Journal of Integrated Pest Management, (2018) 9(1): 27; 1–16
doi: 10.1093/jipm/pmy018
Profile

OXFORD

Hemlock Woolly Adelgid (Hemiptera: Adelgidae): A Non-Native Pest of Hemlocks in Eastern North America

S. Limbu,[1] M. A. Keena,[2,3] and M. C. Whitmore[1]

[1]Department of Natural Resources, Cornell University, Morrison Hall, Ithaca, NY 14850, [2]U.S. Forest Service, Northern Research Station, 51 Mill Pond Road, Hamden, CT 06514, and [3]Corresponding author, e-mail: melody.keena@usda.gov

Disclaimer: The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

Subject Editor: Dawn Gouge

Received 19 September 2018; Editorial decision 21 November 2018

Abstract

Hemlock woolly adelgid, *Adelges tsugae* Annand, is an invasive insect species in eastern North America that was accidentally introduced from southern Japan. It is the single most important pest of hemlocks in eastern North America and has a severe impact on the two susceptible species: eastern hemlock, *Tsuga canadensis* (L.) Carriere (Pinales: Pinaceae) and Carolina hemlock, *Tsuga caroliniana* Engelmann (Pinales: Pinaceae). Since the first report of hemlock woolly adelgid in Virginia in 1951, it has been slowly but steadily increasing its range. Recent establishments outside the contiguous range in Michigan and Nova Scotia have also occurred. At the stand level, hemlock trees are being replaced by hardwood trees in eastern North America, impacting some critical ecosystem processes. Several institutions are actively researching ways to protect the existing hemlock stands from further damage and to restore the ecosystems impacted by their loss. Although several control options for hemlock woolly adelgid have been developed, none are completely effective on their own, so a combination of all available control strategies is being used in an effort to save the existing hemlock stands. High-value hemlocks are being protected using chemicals, while a suite of predators is being released in forested areas. However, biological control has not provided immediate protection for heavily infested trees, so options for restoring hemlocks (hybrids with Asian species and punitively resistant stock) and finding viable replacements are being evaluated.

Key words: *Adelges tsugae*, hemlock, *Tsuga* spp., invasive species

The hemlock woolly adelgid, *Adelges tsugae* Annand, is a tiny aphid-like insect that covers itself with a waxy wool (Fig. 1). It is native to eastern Asia and is thought to have colonized western North America about 20,000 y ago, so it is also considered native to that region (Havill et al. 2016). In both Asia and western North America, this insect is not normally considered a pest and only occasionally will it build to high enough numbers to impact ornamental hemlocks (Chrystal 1916, McClure 1987). A single clone of *A. tsugae* that originated in southern Japan is thought to be the source of the populations in eastern North America (Havill et al. 2006), where it is threatening the health of two hemlock species: eastern hemlock, *Tsuga canadensis* (L.) Carriere (Pinales: Pinaceae), and Carolina hemlock, *Tsuga caroliniana* Engelmann (Pinales: Pinaceae). It was first reported in Richmond, Virginia on ornamental hemlock trees in 1951 (Gouger 1971) and now occurs in 20 eastern states in the United States and in Nova Scotia, Canada (Canadian Food Inspection Agency [CFIA] 2017a, U.S. Department of Agriculture [USDA] 2017).

Although hemlocks are rarely considered valuable timber species, their loss can have a major impact on the ecological, aesthetic, and economic value of forested and residential areas. Hemlock forests provide a unique understory microclimate that supports distinct groups of terrestrial and aquatic organisms. Several studies have demonstrated negative impacts of hemlock woolly adelgid infestation on hemlock-associated organisms (Tingley et al. 2002, Ross et al. 2003). Moreover, infested hemlock stands reduce the aesthetic value of state parks and residential areas, which in turn impacts recreational activities. Additionally, dead or unhealthy hemlock trees in and around residential areas have resulted in a reduction in property values (Li et al. 2014).

Taxonomy

There are 65 species worldwide in the family Adelgidae, and the hemlock woolly adelgid is the only one that uses hemlocks as a secondary host (Favret et al. 2015). Binazzi (1984) provides a key to Adelgidae, and the original description of the hemlock woolly adelgid can be found

Published by Oxford University Press on behalf of Entomological Society of America 2018.

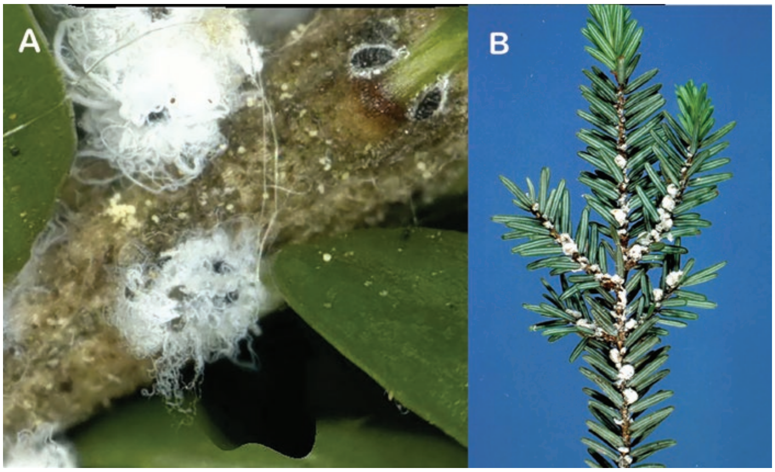

Fig. 1. (A) Hemlock woolly adelgid adults covered with wax and two aestivating sistentes first instars (upper right corner). (B) Hemlock branch with many hemlock woolly adelgids on it. (Photos by M. A. Keena and M. E. Montgomery)

in Annand (1924, 1928). Molecular work has shown that what is called *A. tsugae* worldwide is made up of eight endemic lineages (western North America, northern Japan, Ulleung Island [Korea], Taiwan, and China), which may represent more than one taxa that split at either the species or subspecies level (Havill et al. 2016). The introduced hemlock woolly adelgid in eastern North America includes one COI haplotype and a single microsatellite clone, which matches samples found in southern Japan on *Tsuga sieboldii* Carrière (Havill et al. 2016).

Hemlock woolly adelgid is sometimes incorrectly called an "aphid." For instance, in France it is called "*puceron lanigère de la pruche*" (hemlock aphid) and in Germany "*Laus Hemlockstannen*" (hemlock louse) or "*Tannenlaus Hemlocks*" (hemlock aphid; Centre for Agriculture and Biosciences International [CABI] 2018). In Chinese, it is called "*tiě shān qiú yá*" (hemlock ball aphid) and in Japanese, it is called "*harimori hime kasaaburamushi*" (aphids that produce galls like small cones on tiger spruce; Fig. 2).

Fig. 2. Hemlock woolly adelgid gall on tiger-tail spruce in Japan. (Photo by S. Shiyake)

Description of Life Stages

Adults

In eastern North America, hemlock woolly adelgid goes through two wingless parthenogenic (females that produce females without a male present) forms (often called the sistentes and progredientes) and produces a winged sexupara (female that would seek out the primary host and produce a sexual generation) on hemlock (Fig. 3). The primary distinction between the two parthenogenic forms is that the sistentes diapause during the first instar and the progredientes do not. The two wingless adult forms vary in size and relative lengths of their antennal segments. Sistentes adults measure 1.41 ± 0.17 mm long by 1.05 ± 0.12 mm wide and progrediente adults are smaller measuring 0.87 ± 0.09 mm long by 0.63 ± 0.07 mm wide (McClure 1989). The sistentes are also darker because they are more heavily sclerotized and they have more wax pores on their dorsal surface than the progredientes. The length of the terminal antennal segment of the progredientes is twice the length of the combined other antennal segments while the terminal antennal segment of the sistentes is about the same length as the combined other segments (McClure 1989). The winged sexuparae are of intermediate size measuring 1.09 ± 0.10 mm long by 0.51 ± 0.06 mm wide, are dark brown and heavily sclerotized, have long five-segmented antennae, and compound eyes (Fig. 4; McClure 1989).

Eggs

Hemlock woolly adelgid eggs are laid in a protective white waxy ovisac that resembles a mound of cotton extruded through pores distributed on the body surface (Fig. 1A). The waxy covering provides both physical and chemical protection for the eggs and other stages (Jones et al. 2014a). Newly laid hemlock woolly adelgid eggs are oblong, amber-colored, and darken to a reddish-brown color as the embryo develops (Fig. 5). Eggs laid by sistentes measure 0.35 ± 0.04 mm long by 0.21 ± 0.03 mm wide, while those laid by progredientes measure 0.36 ± 0.04 mm long by 0.23 ± 0.03 mm wide (McClure 1989). The sexuparae can be induced to lay eggs if held with spruce foliage and their eggs measure 0.37 ± 0.05 mm long by 0.25 ± 0.04 mm wide (McClure 1987).

Crawlers

Newly hatched adelgids in all generations are called crawlers because they are the stage that actively moves to locate a feeding site on the host. They have longer legs and antennae than the other instars that follow (Havill and Foottit 2007; Figs. 6

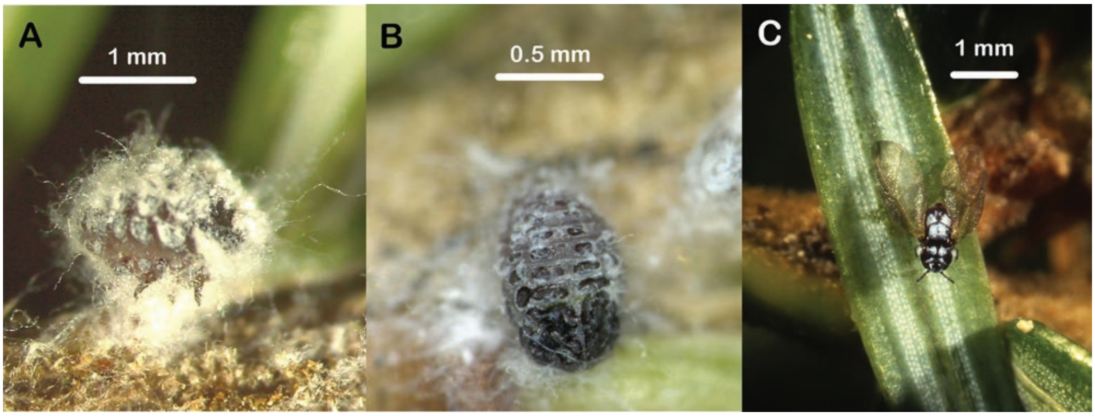

Fig. 3. Hemlock woolly adelgid adults: (A) Sistens adult with most of the wax removed. (B) Progrediens adult with wax removed. (C) Sexupara adult. (Photos by S. Limbu, M. A. Keena, and K. S. Shields)

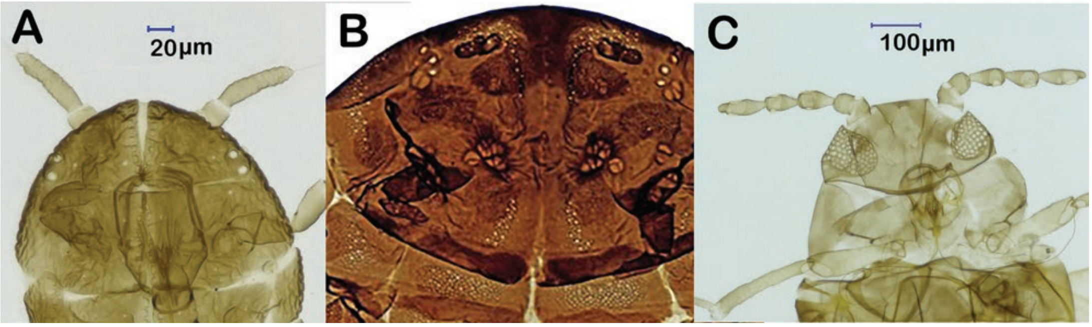

Fig. 4. Slide-mounted hemlock woolly adelgid heads showing antennae of first instar (A), adult (B), and sexupara (C). The sexupara is the only stage with compound eyes. (Photos by N. P. Havill)

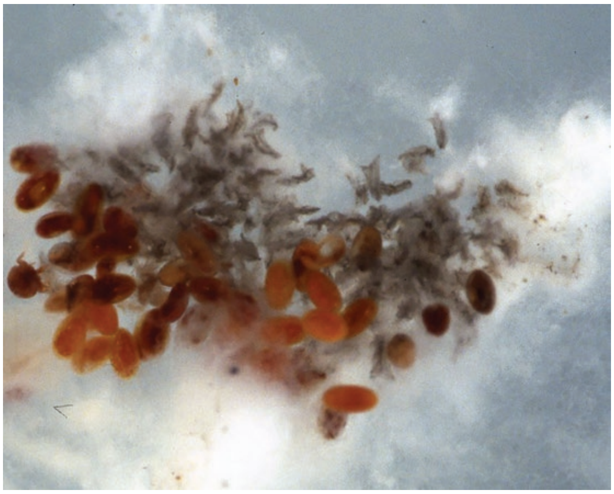

Fig. 5. Hemlock woolly adelgid eggs showing newly laid and darker eggs with maturing embryos with eye spots. (Photo by M. E. Montgomery)

and 7). The stylets that make up their mouthparts are more than three times their body length and have two channels, one to inject saliva and one to suck out the plant nutrients (Havill et al. 2014). Progredientes crawlers are present in the spring and sistentes crawlers are present in the early summer, with the exact timing depending on the climate. The crawlers measure 0.44 ± 0.05 mm long by 0.27 ± 0.03 mm wide and after they settle to feed, become more sclerotized and convex (McClure 1989). The sistentes crawlers enter a summer aestivation (stops developing during hot temperatures) soon after beginning to feed. During aestivation, the first instars are black, have woolly fringe, and resemble a football in shape (Fig. 8).

Nymphs

The hemlock woolly adelgid goes through a total of four nymphal instars (including the crawler) and one can often find the four distinct shed skins next to the adults since the insect does not change location once it settles (Fig. 9). The nymphs of sistentes and progredientes are similar in size and morphology, so can only be distinguished by their timing and location on the host. The settled first-, second-, third-, and fourth-instar nymphs measure 0.43 ± 0.04 mm long by 0.27 ± 0.03 mm wide, 0.57 ± 0.05 mm long by 0.34 ± 0.04 mm wide, 0.67 ± 0.06 mm long by 0.43 ± 0.04 mm wide, and 0.74 ± 0.06 mm long by 0.47 ± 0.05 mm wide, respectively (McClure 1989).

Nymphs of the sexuparae hatch at the same time as the progredientes and eggs of both are produced by the sistentes females. They cannot be distinguished until they reach the second instar, when they differ in size, shape, and morphology. Sexuparae nymphs are larger than the sistentes and progredientes nymphs measuring 0.60 ± 0.07 mm long by 0.35 ± 0.04 mm wide, 0.77 ± 0.07 mm long by 0.47 ± 0.05 mm wide, and 0.89 ± 0.09 mm long by 0.49 ± 0.05 mm wide in the second, third, and fourth instars, respectively (McClure 1989). The sexuparae nymphs also have a suture (visible junction) between the dorsal plates that make up the thorax, a wing bud notch, and the antennae are generally larger and longer than those of the other nymphs (see drawings in McClure 1989 for sexupara nymph morphology).

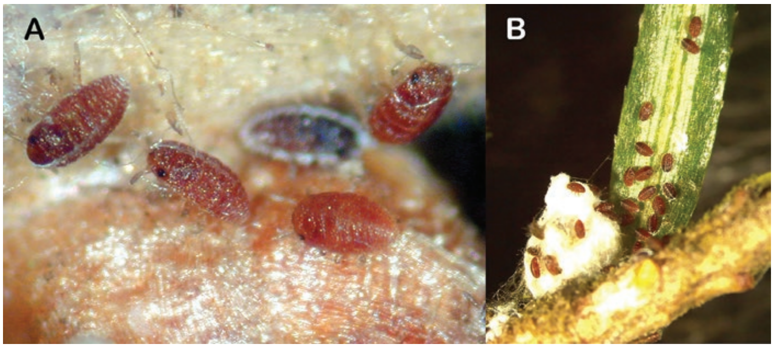

Fig. 6. Hemlock woolly adelgid crawlers (A) and several near an egg mass (B). (Photos by M. E. Montgomery and S. Limbu)

Fig. 7. Hemlock woolly adelgid crawler (first-instar nymph) showing characteristic wax pores, legs, antennae, and long mouthparts. (Photo by N. P. Havill)

Biology

Life Cycle and Stages

Hemlock woolly adelgids have a complex life cycle (including a sexual generation) that takes 2 y to complete in parts of their native range in Asia. In eastern North America, the hemlock woolly adelgid has an abbreviated life cycle that does not have a sexual generation, likely because the primary host species, tiger-tail spruce (*Picea torano* (K. Koch) Koehue (=*Picea polita*)), is absent except rarely in arboreta or ornamental plantings (Fig. 10; Havill et al. 2014). In the introduced range, survival or reproduction of the sexual form (sexuparae) has not been observed.

Sistentes begin to oviposit in early February in Georgia and in mid-February in Connecticut and continue laying for about 16 wk (McClure 1987, Gray and Salom 1996, Joseph et al. 2011). However, during a particularly warm winter in Tennessee, sistentes have been reported to lay eggs as early as the end of December (Leppanen and Simberloff 2017). The eggs of the sistentes give rise to progredientes and the winged generation (sexuparae). The progredientes lay eggs of the sistentes generation starting in mid-May in Georgia and June in Connecticut (McClure 1989, Gray and Salom 1996, Joseph et al. 2011). The last progredientes/sexuparae eggs may be laid only a week before the sistentes eggs first appear so there is substantial overlap of the two generations in early summer (McClure 1987). The sistentes produces more eggs than the progredientes (about 300 and 100 eggs per female, respectively; McClure et al. 2001). Hemlock woolly adelgids lay two to three eggs per female in 48 h at 15°C (Limbu et al. 2016). Eggs hatch in 1–2 wk depending on temperatures (Joseph et al. 2011).

Progredientes/sexuparae crawlers are present in the southeastern United States from early March to mid-June and they begin to hatch in mid-April in the northeastern United States (McClure 1987, Joseph et al. 2011). Crawlers are only active for 1–2 d (McClure 1987). The progredientes/sexuparae crawlers settle primarily near the base of the needles on the previous years' growth and the progredientes remain there for the rest of their lives. The adelgid inserts its stylets through the plant tissue (bark and phloem) and into the host's storage cells (xylem ray parenchyma cells), where it feeds on the starch (Young et al. 1995). The proportion of the spring generation that develops into winged sexuparae increases with sistentes density (McClure 1991, Sussky and Elkinton 2014).

In Connecticut, sistentes eggs hatch into crawlers in June through July and in Georgia from late May to early July (McClure 1987, Joseph et al. 2011). The sistentes crawlers settle quickly near the base of the needles on new shoots if available, become immobile, and then aestivate for the rest of the summer (Fig. 8). Aestivation of first instars is optional rather than required and is induced if the period from egg through second instar is exposed to temperatures of ≥17°C under a long daylight cycle (Salom et al. 2001). The spring generation can also be induced to stop developing if these same abiotic conditions exist at that time of year (Weed et al. 2016). The survival of aestivating sistentes first instars is ≥80% when summer temperatures remain <25°C, but survival decreases as temperature increases and with the duration of exposure to higher temperatures (Sussky and Elkinton 2015, Mech et al. 2017). Exposure to direct sunlight can

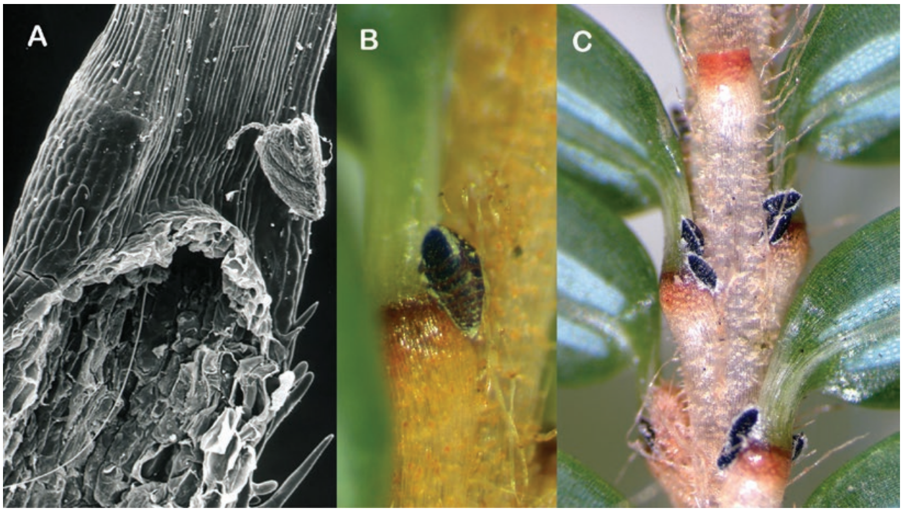

Fig. 8. Aestivating hemlock woolly adelgid sistentes first instars: (A) scanning electron microscope photo showing long mouthparts inside the host, (B) close up of nymph just after it settled, and (C) several aestivating nymphs at the base of needles on a hemlock branch. (Photos by K. S. Shields and M. E. Montgomery)

Fig. 9. Third-instar hemlock woolly adelgid sistens nymph with two exuvia next to it. (Photo by M. A. Keena)

also contribute to reduced survival of aestivating sistentes, perhaps because they are black and will warm to temperatures higher than ambient when in the sun (Brantley et al. 2017, McAvoy et al. 2017a).

The sistentes first instars slowly resume development in the late fall (late September to early October). These nymphs normally complete development by February–March of the following year and no stage-specific temperature response data is available for this generation. The progredientes nymphs complete development in about a month and a half in Georgia (Salom et al. 2002). The lower temperature threshold is 3.9°C and the upper threshold is between 22 and 27°C for the second instar to adult. The number of degree-days required to develop from second instar to adult is 222 (base 3.9°C) in the laboratory and slightly higher under field conditions (Salom et al. 2002).

Colder winter temperatures in northeastern North America result in substantial mortality of the sistentes nymphs, which helps to slow the rate of hemlock mortality and determines the adelgids ability to establish in new areas with colder temperatures (Skinner et al. 2003, Trotter and Shields 2009). Winter mortality is reported to exceed 90% when temperatures fall below −20°C and approach 100% at temperatures below −35 to −40°C (Parker et al. 1998, 1999; Butin et al. 2005; Paradis et al. 2008; Trotter and Shields 2009; Cheah 2017). A recent model using the duration of the cold period, the maximum cold temperature, and temperature conditions before the cold period provides a way to predict winter mortality (McAvoy et al. 2017b). Despite high winter mortality, a few hemlock woolly adelgids survive and populations quickly rebound with individuals selected for cold tolerance (Parker et al. 1998, Elkinton et al. 2017). Hemlock woolly adelgids in northeastern North America are already showing signs of genetic adaptation to colder winter temperatures than those that occur in the southeastern United States (Skinner et al. 2003, Butin et al. 2005, Elkinton et al. 2017, Lombardo and Elkinton 2017). A laboratory experiment shows that exposing adelgids to cold temperature for a short time results in induction of cold tolerance, which lowers the temperature at which they freeze (Elkinton et al. 2017).

Sistentes adults are present from February to March in Connecticut and early January to mid-May in Georgia, depending on the winter–spring temperatures (McClure and Cheah 1999, Joseph et al. 2011). Progredientes adults are present from late May to early July in Connecticut and May and June in Georgia (McClure and Cheah 1999, Joseph et al. 2011).

Hemlock woolly adelgids harbor endosymbiotic bacteria, some of which are transmitted from mother to egg, and may be necessary for their survival (von Dohlen et al. 2013, Weglarz et al. 2018). The specific role these bacteria play is not known but killing them with antibiotics results in the death of the adelgids (Shields and Hirth 2005). Further research on these bacteria may provide novel control options and provide more information on their symbiotic relationship with the adelgid.

Hosts and Distribution

There are 10 hemlock species; among these four are native to North America. Eastern hemlock, *T. canadensis* and Carolina hemlock, *T. caroliniana* are found in eastern North America, whereas Mountain hemlock, *Tsuga mertensiana* (Bongard) Carrière and Western hemlock, *Tsuga heterophylla* (Rafinesque-Schmaltz) Sargent are endemic to the western North America (Farjon 2010, Holman et al. 2017). The eastern hemlock is distributed from the southeastern coast of Canada, south to the northern parts of Georgia and Alabama, and west to the eastern parts of Minnesota

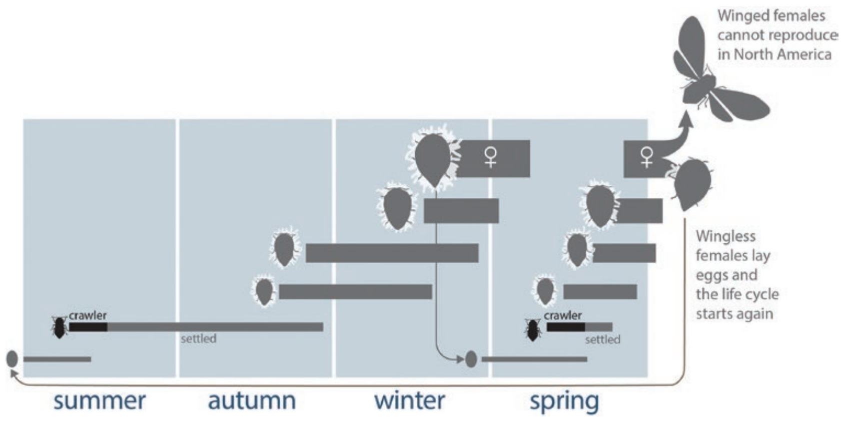

Fig. 10. Simplified life cycle of hemlock woolly adelgid. The anholocycle part is all that occurs in eastern North America. The full holocycle occurs in Japan where this invasive insect originated. (Illustration by N. P. Havill and V. D'Amico)

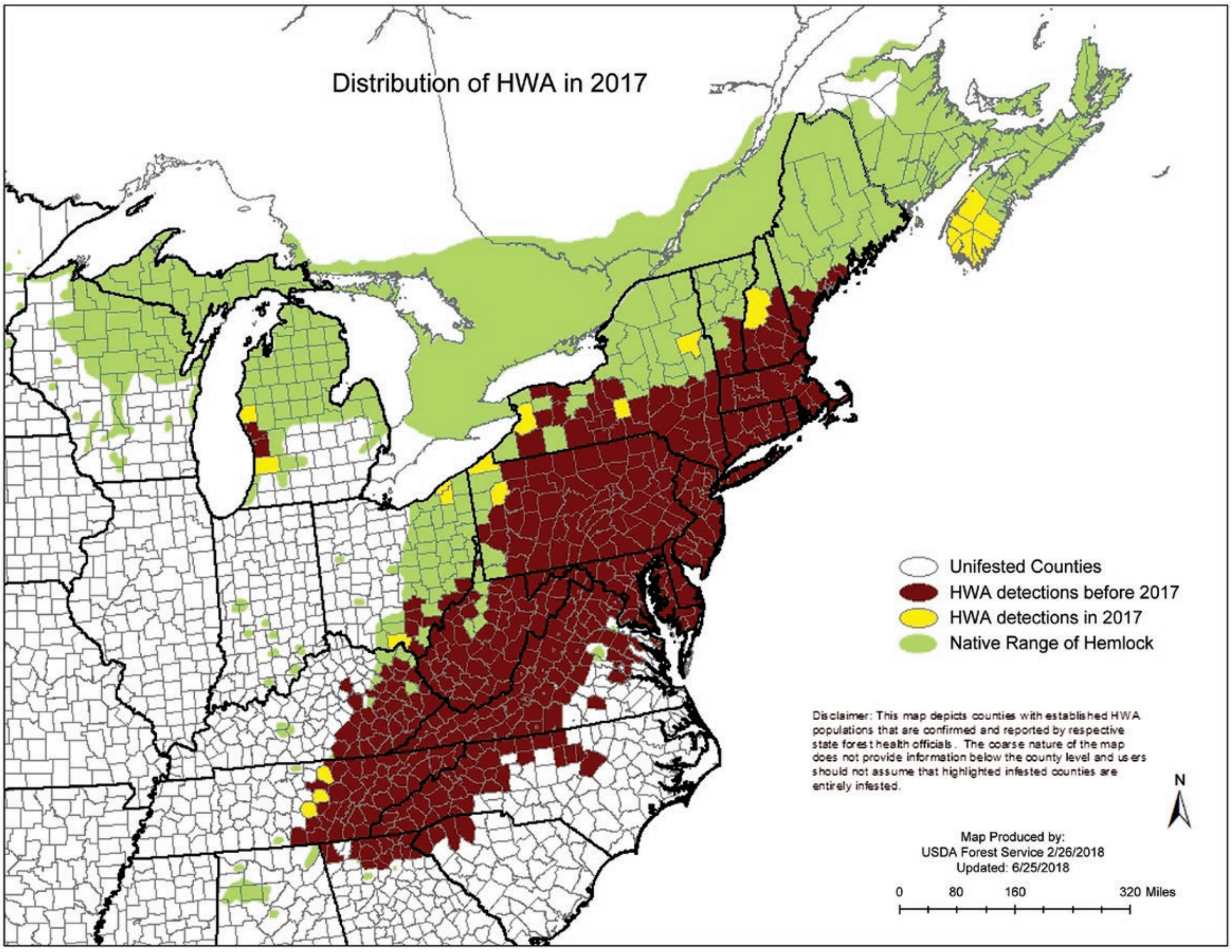

Fig. 11. Hemlock woolly adelgid distribution in eastern North America.

(Godman and Lancaster 1990). Carolina hemlocks are found in southern Virginia to northern Georgia (Jetton et al. 2008). Hemlocks are an important foundation tree species and dominate about 1 million hectares of eastern North American forests (McWilliams and Schmidt 2000).

Since its introduction near Richmond, Virginia before 1951, the hemlock woolly adelgid has spread and currently occupies about half of the hemlock range in eastern North America (Fig. 11). Recently, there have been some new isolated range expansions possibly resulting from the movement of infested ornamental hemlocks into Michigan, southern Ontario, and Nova Scotia. Isolated infestations in Michigan were initially targeted for eradication efforts, but now the infestations have spread too far such that the eradication efforts have been abandoned.

Ecology

Hemlocks are long-lived and one of the most abundant tree species in eastern North America (Fig. 12; McWilliams and Schmidt 2000, Lorimer et al. 2001). Moreover, hemlocks are shade-tolerant, co-evolved in mixed deciduous forests, and are known for their ability to mediate soil moisture, stabilize stream base-flow, and regulate stream temperatures (Barden 1979, Brantley et al. 2013). They create cool, moist microclimates with slow rates of nitrogen cycling because of deep shade, resulting in slow decomposition of acidic organic litter that is unique to hemlock-dominated forests (Ellison et al. 2010). Thus, hemlocks provide and support a unique community of terrestrial and aquatic organisms; there are no other known tree species that can replace its ecological functions (Ward et al. 2004).

Since its arrival, the hemlock woolly adelgid has decimated many hemlock stands in eastern North America. Dead hemlocks and needle loss in a hemlock-dominated forest can increase light levels and temperature on the forest floor. This alteration in microclimate due to hemlock decline has disrupted forest ecosystem processes with a direct impact on carbon cycling. Hemlock woolly adelgid infestation has reduced hemlock basal area (the area of a given section of land that is occupied by the cross-section of tree trunks), litter input, and fine root biomass over time leading to a reduction of CO_2 production in the soil (Nuckolls et al. 2009). Similarly, Jenkins et al. (1999) reported that hemlock woolly adelgid infestation accelerated formation of ammonium and nitrates in the soil which can serve as fertilizers and their production can lead to more acidic soils. All these alterations in microclimate, soil moisture, and nutrient status will likely bring changes in stand composition and species diversity (Stadler et al. 2005, Spaulding and Rieske 2010). Studies have reported negative impact of hemlock stand loss on six bird species (Tingley et al. 2002), fish in adjacent streams (Ross et al. 2003), and the associated invertebrate community (Adkins and Rieske 2015, Benton et al. 2017).

Dispersal

In eastern North America, the hemlock woolly adelgid spends most of its life cycle in sedentary stages. Only the crawler and winged stages (sexuparae) are mobile; but the sexuparae cannot find suitable hosts or produce viable offspring. However, it only takes one adelgid to start a new infestation (Tobin et al. 2013) and the tiny eggs and crawlers are dispersed by wind, birds, animals, and humans (McClure 1990). Airborne adelgids have been captured 600 m from an infestation (McClure 1990). Over 80% of the birds trapped near infested hemlocks had eggs and crawlers on them and deer that browsed on infested hemlocks can carry the eggs and crawlers as well (McClure 1990). Transfer by birds has been shown to be highest when peak crawler emergence occurs during bird migrations (Russo et al. 2016). The insect is estimated to spread about 15 km per year in the South and 8 km per year in the North (Evans and Gregoire 2007a). Variability in the rate of spread is potentially attributed to colder temperatures in the North. Human-aided spread occurs primarily through transportation of hemlock woolly adelgid infested nursery stock or logs from infested regions that have eggs or crawlers on them that can survive an extended period of time without nourishment (McClure 1990). It is believed that the pest was introduced into the United States from Japan through infested seedlings. Movement of infested materials both within and out of infested areas is restricted by regulatory agencies to prevent further human-aided spread (CFIA 2017b, MDARD 2017).

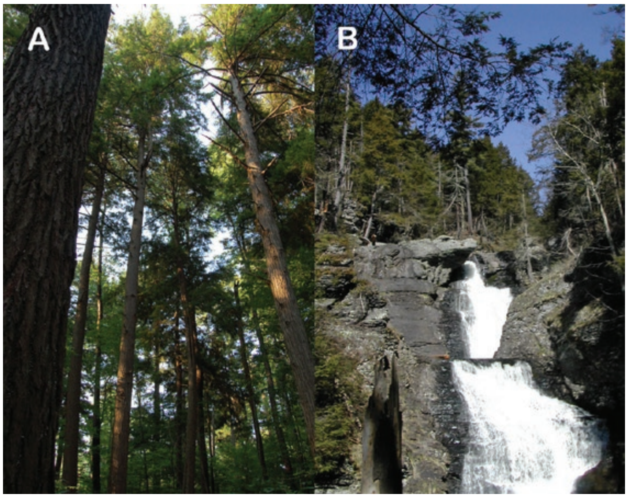

Fig. 12. Healthy hemlocks. (A) Old growth hemlocks in Pennsylvania and (B) hemlocks in a riparian area. (Photos by M. A. Keena)

Sampling and Scouting Procedures

Damage

As a hemipteran, hemlock woolly adelgid has piercing and sucking mouthparts, similar to those of most aphids. However, hemlock woolly adelgid's mouth parts are much longer than that of aphids, which enables it to gain access to the cells where the tree stores nutrients. A study on feeding biology of hemlock woolly adelgid suggests that these insects may insert saliva into the tree and digest the nutrients before sucking them back up and by doing this cause a tree-wide defensive response (Oten et al. 2014). Hemlock woolly adelgid feeding causes hemlock trees to reduce photosynthesis, produce false tree rings, and exhibit signs of water stress (e.g., reduced water mobility within the tree, and exchange of water and carbon dioxide with the outside air; Gonda-King et al. 2012, 2014; Domec et al. 2013). This may explain why infested hemlocks exposed to drought may die much more quickly than if the trees are well watered. As adelgid infestation levels increase the tree stops producing new growth, which forces adelgid populations to settle in less nutritious old growth, causing adelgid populations to decline. This is often followed by an increase in tree health and reinfestation by adelgids (McClure 1991, Jones et al. 2016). Similar adelgid population cycles also occur following high winter or summer adelgid mortality.

Hemlock woolly adelgid feeding on hemlock causes yellowing and desiccation of the hemlock needles (Fig. 13A). Buds start to die resulting in little to no new growth on the tree. Needles fall off and dieback symptoms become visible within 2–4 y in northeastern North America (Fig. 13B; Cheah et al. 2004). Hemlock woolly adelgid infestation can kill a tree in less than 1–3 y in the southeastern United States and 5–15 y in northeastern North America (Fig. 13C; Ellison et al. 2010).

Detection Methods

There is no pheromone or baited trap available for hemlock woolly adelgid detection. Visual survey is the primary tool used to detect new infestations and range of spread. Visual detection of hemlock woolly adelgid may be challenging during the summer when they are not developing nor covered with wool, and at an early stage of infestation when adelgid density is low. Hemlock woolly adelgid infestation is detected by looking for tiny white balls of wool on the underside of the terminal shoots during late October to mid-July (Fig. 1B). If trees are heavily infested, the pest density is slightly

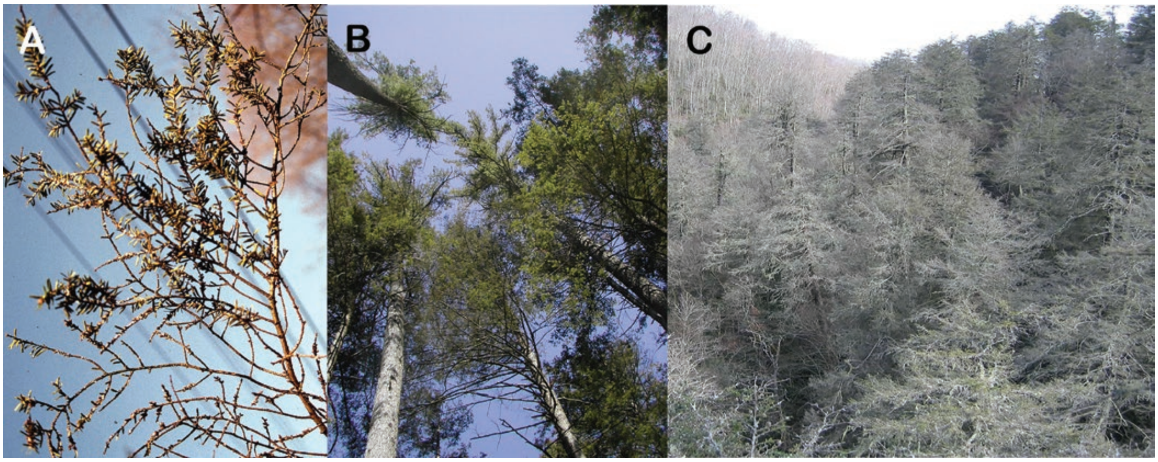

Fig. 13. Hemlock woolly adelgid damage on a branch showing yellowing and needle loss (A), crown thinning and dieback (B), and many "gray ghost" dead hemlocks in the Great Smoky Mountains National Park (C). (Photos by M. E. Montgomery, M. A. Keena, and K. Gottschalk)

higher on the lower branches, and if a tree is lightly infested hemlock woolly adelgid may be concentrated on the upper branches (Evans and Gregoire 2007b). At all densities, North-pointing branches usually have a higher density of hemlock woolly adelgid, so surveying branches on the north side may increase the probability of locating an infestation (Evans and Gregoire 2007b).

Several techniques are being employed to sample at all levels of the crown of a tree. Nondestructive sampling guidelines have been developed for both the progredientes and sistentes generations (Costa and Onken 2006, Fidgen et al. 2006). The simplest method involves examining one branch, and if no white woolly masses are found, a second branch on the opposite side should be selected and checked (Costa and Onken 2006). A binomial (present or absent) sequential sampling plan for detecting sistentes on new growth found that sampling 20–80 shoots per tree was needed to make a determination, which took <2 min per tree to complete (Fidgen et al. 2006). Detecting a single infested tree is sufficient evidence of hemlock woolly adelgid presence. To sample the middle and upper crown of a tree, a HYPERDOG ball launcher (HYPER PET, Wichita, KS) can be used to launch a Velcro (Velcro USA, Manchester, NH) covered racket ball (PennUltra-Blue, Phoenix, AZ) into the tree that can pick up adelgids or their waxy wool covering (Fig. 14). Less than 10 samples per tree are enough to detect the pest at a low level infestation using this method (Fidgen et al. 2016). Pole pruners can also be used to sample otherwise inaccessible branches; examining broken or chewed off branches found on the ground is also recommended (Coots et al. 2015, MDARD 2016). There are commercially available sticky traps (green prism traps, Synergy Semiochemicals Corp., Burnaby, BC, Canada) that can be nailed horizontally on the top end of a wooden stake (2.5 × 2.4 × 200 cm) to monitor airborne adelgid eggs, crawlers, and the winged generation (Fidgen et al. 2017), but the captured insects need to be carefully examined to distinguish them from other adelgid species that might be present in eastern forests such as *Adelges piceae* (Ratzeburg) or *Pineus strobi* (Hartig). Hemlock health can be measured at a landscape scale using remote sensing or satellite imagery (Royle and Lathrop 1997, Bonneau et al. 1999). Hemlock crown health has been directly correlated with hemlock woolly adelgid damage and can be used as a way to measure tree health at the tree and stand levels using either visual estimates or indices derived from branch samples (Mayfield et al. 2015, Benton et al. 2016). Although this is not an accurate measure to detect the adelgid at lower population densities, it helps to identify the location and stage of adelgid damage.

Fig. 14. Ball with velcro on it shot into the upper canopy of hemlock trees using the slingshot to sample for hemlock woolly adelgid. (Photo by S. Limbu)

Management Options

Eradication

Eradication of hemlock woolly adelgid has been attempted in newly infested regions in North America by removing and destroying infested trees and treating healthy trees in the vicinity with systemic insecticides. Surveys were performed in the area for multiple years post-treatment to ensure eradication (MDARD 2013). However, most attempts at eradication have not been successful. For example, a hemlock woolly adelgid infestation was detected in Michigan for the first time in 2006. Efforts were made to isolate and eradicate the pest population immediately following the detection. By 2013, it was believed that hemlock woolly adelgid had been successfully eradicated from Michigan. However, the pest reappeared in different counties in 2015, possibly indicating a low level of the pest that remained undetected during the 2013 and 2014 surveys (MDARD 2018). Currently, the state has abandoned eradication and is focused on monitoring, management, and regulation of hemlock woolly adelgid. Conversely, in Canada, infestations located in Ontario were reported to have been eradicated. Only mechanical eradication was used, which involved on-site cutting and burning of infested trees. Surveys have been performed since then to ensure the success of the eradication and prevent further spread (CFIA 2017b).

Silvicultural Control

Silvicultural treatments for control of hemlock woolly adelgid have been used and are being evaluated (Fajvan 2008). For example, thinning, pruning, or selective harvest of overstory trees reduces the shade on understory hemlock trees in a mixed forest setting. Artificially and naturally shaded trees have better hemlock woolly adelgid survival than unshaded trees, indicating positive impacts of these silvicultural practices on hemlock health (Brantley et al. 2017, McAvoy et al. 2017a). There was no effect of thinning on hemlock foliar nutrients, suggesting that thinning did not increase the attractiveness of hemlock trees to hemlock woolly adelgid (Piatek et al. 2016). Removing adjacent trees to increase sun exposure, planting hemlock trees in a sunny location, and pruning new growth after hemlock woolly adelgid sistentes eggs have hatched and sistentes crawlers are settled are recommended to reduce hemlock woolly adelgid density in horticultural settings (McAvoy et al. 2017a). Although silvicultural treatments show promise for reducing hemlock woolly adelgid density, it is not known how increased light intensity and soil temperature affect other trees, wildlife, and insects associated with hemlock trees. At present, silviculture is a practical option for ornamental hemlock stands, but further studies are underway to develop protocols that would apply to a hemlock forest. The studies that are underway aim to determine the degree of thinning, the combination of treatments, and their timing in a hemlock forest to achieve reductions in hemlock woolly adelgid density.

Application of nitrogen containing fertilizer on shaded hemlock trees may increase hemlock woolly adelgid density (McAvoy et al. 2017a). Application of fertilizer increases foliar nutrients that are acquired by sap sucking insects like hemlock woolly adelgid, hence, fertilizer application may promote hemlock woolly adelgid population growth (McClure 1992). Also, fertilizer application may result in ineffective silvicultural or pesticide treatment if applied together. However, if low rates of insecticide are combined with fertilization, it can benefit predators and help improve hemlock health through an integrated approach (Joseph et al. 2011).

Development of hemlock woolly adelgid resistant or tolerant hemlock hybrids have been explored for hemlock woolly adelgid control, but this involves long-term research to develop and test tree lines, which have not yet been completed. *Tsuga chinensis* (Franch.) E. Pritz is found in China, and hybrids of *T. chinensis* with *T. caroliniana* are comparatively more resistant to hemlock woolly adelgid than native species in eastern North America (Montgomery et al. 2009). These hybrids may be suitable for landscape or horticultural use but use in hemlock woolly adelgid-invaded forest settings and success in replacing native hemlocks are still being evaluated (Montgomery et al. 2009). Impacts of replacement on biodiversity and sustainability of hybrids in eastern forests are being explored. Crosses between *T. canadensis* and Asian hemlock species have been unsuccessful because of incompatibilities between the species. There have also been 30 putatively resistant *T. canadensis* trees from five different states found in areas where the adelgid has killed all other trees that are being evaluated (Ingwell and Preisser 2011). Preliminary assessments show some differences in adelgid survival between known susceptible trees and these putative resistant trees when using rooted cuttings.

Biological Control

Entomopathogenic Fungi

Several insect-killing fungi associated with hemlock woolly adelgid have been identified from eastern North America and southern China and their efficacy to control adelgids has been evaluated. A laboratory study shows that there is variation among fungal species in virulence, rate of growth, and sporulation; some isolates of *Metarhizium anisopliae* (Metchnikoff) Sorokin, *Lecanicillium lecanii* R. Zare & W. Gams, and *Beauveria bassiana* (Balsamo-Crivelli) Vuillemin were identified as the most effective at killing hemlock woolly adelgid (Reid et al. 2010). These naturally occurring fungi caused 42–82% hemlock woolly adelgid mortality in the laboratory when applied at the rate 1×10^8 spores/ml (Gouli et al. 1997). Field efficacy testing performed in 2001 and 2003 using fungal products that are commercially available for other uses demonstrated that insect-killing fungi are effective when applied during late summer and fall when first-instar sistentes are present without their protective waxy wool (Parker et al. 2004). However, insect-killing fungi have specific temperature and moisture requirements to be efficacious, and field conditions may not be as ideal as laboratory conditions. Commercially available products are of limited usefulness and further study would be needed to select an appropriate pathogen that can survive variable field conditions; also needed are improvements in production methods, application methods, and data to meet the requirements for registration before a hemlock woolly adelgid-specific product would be available.

Predators

Native natural enemies such as predaceous gall midges (Diptera: Cecidomyiidae), lacewings (Neuroptera: Chrysopidae and Hemerobiidae), lady beetles (Coleoptera: Coccinellidae), and flower flies (Diptera: Syrphidae) prey on hemlock woolly adelgid in low densities in eastern North America (McClure 1987, Montgomery and Lyon 1995, Wallace and Hain 2000). However, these predators tend to be generalists (eat a wide range of insects) and are not sufficient to control hemlock woolly adelgid infestations. Therefore, for several years, research has focused on developing a complex of non-native natural enemies of hemlock woolly adelgid for reducing pest populations in eastern North America. Many predatory insect species have been evaluated for potential biocontrol of hemlock woolly adelgid (Onken and Reardon 2011). Thus far, eight species of non-native predatory insects have been released in eastern North America (Table 1). Two of these predator species were imported from Japan, four from the Pacific Northwest in North America, and two from China (Onken and Reardon 2011).

Sasajiscymnus tsugae (Coleoptera: Coccinellidae) Sasaji and McClure was one of the earliest exotic lady beetles released for biological control of hemlock woolly adelgid. It was brought to the United States from southern Japan in 1994 and 1995. Later the genetic diversity of the colony in the United States was increased by including *S. tsugae* from other parts of Japan (Cheah 2011). It is a tiny black beetle measuring 1.60 mm by 1.05 mm with slightly brown antennae (Fig. 15D). This predator is widespread and is reported to be an effective predator of hemlock woolly adelgid in Japan (McClure 1995, Sasaji and McClure 1997). *Sasajiscymnus tsugae* can go through more than one generation per year and produces an average of 280 eggs over a 14-wk period, which makes it a good candidate for mass rearing (Cheah and McClure 2000). It was first released in Connecticut in 1995 and subsequently, millions were released in 16 eastern states (Cheah 2011). In Tennessee and Georgia, the predator was established and found to coexist with other non-native and native predators of hemlock woolly adelgid (Hakeem et al. 2011, Jones et al. 2014b). Studies have suggested that hemlock trees recovered after predator release, but there were only a few individuals recovered in Connecticut where this work was

Table 1. *Adelges tsugae* non-native predator source, first release date and locations, and establishment status in eastern North America to date

Predator species	Native range	First release date and locations	Released locations	Establishment status
Sasajiscymnus tsugae	Japan	1995 (CT)	16 states from SC to ME	Established in TN
Laricobius nigrinus	Pacific Northwest	2003 (VA)	8 states from MA to GA	Established in PA, MD, VA, NC, and TN
Laricobius osakensis	Japan	2012 (VA and WV)	NC, PA, SC, TN, VA, and WV	Established in PA and VA
Scymnus sinuanodulus	China	2004–2011	8 states from CT to GA	Unknown
Scymnus ningshanensis	China	2007	MA, CT, and NC	Unknown
Scymnus coniferarum Abbot and Smith	Pacific Northwest	2015	NC+	Unknown
Leucopis piniperda	Pacific Northwest	2016	NY, TN	Not verified
Leucopis argenticollis	Pacific Northwest	2016	NY, TN	Not verified

CT = Connecticut, GA = Georgia, MA = Massachusetts, ME = Maine, MD = Maryland, NC = North Carolina, NY = New York, PA = Pennsylvania, SC = South Carolina, TN = Tennessee, VA = Virginia, WV = West Virginia, and '+' indicates that other locations are unknown but exist.

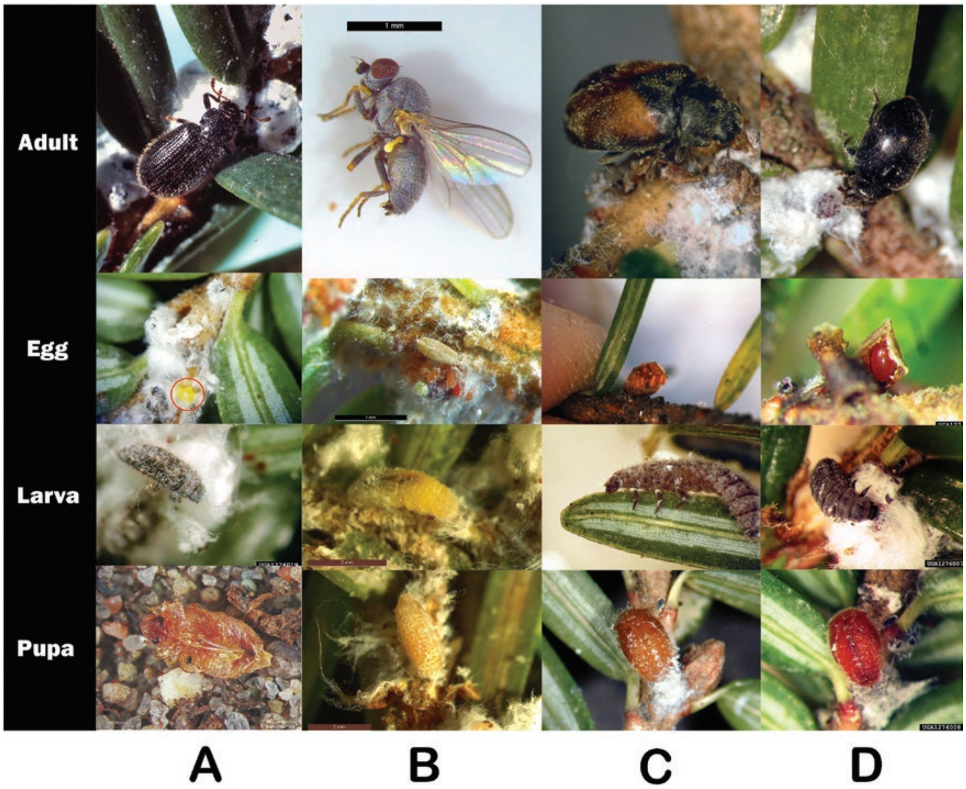

Fig. 15. Hemlock woolly adelgid predator life stages; representatives from each genus. (A) *Laricobius nigrinus* (Coleoptera: Derodontidae, egg is light yellow inside the red ring), (B) *Leucopis argenticollis*, (C) *Scymnus camptodromus* (Coleoptera: Coccinellidae), and (D) *Sasajiscymnus tsugae* (Coleoptera: Coccinellidae). The stages of the other species in the genus look very similar and the adults require either examination under a microscope or molecular analysis to tell them apart. (Photos by M. A. Keena, S. Limbu, M. E. Montgomery, K. O'Connor, R. J. Kay, C. Cheah, and A. Lamb Galloway). Note: Keena, Shields, Montgomery, Havill, D'Amico, and Gottschalk are all Forest Service employees so the photos are in the public domain (permissions also granted). Whitmore, Limbu, Kay, and O'Connor are all from Cornell and in the same lab (permissions also granted). We have e-mail permissions from Cheah and Lamb to use their photos that are available through Bugwood. Shigehiko Shiyake has given permission to use his photo through Nathan Havill.

done despite a significant number of releases (70,000 total; Cheah and McClure 2002). There is no concrete evidence to show that this predator is established and surviving across the full range where it was released or that it is providing control.

During 1995, several Chinese predators of hemlock woolly adelgid were studied as potential biological control agents. *Scymnus* (*Neopullus*) *camptodromus* Yu and Liu (Coleoptera: Coccinellidae), *Scymnus* (*Neopullus*) *sinuanodulus* Yu and Yao, and *Scymnus* (*Neopullus*) *ningshanesis* Yu and Yao were considered the most promising for classical biological control of hemlock woolly adelgid as they were found in abundance, consume large numbers of hemlock woolly adelgid eggs, and their phenology matches that of hemlock woolly adelgid in China (Montgomery and Keena 2011). *Scymnus sinuanodulus* and *S. ningshanesis* were released into eastern North America in 2004 and 2007, respectively, and are not known to have established (Montgomery and Keena 2011, Keena et al. 2012). Establishment has not been confirmed for *S. sinuanodulus* despite being released in considerable numbers in multiple locations, while *S. ningshanesis* was released in small numbers. *Scymnus camptodromus* (Fig. 15C), despite displaying a potential for biological control of hemlock woolly adelgid, was never released in eastern North America because it is difficult to rear in the laboratory due to its egg aestivation and the need to obtain official permission for field release.

In eastern North America, there is only one native *Laricobius* species; *Laricobius rubidus* LeConte (Coleoptera: Derodontidae; Leschen 2011). Pine bark adelgid, *P. strobi*, is a primary host for *L. rubidus*; however, the predator has been found occasionally feeding on hemlock woolly adelgid in eastern North America (Wallace and Hain 2000, Fischer et al. 2015). Although this predator can survive and develop on hemlock woolly adelgid, it prefers to oviposit on eastern white pine (*Pinus strobus* L.), indicating its preference for pine bark adelgid (Zilahi-Balogh 2005). Because *L. rubidus* is not a specialist on hemlock woolly adelgid, it alone will not control this pest in eastern North America. During further exploration for biological control candidates, researchers discovered two non-native *Laricobius* species: *Laricobius nigrinus* Fender and *Laricobius osakensis* Montgomery and Shiyake. Both *L. nigrinus*, which is native to the Pacific Northwest of North America (Fig. 15A; Zilahi-Balogh et al. 2006), and *L. osakensis*, which is native to Japan (Montgomery et al. 2011), are hemlock woolly adelgid specialists that have been imported and reared in the laboratory for release in eastern North America. *Laricobius nigrinus* has also been released after being wild-caught in the Pacific Northwest of the United States (Mausel et al. 2010).

Laricobius nigrinus adults are black in color and measure about 2.3–2.9 mm in length (Zilahi-Balogh et al. 2006). This predator is a specialist on hemlock woolly adelgid and will not develop on other adelgid species (Zilahi-Balogh et al. 2002). *Laricobius nigrinus* has one generation a year and the larval stage requires approximately 226–252 hemlock woolly adelgid eggs at 12–18°C to complete development (Zilahi-Balogh et al. 2003). These beetles have been released in eastern North America since 2003 and are reported to have established at most sites in cold hardiness zones 6a, 6b, and 5b (Mausel et al. 2010). *Laricobius nigrinus* collected from the coastal Pacific Northwest (Oregon and Washington) show slight genetic differentiation from those found more inland (Idaho, Montana, and interior British Columbia; Davis et al. 2011, Havill et al. 2012). The inland populations exhibited more cold tolerance as evidenced by higher survival in Massachusetts field releases and a lower freezing point than the coastal population (Mausel et al. 2011). This indicates that climate-matching predators to the planned location of release may be critical for improving biological control since hemlock woolly adelgid is found across a wide range of plant cold hardiness zones.

Another *Laricobius* species, *L. osakensis*, discovered in Japan in 2005, has recently been added to the predator complex for hemlock woolly adelgid (Montgomery et al. 2011). Laboratory studies show that this predator is a specialist on hemlock woolly adelgid and adults will consume more hemlock woolly adelgid ovisacs than *L. nigrinus* (Lamb et al. 2010, Story et al. 2012). *Laricobius osakensis* has one generation a year like *L. nigrinus* but females are more fecund than *L. nigrinus* (Vieira et al. 2012). The first open-field releases of *L. osakensis* beetles occurred in 2012 in Virginia and West Virginia. The release was delayed due to the discovery of a cryptic population of *Laricobius naganoensis* Leschen in the *L. osakensis* colony that was accidentally imported along with *L. osakensis* from Japan. Therefore, before release, the predator population had to be purified in the laboratory to ensure only *L. osakensis* were released in the field (Fischer et al. 2014). Recovery of pure *L. osakensis* has been confirmed at two Virginia and one Pennsylvania release sites but it is too early to know if it will establish across a wide climatic range (Toland et al. 2018).

There are some morphological characters that can be used to distinguish the different *Laricobius* species, but molecular tools must be used to confirm the species identification and distinguish hybrids that can occur. For example, *L. nigrinus* is black in color and *L. rubidus* is bicolored with back and red elytra (hard outer wings). On the other hand, absence of ocelli (simple eyes) in *L. osakensis* distinguishes it from all the other *Laricobius* species released thus far (Montgomery et al. 2011). However, reliably identifying all the species by observing external morphology in the field is extremely challenging because *L. rubidus* and *L. nigrinus* can hybridize; the proportion of hybrids may be stabilizing at around 10%, and the hybrids may resemble either parents or exhibit intermediate morphological characteristics (Havill et al. 2012). *Laricobius osakensis* females can resemble *L. rubidus* with bicolored reddish black elytra (Montgomery et al. 2011). This *Laricobius* species is not known to hybridize with *L. nigrinus*, which minimizes increasing complications of positive identification (Fischer et al. 2015).

Recently, two *Leucopis* species (Diptera: Chamaemyiidae), commonly known as silver flies, are being evaluated as biocontrol options for hemlock woolly adelgid. *Leucopis* species were first viewed as a potential biocontrol agent for hemlock woolly adelgid when they were found to be in abundance during a field survey of predators of hemlock woolly adelgid in the Pacific Northwest (Kohler et al. 2008). *Leucopis argenticollis* Zetterstedt and *Leucopis piniperda* Malloch found in the Northwest are now being released and evaluated as biocontrol candidates for hemlock woolly adelgid in eastern North America (Fig. 15B). The *Leucopis* species larvae prefer hemlock woolly adelgid but they can feed and develop on other adelgid species as well. In the Pacific Northwest, peak abundance of *Leucopis* species coincides with the presence of progredientes and sistentes eggs and adults, which shows its close association with hemlock woolly adelgid (Grubin et al. 2011). While there are native *L. argenticolis* and *L. piniperda* in eastern North America, they are genetically distinct from those found in western North America and have not been found feeding on hemlock woolly adelgid suggesting western *Leucopis* prefer hemlock woolly adelgids and eastern *Leucopis* prefer pine adelgids (Havill et al. 2018). Therefore, western genotypes of these *Leucopis* species are being released for biological control of hemlock woolly adelgid in eastern North America. The biological control program could benefit from this predator because *Leucopis* species will feed on both generations of hemlock woolly adelgid eggs and have more than one generation a year (Kohler et al. 2008). There are ongoing investigations of these silver flies to understand what role they might play in the hemlock woolly adelgid predator complex and to determine if they can establish across the climatic range of hemlock woolly adelgid in eastern North America.

Chemical Control

Horticultural oils, insecticidal soaps, and insecticides in the organophosphate and neonicotinoid groups can be used to significantly reduce hemlock woolly adelgid populations on hemlocks (McClure 1987, Cowles et al. 2006). Contact insecticides such as insecticidal oils, soaps, and other petrochemicals were used in earlier attempts to control hemlock woolly adelgid and were successful if full cover of foliage was obtained, which is very difficult to accomplish in forest settings (McClure 1987). Currently, imidacloprid is the most commonly used systemic insecticide against hemlock woolly adelgid and is more effective if applied to the soil rather than trunk injected (Cowles et al. 2006, Dilling et al. 2010). Imidacloprid can be applied as a soil drench, soil injection, time-release pellets, or basal bark spray. It is recommended to remove the top organic layer before imidacloprid application as a soil drench because the pesticide will bind to the organic matter (Benton and Cowles 2016). Imidacloprid moves slowly into the tree canopy, often taking a year to show its full effect; however, it can suppress hemlock woolly adelgid populations for multiple years with a single application (Cowles et al. 2006, Doccola et al. 2007, Cowles and Lagalante 2009). Because it moves slowly into the canopy, imidacloprid is not recommended when immediate hemlock woolly adelgid control is required. Alternatively, dinotefuran, another systemic neonicotinoid, is highly water soluble and provides rapid control (within 2–3 wk) of hemlock woolly adelgid, but its efficacy is short-lived (Cowles and Lagalante 2009, Faulkenberry et al. 2012). Because dinotefuran is fast-acting and imidacloprid is a long-lasting insecticide, these two systemic insecticides are considered to be complementary to each other and can be applied at the same time.

Chemical treatments are quick and effective methods to control hemlock woolly adelgids but may have non-target effects, raising concern for broader ecological impacts in forests (Kung et al. 2015, Morrissey et al. 2015). Because dinotefuran is water soluble it can easily leach into water sources. Similarly, imidacloprid and its metabolite, olefin, persist in tree foliage for multiple years (Benton et al. 2015) and these compounds can be a threat to non-target organisms. Optimized doses of active ingredient per tree is recommended to minimize risk of leaching and effects on non-target organisms (Cowles 2009). Benton and Cowles (2016) have developed easy to use guidelines for imidacloprid and recommend not applying the insecticide within 10 feet of water sources.

Integrated Biological and Chemical Treatments

Chemical treatments may have negative impacts on released predators of hemlock woolly adelgid (Eisenback et al. 2010). However, recent studies indicate that using low rates of imidacloprid on hemlock trees provides sufficient control of hemlock woolly adelgid populations, promotes hemlock health, and will not impact hemlock woolly adelgid predators after insecticide concentration has diminished in the trees (Eisenback et al. 2014, Mayfield et al. 2015). This indicates that chemical and biological control may be compatible for management of hemlock woolly adelgid; however, further studies are required to determine the selective timing for application of these treatments and behavior of predator consuming prey with sublethal doses of insecticide. Biocontrol laboratories and pesticide application professionals have to work together for successful integrated management of hemlock woolly adelgid in forests. Documentation of insecticide treatment in and around areas where predators have been released would be valuable for investigations on the compatibility of biological control and insecticide treatments.

Conclusion

Currently, available control measures are not sufficiently effective to reduce the spread of hemlock woolly adelgid in eastern North America. The pest is increasing its range in northeastern North America, even where cold winter conditions do result in increased mortality and slow it's spread, but annual variation in weather and adelgid adaptation to colder climates have allowed it to continue to spread. Biological control is the most explored, long-term option to control hemlock woolly adelgid, but it will demand time for predator establishment and sustained population growth. The sheer numbers of hemlock woolly adelgid present in a single tree, let alone a forest, will require large numbers of predators to bring population densities to levels that will not cause damage to the trees. Models suggest that removing 90% or more of the sistentes generation, as often occurs with cold winter temperatures, is not enough to prevent hemlock woolly adelgid populations from quickly rebounding, therefore, maintaining predator pressure throughout the life cycle is essential in reducing the pest populations (Elkinton et al. 2011). This is why a guild of predators is being released that will attack all life stages of hemlock woolly adelgid. Currently, only the *Leucopis* flies are available and being released to feed on the summer progredientes generation and we know little about their phenology or how they will eventually perform in eastern North America. Long-term research to find resistant hemlocks for use in restoring hemlock woolly adelgid impacted ecosystems is underway but will take years and more resources than are currently being directed for that purpose. Furthermore, additional work is needed to evaluate the combination of existing tools (e.g. chemical, biological, and silvicultural) in the same stands and forests. Continued progress in all these areas is critical to protect the unique and valuable ecosystems that hemlocks provide.

Acknowledgments

We thank Nathan Havill, Kelli Hoover, and Noel Schneeberger for their critical review of this paper and two anonymous reviewers for suggestions that made this a better paper. We thank all of those who have agreed to let us use their photos for this paper.

References Cited

Adkins, J. K., and L. K. Rieske. 2015. A terrestrial invader threatens a benthic community: potential effects of hemlock woolly adelgid-induced loss of eastern hemlock on invertebrate shredders in headwater streams. Biol. Invasions 17: 1163–1179.

Annand, P. N. 1924. A new species of *Adelges* (Hemiptera, Phylloxeridae). Pan-Pac. Entomol. 1: 79–82.

Annand, P. N. 1928. A contribution toward a monograph of the Adelginae (Phylloxeridae) of North America. Stanford University Press, Palo Alto, CA.

Barden, L. S. 1979. Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. Oecologia 44: 141–142.

Benton, E. P., J. F. Grant, R. J. Webster, R. J. Nichols, R. S. Cowles, A. F. Lagalante, and C. I. Coots. 2015. Assessment of imidacloprid and its metabolites in foliage of eastern hemlock multiple years following treatment for hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae), in forested conditions. J. Econ. Entomol. 108: 2672–2682.

Benton, E. P., and R. S. Cowles. 2016. Optimized insecticide dosage for hemlock woolly adelgid control in hemlock trees. WSFNR-17-01, The University of Georgia Warnell School of Forestry and Natural Resources, Tifton, GA.

Benton, E. P., J. F. Grant, R. J. Webster, R. S. Cowles, A. F. Lagalante, A. M. Saxton, R. J. Nichols, and C. I. Coots, 2016. Hemlock woolly adelgid (Hemiptera: Adelgidae) abundance and hemlock canopy health numerous years after imidacloprid basal drench treatments: implications for management programs. J. Econ. Entomol. 109: 2125–2136.

Benton, E. P., J. F. Grant, R. J. Nichols, R. J. Webster, J. S. Schwartz, and J. K. Bailey. 2017. Risk assessment of imidacloprid use in forest settings on the aquatic macroinvertebrate community. Environ. Toxicol. Chem. 36: 3108–3119.

Binazzi, A. 1984. Chiave per le specie afidiche più note delle conifere in Europa. Redia 67: 547–571.

Bonneau, L. R., K. S. Shields, and D. L. Civco. 1999. Using satellite images to classify and analyze the health of hemlock forests infested by the hemlock woolly adelgid. Biol. Invasions 1: 255–267.

Brantley, S., C. R. Ford, and J. M. Vose. 2013. Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests. Ecol. Appl. 23: 777–790.

Brantley, S. T., A. E. Mayfield, R. M. Jetton, C. F. Miniat, D. R. Zietlow, C. L. Brown, and J. R. Rhea. 2017. Elevated light levels reduce hemlock woolly adelgid infestation and improve carbon balance of infested eastern hemlock seedlings. Forest Ecol. and Manag. 385: 150–160.

Butin, E., A. H. Porter, and J. Elkinton. 2005. Adaptation during biological invasions and the case of *Adelges tsugae*. Evol. Ecol. Res. 7: 887–900.

Canadian Food Inspection Agency (CFIA). 2017a. Hemlock woolly adelgid infestation confirmed in Nova Scotia. (https://www.canada.ca/en/food-inspection-agency/news/2017/08/hemlock_woolly_adelgidconfirmedinnovascotia.html) (accessed 10 December 2018).

Canadian Food Inspection Agency (CFIA). 2017b. Phytosanitary requirements to prevent the introduction and spread of the hemlock woolly adelgid (*Adelges tsugae* Annand) from the United States and within Canada. (http://www.inspection.gc.ca/plants/plant-pests-invasive-species/directives/forestry/d-07-05/eng/1323754212918/1323754664992) (accessed 10 December 2018).

Centre for Agriculture and Biosciences International (CABI). 2018. *Adelges tsugae* (hemlock woolly adelgid). *In* Invasive Species Compendium. CAB International, Wallingford, UK. (https://www.cabi.org/isc/datasheet/3270) (accessed 10 December 2018).

Cheah, C. A. J. 2011. *Sasajiscymnus* (=*Pseudoscymnus*) *tsugae*, a ladybeetle from Japan, Chapter 4, pp. 42–53. *In* B. Onken and R. C. Reardon (eds.), Implementation and status of biological control of the hemlock woolly adelgid. USDA Forest Service, Forest Health Technology enterprise Team, Publication FHTET-2011-04, Morgantown, WV.

Cheah, C. A. S. J. 2017. Predicting hemlock woolly adelgid winter mortality in Connecticut forests by climate divisions. Northeast. Nat. 24: B90–B118.

Cheah, C. A. J., and M. S. McClure. 2000. Seasonal synchrony of life cycles between the exotic predator, *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae) and its prey, the hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae). Agr. and Forest Entomol. 2: 241–251.

Cheah, C. A. S.-J., and M. S. McClure. 2002. *Pseudoscymnus tsugae* in Connecticut forests: the first five years, pp. 150–165. *In* B. Onken, R. Reardon, and J. Lashomb (eds.), Proceedings, Symposium on Hemlock Woolly Adelgid in the Eastern United States, 5–7 February 2002, East Brunswick, NJ. Rutgers University, New Brunswick, NJ.

Cheah, C. A. J, M. E. Montgomery, S. Salom, B. L. Parker, S. Costa, and M. Skinner. 2004. Biological control of hemlock woolly adelgid. U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.

Chrystal, R. N. 1916. The forest insect problem in Stanley Park. Proceed. Entomol. Soc. B.C. 9: 63–66.

Coots, C., P. Lambdin, J. Franklin, J. Grant, and R. Rhea. 2015. Influence of hemlock woolly adelgid infestation levels on water stress in eastern hemlocks within the Great Smoky Mountains National Park, USA. Forests 6: 271–279.

Costa, S., and B. Onken. 2006. Standardizing sampling for detection and monitoring of hemlock woolly adelgid in eastern hemlock forests. U.S. Department of Agriculture, Forest Service, Washington, DC.

Cowles, R. S. 2009. Optimizing dosage and preventing leaching of imidacloprid for management of hemlock woolly adelgid in forests. Forest Ecol. Manag. 257: 1026–1033.

Cowles, R. S., M. E. Montgomery, and C. A. Cheah. 2006. Activity and residues of imidacloprid applied to soil and tree trunks to control hemlock woolly adelgid (Hemiptera: Adelgidae) in forests. J. Econ. Entomol. 99: 1258–1267.

Cowles, R. S., and A. F. Lagalante. 2009. Activity and persistence of systemic insecticides for managing hemlock woolly adelgids, pp. 17–18. *In* K. A. McManus and K. W. Gottschalk (eds.), Proceedings, 20th U.S. Department of Agriculture Interagency Research Forum on Invasive Species 2009, 13–16 January 2009, Annapolis, MD. Gen. Tech. Rep. NRS-P-51, U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Davis, G. A., N. P. Havill, Z. N. Adelman, A. Caccone, L. T. Kok, and S. M. Salom. 2011. DNA barcodes and molecular diagnostics to distinguish an introduced and native *Laricobius* (Coleoptera: Derodontidae) species in eastern North America. Biol. Control 58: 53–59.

Dilling, C., P. Lambdin, J. Grant, and R. Rhea. 2010. Spatial and temporal distribution of imidacloprid in eastern hemlock in the southern Appalachians. J. Econ. Entomol. 103: 368–373.

Doccola, J. J., E. J. Bristol, S. D. Sifleet, J. Lojko, and P. M. Wild. 2007. Efficacy and duration of trunk-injected imidacloprid in the management of hemlock woolly adelgid (*Adelges tsugae*). Arbor. Urban Forestry 33: 12.

Domec, J. C., L. N. Rivera, J. S. King, I. Peszlen, F. Hain, B. Smith, and J. Frampton. 2013. Hemlock woolly adelgid (*Adelges tsugae*) infestation affects water and carbon relations of eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*). New Phytol. 199: 452–463.

Eisenback, B. M., S. M. Salom, L. T. Kok, and A. F. Lagalante. 2010. Lethal and sublethal effects of imidacloprid on hemlock woolly adelgid (Hemiptera: Adelgidae) and two introduced predator species. J. Econ. Entomol. 103: 1222–1234.

Eisenback, B. M., S. M. Salom, L. T. Kok, and A. F. Lagalante. 2014. Impacts of trunk and soil injections of low rates of imidacloprid on hemlock woolly adelgid (Hemiptera: Adelgidae) and eastern hemlock (Pinales: Pinaceae) health. J. Econ. Entomol. 107: 250–258.

Elkinton, J. S., R. T. Trotter, and A. F. Paradis. 2011. Chapter 2: simulations of population dynamics of hemlock woolly adelgid and potential impact of biological control agents, pp. 15–24. *In* B. Onken and R. Reardon (eds.), Implementation and status of biological control of the hemlock woolly adelgid. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.

Elkinton, J. S., J. A. Lombardo, A. D. Roehrig, T. J. McAvoy, A. Mayfield, and M. Whitmore. 2017. Induction of cold hardiness in an invasive herbivore: the case of hemlock woolly adelgid (Hemiptera: Adelgidae). Environ. Entomol. 46: 118–124.

Ellison, A. M., A. A. Barker-Plotkin, D. R. Foster, and D. A. Orwig. 2010. Experimentally testing the role of foundation species in forests: the Harvard Forest hemlock removal experiment. Methods Ecol. Evol. 1: 168–179.

Evans, A. M., and T. G. Gregoire. 2007a. A geographically variable model of hemlock woolly adelgid spread. Biol. Invasions 9: 369–382.

Evans, A. M., and T. G. Gregoire. 2007b. The tree crown distribution of hemlock woolly adelgid, *Adelges tsugae* (Hem., Adelgidae) from randomized branch sampling. J. App. Entomol. 131: 26–33.

Fajvan, M. A. 2008. The role of silvicultural thinning in eastern forests threatened by hemlock woolly adelgid (*Adelges tsugae*), pp. 247–256. *In* R. L. Deal (tech. ed.), Integrated Restoration of Forested Ecosystems to Achieve Multiresource Benefits: Proceedings of the 2007 National Silviculture Workshop, 7–10 May 2007, Ketchikan, AK. Gen. Tech. Rep. PNW-733, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Farjon, A. 2010. A handbook of the world's conifers. Brill, Boston, MA.

Faulkenberry, M. S., J. D. Culin, S. N. Jeffers, M. B. Riley, and W. C. Bridges. 2012. Efficacy of imidacloprid and dinotefuran applied as soil drenches or trunk sprays for managing *Adelges tsugae* (Hemiptera: Adelgidae) on mature hemlock trees in a forest. J. Entomol. Sci. 47: 369–374.

Favret, C., N. P. Havill, G. L. Miller, M. Sano, and B. Victor. 2015. Catalog of the adelgids of the world (Hemiptera, Adelgidae). Zookeys 2015: 35–54.

Fidgen, J. G., D. E. Legg, and S. M. Salom. 2006. Binomial sequential sampling plan for hemlock woolly adelgid (Hemiptera: Adelgidae) sistens infesting individual eastern hemlock trees. J. Econ. Entomol. 99: 1500–1508.

Fidgen, J. G., M. C. Whitmore, and J. J. Turgeon. 2016. Ball sampling, a novel method to detect *Adelges tsugae* (Hemiptera: Adelgidae) in hemlock (Pinaceae). Can. Entomol. 148: 118–121.

Fidgen, J. G., M. C. Whitmore, and J. J. Turgeon. 2017. Detection of hemlock woolly adelgid (Hemiptera: Adelgidae) infestations with sticky traps. Great Lakes Entomol. 48: 125–131.

Fischer, M. J., N. P. Havill, C. S. Jubb, S. W. Prosser, B. D. Opell, S. M. Salom, and L. T. Kok. 2014. Contamination delays the release of *Laricobius osakensis* for biological control of hemlock woolly adelgid: cryptic diversity in Japanese *Laricobius* spp. and colony-purification techniques. Southeast. Naturalist 13: 178–191.

Fischer, M. J., C. C. Brewster, N. P. Havill, S. M. Salom, and L. T. Kok. 2015. Assessment of the potential for hybridization between *Laricobius nigrinus* (Coleoptera: Derodontidae) and *Laricobius osakensis*, predators of the hemlock woolly adelgid (Hemiptera: Adelgidae). Biocontrol Sci. and Technol. 25: 1467–1482.

Godman, R. M., and K. Lancaster. 1990. *Tsuga canadensis* (L.) Carriere, pp. 605–612. *In* R. M. Burns and B. H. Honkala (eds.), Silvics of North America: conifers; agriculture handbook 654, vol. 1. USDA Forest Service, Washington, DC.

Gonda-King, L., L. Radville, and E. L. Preisser. 2012. False ring formation in eastern hemlock branches: impacts of hemlock woolly adelgid and elongate hemlock scale. Environ. Entomol. 41: 523–531.

Gonda-King, L., S. Gomez, J. L. Martin, C. M. Orians, and E. L. Preisser. 2014. Tree responses to an invasive sap-feeding insect. Plant Ecol. 215: 297–304.

Gouger, R. J. 1971. Control of *Adelges tsugae* on hemlock in Pennsylvania. Scientific Tree Topics 3: 6–9.

Gouli, S., B. L. Parker, and M. Skinner. 1997. Isolation of fungi associated with hemlock woolly adelgid (Homoptera: Adelgidae). J. Invert. Path. 70: 76–77.

Gray, D. R., and S. M. Salom. 1996. Biology of the hemlock woolly adelgid in the southern Appalachians, pp. 26–35. *In* S. M. Salom, T. C. Tigner, and R. C. Reardon (eds.), Proceedings of the First Hemlock Woolly Adelgid Review, 12 October 1995, Charlottesville, VA. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.

Grubin, S. M., D. W. Ross, and K. F. Wallin. 2011. Prey suitability and phenology of *Leucopis* spp. (Diptera: Chamaemyiidae) associated with hemlock woolly adelgid (Hemiptera: Adelgidae) in the Pacific Northwest. Environ. Entomol. 40: 1410–1416.

Hakeem, A., J. F. Grant, G. J. Wiggins, P. L. Lambdin, and J. R. Rhea. 2011. Establishment and coexistence of two predators, *Laricobius nigrinus*, and *Sasajiscymnus tsugae*, introduced against hemlock woolly adelgid on eastern hemlock. Biocontrol Sci. Tech. 21:687–691.

Havill, N. P., M. E. Montgomery, G. Y. Yu, S. Shiyake, and A. Caccone. 2006. Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. Ann. Entomol. Soc. Am. 99: 195–203.

Havill, N. P., and R. G. Foottit. 2007. Biology and evolution of adelgidae. Annu. Rev. Entomol. 52: 325–349.

Havill, N. P., G. Davis, D. L. Mausel, J. Klein, R. McDonald, C. Jones, and A. Caccone. 2012. Hybridization between a native and introduced predator of Adelgidae: an unintended result of classical biological control. Biol. Control 63: 359–369.

Havill, N. P., L. C. Vieira, S. M. Salom. 2014. Biology and control of hemlock woolly adelgid. FHTET-2014-05, U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.

Havill, N. P., S. Shiyake, A. Lamb Galloway, R. G. Foottit, G. Yu, A. Paradis, J. Elkinton, M. E. Montgomery, M. Sano, and A. Caccone. 2016. Ancient and modern colonization of North America by hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae), an invasive insect from East Asia. Mol. Ecol. 25: 2065–2080.

Havill, N. P., S. D.Gaimari, and A. Caccone. 2018. Cryptic east-west divergence and molecular diagnostics for two species of silver flies (Diptera: Chamaemyiidae: Leucopis) from North America being evaluated for biological control of hemlock woolly adelgid. Biol. Control 121: 23–29.

Holman, G., P. D. Tredici, N. Havill, N. S. Lee, R. Cronn, K. Cushman, S. Mathews, L. Raubeson, and C. S. Campbell. 2017. A new species and introgression in eastern Asian hemlocks (Pinaceae: Tsuga). Syst. Botany 42: 733–746.

Ingwell, L. L., and E. L. Preisser. 2011. Using citizen science programs to identify host resistance in pest-invaded forests. Conserv. Biol. 25: 182–188.

Jenkins, J. C., J. D. Aber, and C. D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Can. J. Forest Res. 29: 630–645.

Jetton, R. M., W. S. Dvorak, and A. A. Whittier. 2008. Ecological and genetic factors that define the natural distribution of Carolina hemlock in the southeastern United States and their role in ex situ conservation. Forest Ecol. and Manag. 255: 3212–3221.

Jones, A. C., D. E. Mullins, T. H. Jones, and S. M. Salom. 2014a. Characterization of physical and chemical defenses in the hemlock woolly adelgid. J. Chem. Ecol. 40: 560–568.

Jones, C. E., N. P. Havill, J. L. Hanula, and S. K. Braman. 2014b. Post release recovery of hemlock woolly adelgid predators in the north Georgia mountains. J. Entomol. Sci. 49: 383–400.

Jones, A. C., D. E. Mullins, C. Brewster, J. P. Rhea, and S. M. Salom. 2016. Fitness and physiology of *Adelges tsugae* (Hemiptera: Adelgidae) in relation to the health of the eastern hemlock. Insect Sci. 23: 843–853.

Joseph, S. V., A. E. Mayfield, M. J. Dalusky, C. Asaros, and C. W. Berisford. 2011. Phenology of the hemlock woolly adelgid (Hemiptera: Adelgidae) in northern Georgia. J. Entomol. Sci. 46: 315–324.

Keena, M. A., R. T. Trotter, 3rd, C. Cheah, and M. E. Montgomery. 2012. Effects of temperature and photoperiod on the aestivo-hibernal egg diapause of *Scymnus camptodromus* (Coleoptera: Coccinellidae). Environ. Entomol. 41: 1662–1671.

Kohler, G. R., V. L. Stiefel, K. F. Wallin, and D. W. Ross. 2008. Predators associated with the hemlock woolly adelgid (Hemiptera: Adelgidae) in the Pacific Northwest. Environ. Entomol. 37: 494–504.

Kung, W. Y., K. Hoover, R. Cowles, and R. T. Trotter III. 2015. Long-term effects of imidacloprid on eastern hemlock canopy arthropod biodiversity in New England. Northeastern Nat. 22: 40–55.

Lamb, A., L. C. Vieira, S. Shiyake, H. Story, T. McAvoy, and S. Salom. 2010. Suitability of *Laricobius osakensis* as a potential biological control agent of hemlock woolly adelgid, pp. 17–20. *In* B. Onken and R. C. Reardon (eds.), Fifth Symposium on Hemlock Woolly Adelgid in the Eastern United States. USDA Forest Service Publication FHTET-2010-07, Morgantown, WV.

Leppanen, C., and D. Simberloff. 2017. Implications of early production in an invasive forest pest. Agri. and Forest Entomol. 19: 217–224.

Leschen, R. A. B. 2011. World review of *Laricobius* (Coleoptera: Derodontidae). Zootaxa 2908: 1–44.

Li, X., E. L. Preisser, K. J. Boyle, T. P. Holmes, A. Liebhold, and D. Orwig. 2014. Potential social and economic impacts of the hemlock woolly adelgid in southern New England. Southeast. Nat. 13:130–146.

Limbu, S., K. Cassidy, M. Keena, P. Tobin, and K. Hoover. 2016. Host range specificity of *Scymnus camptodromus* (Coleoptera: Coccinellidae), a predator of hemlock woolly adelgid (Hemiptera: Adelgidae). Environ. Entomol. 45: 94–100.

Lombardo, J. A., and J. S. Elkinton. 2017. Environmental adaptation in an asexual invasive insect. Ecol. Evol. 7: 5123–5130.

Lorimer, C. G., S. E. Dahir, and E. V. Nordheim. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. J. Ecol. 89: 960–971.

Mausel, D. L., S. M. Salom, L. T. Kok, and G. A. Davis. 2010. Establishment of the hemlock woolly adelgid predator, *Laricobius nigrinus* (Coleoptera: Derodontidae), in the Eastern United States. Environ. Entomol. 39: 440–448.

Mausel, D. L., R. G. Van Driesche, and J. S. Elkinton. 2011. Comparative cold tolerance and climate matching of coastal and inland *Laricobius nigrinus* (Coleoptera: Derodontidae), a biological control agent of hemlock woolly adelgid. Biol. Control 58: 96–102.

Mayfield, A. E., B. C. Reynolds, C. I. Coots, N. P. Havill, C. Brownie, A. R. Tait, J. L. Hanula, S. V. Joseph, and A. B. Galloway. 2015. Establishment, hybridization and impact of *Laricobius* predators on insecticide-treated hemlocks: exploring integrated management of the hemlock woolly adelgid. For. Ecol. Manage. 335: 1–10.

McAvoy, T. J., R. Mays, N. G. Johnson, and S. M. Salom. 2017a. The effects of shade, fertilizer, and pruning on eastern hemlock trees and hemlock woolly adelgid. Forests 8: 156.

McAvoy, T. J., J. Regniere, R. St-Amant, N. F. Schneeberger, S. M. Salom. 2017b. Mortality and recovery of hemlock woolly adelgid (*Adelges tsugae*) in response to winter temperatures and predictions for the future. Forests 8: 497.

McClure, M. S. 1987. Biology and control of hemlock woolly adelgid (vol. 851). Connecticut Agricultural Experiment Station, New Haven, CT.

McClure, M. S. 1989. Evidence of a polymorphic life-cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera, Adelgidae). Ann. Ent. Soc. Am. 82: 50–54.

McClure, M. S. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). Environ. Entomol. 19: 36–43.

McClure, M. S. 1991. Density-dependent feedback and population-cycles in *Adelges tsugae* (Homoptera, Adelgidae) on *Tsuga canadensis*. Environ. Entomol. 20: 258–264.

McClure, M. S. 1992. Effects of implanted and injected pesticides and fertilizers on the survival of *Adelges tsugae* (Homoptera: Adelgidae) and on the growth of *Tsuga canadensis*. J. Econ. Entomol. 85: 468–472.

McClure, M. S. 1995. Using natural enemies from Japan to control hemlock woolly adelgid. Front. Plant Sci. 47: 5–7.

McClure, M. S., and C. A. S. J. Cheah. 1999. Reshaping the ecology of invading populations of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in eastern North America. Biol. Invasions 1: 247–254.

McClure, M. S., S. M. Salom, K. S. Shields. 2001. Hemlock woolly adelgid. FHTET-2001-03, U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.

McWilliams, W. H., and T. L. Schmidt. 2000. Composition, structure, and sustainability of hemlock ecosystems in eastern North America, pp. 5–10. *In* Proceedings, Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. Gen. Tech. Rep. NE-267, United States Department of Agriculture, Forest Service, Northeastern Experiment Station, Newtown Square, PA.

MDARD. 2013. Hemlock woolly adelgid draft. (http://www.michigandnr.com/FTP/forestry/Mech/FHH/2013/hwa/Article) (accessed 10 December 2018).

MDARD. 2016. Hemlock woolly adelgid informational meeting presentation. (https://www.michigan.gov/documents/mdard/Hemlock_Woolly_Adelgid_Informational_Meeting_Presentation_from_10-3-16_and_10-5-16_536733_7.pdf) (accessed 10 December 2018).

MDARD. 2017. Quarantine information. (https://www.michigan.gov/invasives/0,5664,7-324-68002_71241-367635--,00.html) (accessed 10 December 2018).

MDARD. 2018. Hemlock woolly adelgid infestation history in Michigan. (https://www.michigan.gov/documents/mdard/Hemlock_Woolly_Adelgid_Infestation_History_in_Michigan_500168_7.pdf) (accessed 10 December 2018).

Mech, A. M., P. C. Tobin, R. O. Teskey, J. R. Rhea, and K. J. K. Gandi. 2017. Increases in summer temperatures decrease the survival of an invasive forest insect. Biol. Invasions 20: 365–374.

Montgomery, M. E., and M. A. Keena. 2011. Chapter 5: *Scymnus* (*Neopullus*) lady beetles from China, pp. 53–76. *In* B. Onken and R. C. Reardon (eds.), Implementation and status of biological control of the hemlock woolly adelgid. USDA Forest Service, Forest Health Technology enterprise Team, Publication FHTET-2011-04, Morgantown, WV.

Montgomery, M. E., and S. M. Lyon. 1995. Natural enemies of adelgids in North America: their prospect for biological control of *Adelges tsugae* (Homoptera: Adelgidae), pp. 89–102. *In* S. M. Salom, T. C. Tigner, and R. C. Reardon (eds.), Proceedings of the First Hemlock Woolly Adelgid Review, 12 October 1995, Charlottesville, VA. U.S. Department of Agriculture Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.

Montgomery, M. E., S. E. Bentz, and R. T. Olsen. 2009. Evaluation of hemlock (*Tsuga*) species and hybrids for resistance to *Adelges tsugae* (Hemiptera: Adelgidae) using artificial infestation. J. Econ. Entomol. 102: 1247–1254.

Montgomery, M. E., S. Shiyake, N. P. Havill, and R. A. B. Leschen. 2011. A new species of *Laricobius* (Coleoptera: Derodontidae) from Japan with phylogeny and a key for native and introduced congeners in North America. Ann. Ent. Soc. Am. 104: 389–401.

Morrissey, C. A., P. Mineau, J. H. Devries, F. Sanchez-Bayo, M. Liess, M. C. Cavallaro, and K. Liber. 2015. Neonicotinoid contamination of global surface waters and associated risk to aquatic invertebrates: a review. Environ. Int. 74: 291–303.

Nuckolls, A. E., N. Wurzburger, C. R. Ford, R. L. Hendrick, J. M. Vose, and B. D. Kloeppel. 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: impacts on the carbon cycle of southern Appalachian forests. Ecosystems 12: 179–190.

Onken, B., and R. Reardon (eds.). **2011**. Implementation and status of biological control of the hemlock woolly adelgid. U.S. Department of Agriculture, Forest Service, Publication FHTET-2011-04, Morgantown, WV.

Oten, K. L. F., A. C. Cohen, and F. P. Hain. 2014. Stylet bundle morphology and trophically related enzymes of the hemlock woolly adelgid (Hemiptera: Adelgidae). Ann. Entomol. Soc. Am. 107: 680–690.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitig. Adapt. Strat. Gl. 13: 541–554.

Parker, B. L., M. Skinner, S. Gouli, T. Ashikaga, and H. B. Teillon. 1998. Survival of hemlock woolly adelgid (Homoptera: Adelgidae) at low temperatures. Forest Sci. 44: 414–420.

Parker, B. L., M. Skinner, S. Gouli, T. Ashikaga, and H. B. Teillon. 1999. Low lethal temperature for hemlock woolly adelgid (Homoptera: Adelgidae). Environ. Entomol. 28: 1085–1091.

Parker, B. L., S. Costa, and M. Skinner. 2004. Pathogens, pp. 13–14. *In* C. Cheah, M. E. Montgomery, S. Salom, B. L. Parker, S. Costa, and M. Skinner (eds.), *Biological control of hemlock woolly adelgid*. USDA, Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.

Piatek, K. B., M. A. Fajvan, and R. M. Turcotte. 2016. Thinning effects on foliar elements in eastern hemlock: implications for managing the spread of the hemlock woolly adelgid. Can. J. Forest Res. 47: 81–88.

Reid, W. R., B. L. Parker, S. Y. Gouli, M. Skinner, V. V. Gouli, and H. B. Teillon. 2010. Fungi associated with the hemlock woolly adelgid, *Adelges tsugae*, and assessment of entomopathogenic isolates for management. J. Insect Sci. 10: 62.

Ross, R. M., R. M. Bennett, C. D. Snyder, J. A. Young, D. R. Smith, and D. P. Lemarie. 2003. Influence of eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River Basin. Ecol. Freshwater Fish 12: 60–65.

Royle, D. D., and R. G. Lathrop. 1997. Monitoring hemlock forest health in New Jersey using Landsat TM data and change detection techniques. Forest Sci. 43: 327–335.

Russo, N. J., C. A. Cheah, and M. W. Tingley. 2016. Experimental evidence for branch-to-bird transfer as a mechanism for avian dispersal of the hemlock woolly adelgid (Hemiptera: Adelgidae). Environ. Entomol. 45: 1107–1114.

Salom, S. M., A. A. Sharov, W. T. Mays, and J. W. Neal Jr. 2001. Evaluation of aestival diapause in hemlock woolly adelgid (Homoptera: Adelgidae). Environ. Entomol. 30: 877–882.

Salom, S. M., A. A. Sharov, W. T. Mays, and D. R. Gray. 2002. Influence of temperature on development of hemlock woolly adelgid (Homoptera: Adelgidae) progredientes. J. Entomol. Sci. 37: 166–176.

Sasaji, H., and M. S. McClure. 1997. Description and distribution of *Pseudoscymnus tsugae* sp. nov. (Coleoptera: Coccinellidae), an important predator of hemlock woolly adelgid in Japan. Ann. Ent. Soc. Am. 90: 563–568.

Shields, K. S. H., and R. T. Hirth. 2005. Bacterial endosymbionts of *Adelges tsugae* Annand: potential targets for biocontrol?, pp. 357–59. *In* B. Onken and R. Reardon (eds.), Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, 1–3 February 2005, Asheville, NC. USDA Forest Service, Morgantown, WV.

Skinner, M., B. L. Parker, S. Gouli, and T. Ashikaga. 2003. Regional responses of hemlock woolly adelgid (Homoptera: Adelgidae) to low temperatures. Environ. Entomol. 32: 523–528.

Spaulding, H. L., and L. K. Rieske. 2010. The aftermath of an invasion: structure and composition of Central Appalachian hemlock forests following establishment of the hemlock woolly adelgid, *Adelges tsugae*. Biol. Invasions 12: 3135–3143.

Stadler, B., T. Müller, D. Orwig, and R. Cobb. 2005. Hemlock woolly adelgid in New England forests: canopy impacts transforming ecosystem processes and landscapes. Ecosystems 8: 233–247.

Story, H. M., L. C. Vieira, S. M. Salom, and L. T. Kok. 2012. Assessing performance and competition among three *Laricobius* (Coleoptera: Derodontidae) species, predators of hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae). Environ. Entomol. 41: 896–904.

Sussky, E. M., and J. S. Elkinton. 2014. Density-dependent survival and fecundity of hemlock woolly adelgid (Hemiptera: Adelgidae). Environ. Entomol. 43: 1157–1167.

Sussky, E. M., and J. S. Elkinton. 2015. Survival and near extinction of hemlock woolly adelgid (Hemiptera: Adelgidae) during summer aestivation in a hemlock plantation. Environ. Entomol. 44: 153–159.

Tingley, M. W., D. A. Orwig, R. Field, and G. Motzkin. 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. J. Biogeography 29: 1505–1516.

Tobin, P. C., R. M. Turcotte, and D. A. Snider. 2013. When one is not necessarily a lonely number: initial colonization dynamics of *Adelges tsugae* on eastern hemlock, *Tsuga canadensis*. Biol. Invasions 15: 1925–1932.

Toland, A., C. Brewster, K. Mooneyham, and S. Salom. 2018. First report on establishment of *Laricobius osakensis* (Coleoptera: Derodontidae), a biological control agent for hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae), in the Eastern U.S. Forests 9: 496.

Trotter, R. T., 3rd, and K. S. Shields. 2009. Variation in winter survival of the invasive hemlock woolly adelgid (Hemiptera: Adelgidae) across the eastern United States. Environ. Entomol. 38: 577–587.

U.S. Department of Agriculture (USDA). 2017. Hemlock woolly adelgid infestation map. (http://hiro.ento.vt.edu/hwa/wp-content/uploads/2018/06/HWA2017.pdf) (accessed 10 December 2018).

Vieira, L. C., S. M. Salom, and L. T. Kok. 2012. Functional and numerical response of *Laricobius* spp. predators (Coleoptera: Derodontidae) on hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae). Biol. Control 61: 47–54.

von Dohlen, C. D., U. Spaulding, K. Shields, N. P. Havill, C. Rosa, and K. Hoover. 2013. Diversity of proteobacterial endosymbionts in hemlock woolly adelgid (*Adelges tsugae*) (Hemiptera: Adelgidae) from its native and introduced range. Environ. Microbiol. 15: 2043–2062.

Wallace, M. S., and F. P. Hain. 2000. Field surveys and evaluation of native and established predators of the hemlock woolly adelgid (Homoptera: Adelgidae) in the southeastern United States. Environ. Entomol. 29: 638–644.

Ward, J. S., M. E. Montgomery, C. A. S.-J. Cheah, B. P. Onken, and R. S. Cowles. 2004. Eastern hemlock forests: guidelines to minimize the impacts of hemlock woolly adelgid. NA-TP-03-04, USDA Forest Service, Northeastern Area State and Private Forestry, Morgantown, WV.

Weed, A. S., J. S. Elkinton, and N. K. Lany. 2016. Density-dependent recruitment and diapause in the spring-feeding generation of hemlock woolly adelgid (Hemiptera: Adelgidae) in Western North America. Environ. Entomol. 45: 1352–1359.

Weglarz, K. M., N. P. Havill, G. R. Burke, and C. D. von Dohlen. 2018. Partnering with a pest: genomes of hemlock woolly adelgid symbionts reveal atypical nutritional provisioning patterns in dual-obligate bacteria. Genome Biol. Evol. 10: 1607–1621.

Young, R. F., K. S. Shields, and G. P. Berlyn. 1995. Hemlock woolly adelgid (Homoptera, Adelgidae)—stylet bundle insertion and feeding sites. Ann. Entomol. Soc. Am. 88: 827–835.

Zilahi-Balogh, G. M. G., L. T. Kok, and S. M. Salom. 2002. Host specificity of *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a potential biological control agent of the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). Biol. Control 24: 192–198.

Zilahi-Balogh, G. M. G., S. M. Salom, and L. T. Kok. 2003. Development and reproductive biology of *Laricobius nigrinus*, a potential biological control agent of *Adelges tsugae*. Biocontrol 48: 293–306.

Zilahi-Balogh, G. M. G., C. D. Broeckling, L. T. Kok, and S. M. Salom. 2005. Comparison between a native and exotic adelgid as hosts for *Laricobius rubidus* (Coleoptera: Derodontidae). Biocontrol Sci. Tech. 15: 165–171.

Zilahi-Balogh, G. M. G., L. M. Humble, L. T. Kok, and S. M. Salom. 2006. Morphology of *Laricobius nigrinus* (Coleoptera: Derodontidae), a predator of the hemlock woolly adelgid. Can. Entomol. 138: 595–601.