rely on this cover; however, research on these effects is limited in the southern Appalachians.

The most apparent short-term effects are the impacts on diameter growth and species composition. As HWA infested hemlock trees lose foliage and the canopy declines, their diameter growth rate declines rapidly (Rentch et al., 2009; Ford et al., 2012), with a complete cessation of diameter growth three years after infestation (Ford et al., 2012). Loss of photosynthetic capacity (i.e., reduced leaf area) is the most obvious explanatory variable for this growth decline. Diameter growth of co-occurring hardwood trees (primarily red maple (*Acer rubrum*), sweet birch (*Betula lenta*), and yellow poplar (*Liriodendron tulipifera*)) increased by 25% to 30% in the first two years after infestation, but smaller responses (i.e., 10% increase in diameter growth) were observed thereafter as canopy gaps created by hemlock mortality were refilled (Ford et al., 2012). Where *Rhododendron* was present in the mid- and understory, diameter growth rate increased by 17%. Unlike the response of deciduous overstory trees, *R. maximum* growth is sustained (Ford et al., 2012) because it's evergreen leaves can take advantage of greater light availability in the fall, winter, and spring (Russell et al., 2009). As hemlock dies and is not regenerated, it is lost from the community. In contrast, a 3-fold increase in tree seedlings comprised of red maple, sweet birch, yellow poplar, sourwood (*Oxyendrum arboreum*), scarlet oak (*Quercus coccinea*), and northern read oak (*Quercus rubra*) was observed, but only in areas where *Rhododendron* was absent (Ford et al., 2012). While an increase in seedling density is not likely to significantly alter structural or functional attributes in the short-term, shifting species compositions may have important long-term implications (discussed in Section 3.5).

Ecosystem carbon accumulation exhibited a significant decline initially (Nuckolls et al., 2009), but then recovered as surrounding trees increased diameter (or basal area) growth rates due to reduced competition associated with hemlock loss (Ford et al., 2012). Nutrient pools, cycling rates, and stream chemistry are generally not affected (Roberts et al., 2009; Knoepp et al., 2011), with the possible exception of an increase in phosphorus availability in high elevation hemlock stands (Block et al., 2012). These results contrast with what has been observed with HWA infestations in nearly pure stands of eastern hemlock in New England, where nutrient cycling (particularly N) processes respond rapidly (Orwig et al., 2008). This slow response in carbon and nutrient cycling in the southern Appalachians is likely a result of several factors, but it may be most influenced by the presence of co-occurring trees and shrubs that continue to regulate ecological processes.

3.4. Short-term impacts on aquatic ecosystems

Impacts on aquatic ecosystems may take decades to be fully realized and will differ through time. For short-term responses, as hemlock declines and leaf area is reduced, stream light levels may increase (Siderhurst et al., 2010; Webster et al., 2012); however, the magnitude and timing of light level effects are influenced by the presence of *Rhododendron,* which mutes the light response in all seasons (Roberts et al., 2009). Effects on stream temperature are more variable and inconsistent. For example, Webster et al. (2012) found that stream temperature was negatively related to hemlock foliage mass at the beginning of HWA infestation when foliage mass was still plentiful; i.e., the greater the hemlock foliage mass, the lower the stream temperature. However, there were no significant differences in stream temperature over time, even though HWA had begun to substantially reduce foliage mass over the measurement period. Hence, consistent with the results reported in Roberts et al. (2009) and Siderhurst et al. (2010), linking HWA impacts with changes in stream temperature is confounded by a variety of factors, including the influence of groundwater and the type (e.g., evergreen vs. hardwood) and response of co-occurring vegetation.

3.5. Long-term impacts

Longer-term effects (5–50 years) are likely to be much more substantial. Canopy decline and the subsequent hemlock mortality will increase light levels and accelerate growth of other trees and shrubs, but also has the potential to warm streams, especially in the winter months. For example, four years after initial HWA infestation, light levels were increased by 1.5-fold in the winter (Ford et al., 2012). Furthermore, as the standing dead hemlock trees decompose and begin to shed branches and fall over, large amounts of wood will be added to near stream areas and streams. While downed hemlock wood is an important structural attribute on the forest floor (Webster and Jenkins, 2005) and in streams (Hedman et al., 1996), a large pulse of wood may have some undesirable impacts (discussed in Section 4.1).

Long-term impacts on forest ecosystem structure and function will ultimately be determined by the response of co-occurring trees and shrubs and new species that invade the disturbed areas. A key controlling factor is the presence of *Rhododendron*. In areas where *Rhododendron* cover is substantial, regeneration of trees or other shrubs to fill-in the gaps created by hemlock mortality will be limited (Clinton and Vose, 1996; Hilles Ris Lambers and Clark, 2003; Wurzburger and Hendrick, 2007). Some of these limitations on regeneration may be minimized if the standing dead hemlock trees create canopy gaps as they fall (Beckage et al., 2000). However, a recent study suggests that *Rhododendron* distribution also expanded in response to logging and chestnut blight and a similar response is possible with hemlock mortality (Elliott and Vose, 2012). If hemlock is the predominant overstory species with a *Rhododendron* shrub layer underneath, then the structure of the impacted area may shift to a shrub dominant ecosystem (Elliott and Vose, 2012). In areas where *Rhododendron* is sparse, growth response data, seedling recruitment rates, and modeling suggests that hemlock will be replaced by a mixture of maple, birch, beech, and oaks (Krapfl et al., 2011; Ford et al., 2012). These species provide very different ecological functions (e.g., water, carbon, and nutrient cycling processes; microclimate regulation; wildlife habitat, etc.) than hemlock and long-term changes could be substantial. For example, in areas where deciduous hardwood trees replace hemlock, nutrient cycling rates and water use would be expected to be much higher (Knoepp et al., 2011; Ford and Vose, 2007; Brantley et al., submitted for publication), whereas in areas where sites are dominated by *Rhododendron*, nutrient cycling rates and water use are expected to be much lower (Brantley et al., submitted for publication). With our current state of knowledge and the complexity of the inter-relationships among variables, it is difficult to predict whether these changes will have an overall negative, neutral, or positive effect, and the effects may vary depending on what parameters are being evaluated and how they interact with climate and other variables. For example, during dry years reduced water use by *Rhododendron* may help offset drought impacts on soil moisture, whereas in wet years, soils may be more frequently saturated and anaerobic.

4. Management options for restoring impacted stands

Land managers are now faced with developing management strategies and activities to restore desired structural and functional attributes in stands with significant levels of mortality. It is important to note that the decision to "do nothing" will have consequences for the long-term structure and function of southern Appalachian ecosystems and hence, deciding to forgo restoration activities is as important as decision to implement restoration activities. Although the scope and magnitude of the task is daunting, research suggesting that short-term effects on ecosystem structure and function are relatively minor implies that land managers will have time to plan and implement restoration and recovery activities over the next several years. Management options will be guided by the research results discussed above, but management options will also likely involve novel approaches that will require additional research, monitoring, and adaptive management approaches.

4.1. Managing large inputs of wood

As dead hemlocks begin to decompose and fall, large inputs of wood to streams and hiking trails could have immediate negative impacts on recreational quality as well as human safety. Coarse wood is generally recognized as having a positive aspect in most terrestrial and stream ecosystems (Harmon et al., 1986); however, in areas where hemlock is dominant (i.e., in some cases comprising >50% of the basal area), a large pulse of coarse wood could have negative impacts. Some of these impacts could be minimized by identifying areas with the greatest risk, and using directional felling. In other cases, if large amounts of wood have already been deposited in the streams, management may be required to minimize impacts on stream stability, culvert functioning, etc. This could include removing hemlock wood that has fallen into the stream.

4.2. Managing species composition

The loss of evergreen cover and other ecological functions provided by eastern hemlock will not likely recover without active management. HWA impacts all age classes of hemlock and widespread mortality (Elliott and Vose, 2011) will limit opportunities for large-scale "natural recovery" from surviving hemlocks for decades and perhaps, even centuries. Rapid recovery will likely require more aggressive strategies, such as re-planting areas with hemlock seedlings resistant to HWA (i.e., through breeding, genetically engineered resistance, or planting non-native western or Chinese hemlock) are possible options (Merkel et al., 2007; Jonas et al., 2012); however, in many areas in the southern Appalachians, these strategies will also require the development of new silvicultural prescriptions that control competition from other species, especially *Rhododendron*. While *Rhododendron* provides riparian and near stream evergreen cover that could help maintain cooler water temperatures, it's inhibition of the regeneration of other overstory species (Clinton and Vose, 1996; Hilles Ris Lambers and Clark, 2003) is a key factor shaping future forest composition. Public acceptance of introducing non-native species and chemical controls of *Rhododendron* could limit these restoration options on public lands. Alternatively, land managers can help facilitate the transition to other species (e.g., though selective cutting, planting, etc.) that have at least some of the attributes and ecological functions previously provided by hemlock. For example, eastern white pine (*P. strobus*) is among the most shade tolerant pines in the southern Appalachians and could replace some of the evergreen cover lost by hemlock mortality. However, white pine wood decomposes quickly and would not provide stable supplies of wood to the forest floor and streams.

5. Decision analysis framework for HWA management

Decisions regarding management choices in response to HWA require addressing the potentially irreversible consequences of action or inaction, the uncertainty regarding treatment effects, and the public-good nature of many benefits. These features are not unique to hemlock but rather apply to a larger set of problems now faced by forest land managers, where native ecosystems face substantial restructuring by highly virulent nonnative invasive species.[1]

Classical decision analysis derives from a consideration of the costs, benefits, and probabilistic statements regarding the outcomes of various treatment options. Because the landscape position of hemlock forests in ecological as well as social dimensions affects all three elements, decision rules do not easily resolve to universal statements. For example, we have used the term "iconic"

[1] Other examples include the mortality of Ash (*Fraxinus sp.*) caused by the Emerald Ash Borer (*Agrilus planipennis* Fairmaire) in the Northeastern and Midwestern United States and the rapid extirpation of Red Bay (*Persea borbonia*) from lowland forests in the southeastern United States by Laurel Wilt Disease (caused by a fungus, *Raffaelea lauricola*).

Table 1
Decision options for managing HWA-Hemlock in the southern Appalachians.

Decisions	Outcomes	Implications
1a. Intensify detection monitoring	Increased probability of early detection	Enhanced control opportunities
1b. Casual monitoring	Lowered probability of early detection	Avoided monitoring costs
2a. Apply control treatments	Reduced probability of mortality	Chemical: must be ongoing to avoid mortality, per year costs remain relatively fixed, efficacy on individual trees is very good (e.g., 95%) when applied appropriately, impractical to treat large number of trees Biological: treatment is not ongoing once agents establish and become self-perpetuating, high initial costs incurred in development/delivery but per year costs decrease over time after establishment, efficacy is less certain but some agents showing promise; more practical than chemical on large scales Defers restoration activities and allows for development of new knowledge
2b. Forgo control treatments	Rapid mortality (3–10 years following infestation)	Sets time table of trajectory of ecological changes. May impose constraints on other management choices due to rapid mortality and natural replacement
3a. Alter species composition using native species	Replaces some ecosystem services (e.g., shading)	Silvicultural options are not well defined. Efficacy is challenged by competition with *Rhododendron*
3b. Alter species composition using nonnative hemlocks	Replaces a broader range of ecosystem services	Public acceptance on introducing nonnative species in public lands uncertain
3c. Forgo species management	Species composition determined by site conditions	May result in new forest compositions that may have long-term undesirable implications for structure and function but avoids high costs of species replacement
4a. Post-mortality sanitation	Reduces short run impacts on aquatic systems. Protects recreationists and reduces aesthetic impacts	Reduces uncertainty about long-term impacts of standing dead hemlock, but may initiate a trajectory of change
4b. Forgo sanitation treatments	Short run (5–15 years) impacts on aquatic systems and recreation values	Increases uncertainty about long-term impacts of standing dead hemlock, but allows for a "wait and see" approach

to describe eastern hemlock where the species represents a place or system to a large number of people. It's likely that iconic values are attached to recreation destinations (e.g., the Joyce Kilmer Wilderness Area, the Great Smoky Mountains National Park) or to residential areas with large densities of hemlocks. In addition, we have used the term "keystone species" or "foundation species" to describe hemlocks in cases where it has a disproportionate influence on its ecological community, most notably the headwaters of high elevation streams in the southern Appalachians. These two terms imply very different sets of values flowing from hemlock forests and therefore different benefits accruing to any type of management choice. A critical challenge in this and any analysis of an invasive species is assigning value flows to the retention or loss of an individual species in a complex forest ecosystem. It is also important to emphasize that outcomes may differ by region and that the trajectory of ecosystem change depends critically on the species composition of the surrounding forest. For example, in the southern Appalachians, the presence or absence of a *Rhododendron* understory holds critical sway over the outcomes for associated riparian and aquatic communities.

While managers likely face a continuum of treatment options, we condense them into the set of four decisions described in Table 1. First, natural resource agencies and landowners may choose to accelerate detection and condition monitoring of hemlock forests throughout the region. The benefits could accrue to early detection of infestation and more timely application of control treatments. The second type of decision is whether or not to apply control treatments once a forest is infested. The decision to control would depend on the values at risk from hemlock mortality but also on the costs and likely success rate of the treatment activities. The third type of decision is whether and how to restore degraded areas after the loss of hemlock trees. Here, the manager may deploy other native species (e.g., white pine) or nonnative or interspecific hybrid hemlock species with resistance to the HWA. It's likely that the nonnative or hybrid hemlocks offer the greatest span of "hemlock-like" structural and functional attributes, but may be unacceptable to large segments of society who object to introducing another non-native species into southern Appalachian forests. Post mortality treatments may also include stand sanitation activities intended to remove woody inputs to streams and to reduce safety hazards and mitigate losses of aesthetic services in a subset of important locations.

Choices regarding any given forest will depend on a thorough accounting of the values at risk from the death of hemlock trees, the condition of the surrounding landscape, and the costs of various options. Decisions regarding hemlock will likely be influenced by competing demands for funds and the binding constraints defined by agency/landowner budgets. Opportunity costs defined by other demands such as wildfire protection, recreation, water protection, and other forest pests, may ultimately influence choices regarding any individual forest pest problem.

Acknowledging this decision context, we offer the following set of propositions regarding effective management of HWA in the southern Appalachians:

Proposition 1 - *The costs and environmental constraints of controlling HWA with chemical treatments, coupled with uncertain success of some treatment options (e.g., biological control), will limit successful control efforts to a small subset of infested stands in the southern Appalachians. Given current technologies and effectiveness, chemical controls must be continued on a 3–5 year cycle. If biological control efforts prove successful in the near term (i.e., before most of the hemlock trees in the southern Appalachians have been killed), then this proposition will be invalid; however, long-term and large-scale effectiveness of biological controls are uncertain.*

Proposition 2 - *Optimal treatment strategies may prescribe no control in many areas of the southern Appalachians. This is a corollary to proposition 1. In many areas, mortality has already occurred. In others, high costs or remoteness, low treatment efficacy, and low values at risk preclude application of controls.*

Proposition 3 - *In some specific situations, direct management intervention will provide the best protection of key structural and functional attributes. Hemlocks provision of year-round evergreen cover and structural elements of aquatic ecosystems define a key impact of HWA. These attributes may be best restored by deliberate replacement of shade producing trees as mortality proceeds. We might even imagine cases where accelerating the mortality and replacement of hemlocks with target species could be optimal—providing more effective replacement (i.e., in advance of natural competition) under safer working conditions.*

Proposition 4 - *Setting treatment priorities will influence ultimate effectiveness of programs. Because the effectiveness of widespread treatment has not yet been demonstrated in the southern Appalachians, prioritization of areas based on ecological benefits and iconic values is imperative. Focus needs to be placed on derivative values rather than on the loss of trees per se. Because a decision to treat has long term implications for budget allocations, treatment priorities should span both currently infested and non-infested forests.*

6. Conclusions and management implications

Despite considerable investment in control efforts, large areas of eastern hemlock have already been impacted by HWA in the southern Appalachians and barring a breakthrough in control efforts or an external event, eastern and Carolina hemlock may suffer a similar fate as the American chestnut. Fortunately, most of the short-term impacts of HWA induced mortality appear to be localized and relatively minor and land managers can begin to strategically implement land management decisions to address observed short-term impacts on ecosystem structure and function and plan and manage for projected longer-term impacts.

A continuation of efforts to control HWA is expected and supported by the public, especially for an iconic species such as eastern hemlock. Furthermore, research continues on improved control measures and identification and development of genetic resistance. New discoveries and proliferation of biological control agents may ultimately lead to effective HWA control and options for restoration with native eastern hemlock. However, the continued high rate of hemlock mortality over large areas of the southern Appalachians raises important questions about how scientists, land managers, and forest health specialists should deal with this and other exotic pests and pathogens in the future, as interactions with climate change and other global changes alter the virulence of pest and pathogens, as well as the vulnerability of their hosts (Dukes et al., 2009). For example, when do public land managers begin to move away from active control efforts, and how do they communicate the rationale for these decisions to the public? And, how do they develop and communicate a balanced strategy that recognizes and quantifies the probability of success, as well as costs and benefits of control efforts? This consideration of the balance between control and/or restoration may leave the public and land managers better prepared for novel and perhaps aggressive restoration efforts.

The degree to which we may already be at a leverage point where the costs and benefits of controlling virulent exotic pests over large scales requires a "trade-off" based approach (comparable to the decision analysis described in Table 1) is not known. However, the loss of eastern hemlock in the southern Appalachians will permanently alter the structure and function of southern Appalachian ecosystems. Land managers will be challenged to manage these "novel ecosystems" in ways that may be very different than in the past (Hobbs et al., 2011). For example, in order to maintain ecosystem services, restoration efforts may require equally novel approaches, such as the introduction of non-native or hybridized hemlock species, facilitated movement of native species to new habitats (e.g., white pine), and aggressive management of existing species (e.g., *Rhododendron*) with mechanical removal, fire, or chemicals. Engineering ecosystem structures in such ways will be challenging because science to support restoration efforts has been limited and is mostly speculative based on intensive studies of short-term impacts, and how these impacts interact with current forest conditions unique to the region (e.g., the presence or absence of *Rhododendron*).

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