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Hemlock Woolly Adelgid in the Eastern United States: What Have We Learned?

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1 **RUNNING HEAD: Adelgid overview**

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4 **TITLE: Hemlock Woolly Adelgid in the eastern United States: What have we**
5 **learned?**

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Abstract

23 *Adelges tsugae* Annand (Hemlock Woolly Adelgid) is a small piercing-sucking insect that
24 feeds on hemlock trees (*Tsuga* spp.). Native to Asia and the Pacific Northwest, the Hemlock
25 Woolly Adelgid is invasive in the eastern United States where it attacks *Tsuga canadensis*
26 (Eastern Hemlock) and *T. caroliniana* (Carolina Hemlock). It is currently found in 19 eastern
27 states and has caused extensive mortality to hemlock forests. The ecological and economic
28 impacts of this pest are significant, widespread, and often difficult to quantify. As the Hemlock
29 Woolly Adelgid continues to disperse throughout the range of Eastern and Carolina Hemlocks,
30 management techniques aimed at controlling it are being researched, implemented, and assessed.
31 This introductory paper provides an overview of the biology, life cycle, ecology, and history of
32 this pest in the eastern US as a foundation for this special issue.

33

34

Introduction

35 *Adelges tsugae* Annand (Hemlock Woolly Adelgid) is a small (~3 mm adult) piercing-
36 sucking insect that feeds on conifers in the genus *Tsuga* and *Picea* (Havill and Footitt 2007). The
37 population invasive to the eastern US is native to Japan (Havill et al. 2006). Although it has
38 minimal impact on its native host plants (McClure 1997), it has become a major pest in the
39 eastern US. In the eastern US, the adelgid feeds on *T. canadensis* Carrière (Eastern Hemlock)
40 and *T. caroliniana* Engelmann (Carolina Hemlock), two hemlock species that have little or no
41 defense against this insect (Montgomery et al. 2009). The resulting loss of hundreds of thousands
42 of trees from forests ranging from Georgia to Massachusetts has profoundly affected both local
43 communities and the associated ecosystems (Ellison et al. 2005).

44 This special issue of Northeastern/Southeastern Naturalist explores the adelgid's impacts and
45 the challenges posed by its invasion. It contains articles surveying the wide range of adelgid-
46 related questions researchers are addressing throughout the invaded range. In the following
47 pages, we provide an overview of adelgid biology, its interactions with and impacts on other
48 species at the community and ecosystem level, and the current status of control efforts.

49 **Biogeography and history of the invasion**

50 Hemlock Woolly Adelgid was first described as a species in the early 1920's from
51 infestations on *T. heterophylla* Sargent (Western Hemlock) in the northwestern US (Annand
52 1924). The adelgid is genetically diverse throughout its native range, with different lineages
53 associated with particular regions and host plant species. Hemlock Woolly Adelgid in the
54 northwestern US is genetically different from the population native to Asia and the invasive
55 population in the eastern US, which originated from low-elevation populations infesting *Tsuga*
56 *sieboldii* Carrière (Southern Japanese Hemlock) in central Japan (Havill et al. 2006). Hemlock
57 Woolly Adelgid in the eastern US was first reported in the early 1950s near Richmond, Virginia
58 (Souto et al. 1996). Although it was initially thought to be mainly a pest of ornamentals, by the
59 1980s the adelgid had also begun to harm forest hemlock. It is currently found in 19 eastern
60 states, ranging from northern Georgia to southern Maine (USFS 2012).

61 **Life cycle**

62 The Hemlock Woolly Adelgid has two generations per year in the invaded range (Figure 1).
63 In the early spring, first-instar nymphs of the spring generation (progreiens, plural
64 progredientes) emerge and seek out suitable feeding sites in the leaf cushion at the base of
65 hemlock needles (McClure 1989, Oten et al. 2012). These first-instar nymphs are known as
66 crawlers and can either move actively upon their natal host or be dispersed passively by wind,

67 birds, deer, or humans (McClure 1990, Turner et al. 2011). Once the crawlers find an appropriate
68 feeding site, they settle permanently and use their feeding stylet bundle to probe and feed from
69 xylem ray parenchyma cells (Young et al. 1995). Adelgids go through four larval instars before
70 maturing into adults; because Hemlock Woolly Adelgid in the invaded range reproduces
71 asexually, each mature individual is theoretically capable of producing 20-30 summer-generation
72 (sistens, plural sistentes) offspring in early summer (McClure 1989, Paradis 2011). After the
73 summer-generation crawlers settle at the base of new-growth hemlock needles, they aestivate
74 until late fall, when they begin to feed. They feed throughout the winter, and each adult is
75 theoretically capable of producing 50-100 offspring the following spring (Paradis 2011).

76 While the spring generation is the same in the adelgid's native and invaded range, the
77 summer generation differs substantially between the two areas. Summer-generation eggs hatch
78 into either wingless asexual progrediens that feed on hemlock or winged sexually-reproducing
79 sexuparae that feed on *Picea torano* Carriere (Tiger Tail Spruce) in the native range (Sato 1999).
80 In the invaded range, however, there are no suitable spruce hosts and the sexuparae perish
81 without reproducing. As a result, HWA in the eastern US is obligately asexual and genetic
82 variability is limited. Despite this lack of genetic recombination, however, there is evidence for
83 adaptive genetic variation in cold tolerance in the invaded population (Butin et al. 2005).

84 **Population ecology**

85 Although mature adelgids can produce a large number of offspring, both juvenile and adult
86 adelgids also experience high mortality rates (McClure and Cheah 2002). The dispersing
87 crawlers are wingless, passively dispersed, and stand a high probability of ending up in
88 unsuitable habitat. Even under ideal conditions, early-instar mortality rates can approach 90%
89 (Paradis 2011), and adults are susceptible to extreme heat in the summer and periods of intense

90 cold in the winter (Trotter and Shields 2009). Because even low adelgid densities substantively
91 affect tree health, its survival is highly density-dependent (McClure 1991), with the previous
92 generation's density being the strongest predictor of survival (Paradis 2011). In the invaded
93 range, this density-dependent mortality is compounded by the fact that sexuparae production
94 increases in populations feeding on unhealthy or declining hosts. Both Eastern and Carolina
95 Hemlocks are, however, higher-quality host plants for the invasive adelgid population than many
96 hemlock species that have co-evolved with other lineages of the adelgid (Montgomery et al.
97 2009). This may provide one explanation for why the adelgid is so abundant in its novel range.

98 **Community ecology**

99 The Hemlock Woolly Adelgid has numerous predators in its native range (Cota Vieira et al.
100 2013, Hakeem et al. 2011, McClure and Cheah 1999), but no predators native to the invaded
101 range appear capable of reducing adelgid densities sufficiently to consistently prevent hemlock
102 decline and death (Havill et al., 2012). As a result, its most important intraspecific interactions
103 likely involve those herbivores that co-occur on its host plant. Although *Lambdina fuscicornis*
104 Guenee (Hemlock Looper) has historically been considered a major hemlock pest (Trial and
105 Devine 1995), its densities appear to have declined in southern New England (E. Preisser,
106 personal observation). In this region, the most commonly co-occurring hemlock herbivore is
107 another invasive hemipteran, *Fiorinia externa* Ferris (Elongate Hemlock Scale) (Preisser et al.,
108 2008). This sessile armored scale feeds on the underside of hemlock needles, reproduces
109 sexually, and has one generation per year in the northeastern US and two generations in the
110 South (Abell and Van Driesche 2012, McClure 1978). Its dispersing crawler stage settles on
111 hemlock foliage in late spring, approximately one month after HWA crawlers have begun
112 feeding; because of this, the adelgid was predicted to competitively exclude the scale from

113 hemlock (McClure 1997). In reality, however, both the range and population density of the scale
114 have increased sharply in adelgid-invaded areas of southern New England (Preisser et al. 2008).

115 Because the adelgid and elongate hemlock scale are both sessile and feed on different plant
116 structures, they interact via their impact on the shared host plant. This fact is important because
117 the two species have very different impacts on plant health; both experimental research (Miller-
118 Pierce et al. 2010, Miller-Pierce and Preisser 2012, Preisser and Elkinton 2008) and landscape
119 surveys (Preisser et al. 2008, 2011) have found that while the scale can reach higher densities
120 than the adelgid, the adelgid has a greater impact on plant health. Experimental work assessing
121 their interactions on hemlock branches found that each species decreased the other species'
122 density by ~30% relative to when the species occur by themselves (Preisser and Elkinton 2008);
123 at the whole-tree level, however, intraspecific competition is only measurable when one species
124 arrives several years earlier than the other (Miller-Pierce and Preisser 2012). In such a scenario,
125 HWA densities are 40% lower when settling on trees previously infested with the scale; by
126 contrast, the prior presence of HWA does not significantly reduce scale densities (Miller-Pierce
127 and Preisser 2012). Most recently, experimental work found that HWA crawlers avoided settling
128 on EHS-infested branches, a finding supported by surveys showing that crawlers avoid settling at
129 the base of EHS-infested needles (Gomez et al. 2013). These findings suggest that EHS, despite
130 its apparent disadvantages, may actually be competitively dominant over HWA.

131 **Interaction with hemlock**

132 While HWA is capable of quickly killing hemlock trees (McClure 1991, Orwig et al. 2002),
133 the mechanism underlying such rapid HWA-mediated mortality has only recently begun to be
134 addressed. Following initial infestation, the tree declines in health. This period is marked by
135 needle drop, bud abortion, and inhibition of new growth (McClure 1991). A healthy hemlock can

136 be killed in as little as four years, with many trees (especially in warmer climates) dying within
137 ten years of infestation (McClure 1987, 1991; see the following 'larger-scale effects' section,
138 below, for a more detailed description of adelgid-induced tree mortality). Some scientists
139 hypothesized that hemlocks died from resource depletion; large numbers of adelgids essentially
140 'starved' the tree of nutrients (McClure 1991). This explanation was challenged by work that
141 used scanning electron microscopy to identify the adelgid's precise feeding mode and cellular-
142 level impact (Young et al. 1995). Because these researchers found that adelgid feeding caused
143 relatively little cellular damage, they proposed that the adelgid's impact on tree health was better
144 explained by 'toxicity': fluids secreted by feeding adelgids, or the plant's response to the
145 feeding, had a disproportionately large impact on plant health. This explanation gained credence
146 with the large increase in elongate hemlock scale densities in southern New England; similarly-
147 sized to adelgids but more abundant (Preisser et al. 2008), these scales nonetheless had less
148 impact on hemlock growth and survival (Miller-Pierce et al. 2010, Miller-Pierce and Preisser
149 2012, Preisser and Elkinton 2008, Preisser et al. 2008, 2011).

150 The large amount of damage induced by HWA feeding appears linked to a hypersensitive
151 response in hemlock. The presence of HWA at the base of a needle causes extensive damage
152 (measured by the presence of hydrogen peroxidase) to the needle itself as well as to nearby 'new
153 growth' foliage that had not been colonized by HWA crawlers (Radville et al. 2011). The
154 hypersensitive response acts to isolate sessile herbivores by killing nearby tissue and starving the
155 feeding insect (Fernandes 1990, Fernandes and Negreiros 2001). In the case of HWA, the
156 hypersensitive response causes the induction of 'false growth rings' in infested stems that
157 interfere with solute transport and prevent the stems from obtaining the water necessary for
158 photosynthesis (Domec et al. 2013, Gonda-King et al. 2012). As a result, the plant may

159 experience chronic water stress and eventually be unable to carry out photosynthesis (Domec et
160 al. 2013). Despite widespread cell death, induction of the hypersensitive response appears to
161 cause relatively little harm to feeding adelgids. On the contrary, HWA may themselves
162 biochemically manipulate the plant to induce this response. HWA possesses several enzymes
163 similar to those used by related insects to feed upon and influence their host plants (Oten 2011).
164 A detailed analysis of herbivore-mediated changes in hemlock amino acid concentrations found
165 that adelgids actually induced substantial increases in local nutrient levels (Gómez et al. 2012).
166 This manipulation may be similar to that occurring in galling insects, where sessile herbivores
167 manipulate plant physiology to build protective structures (i.e., galls) that serve as both food and
168 protection (Havill and Footitt 2007).

169 **Larger-scale effects**

170 The Hemlock Woolly Adelgid has killed so many hemlocks in the eastern US that the
171 International Union for Conservation of Nature (IUCN) recently labeled Eastern Hemlock 'near
172 threatened' and placed it on the Red List of Threatened Species (Farjon 2013). At the local level,
173 adelgid-induced hemlock mortality has substantially impacted many natural areas; Virginia's
174 Shenandoah National Park, for example, has lost ~90% of its mature hemlocks (Townsend and
175 Riese-Kinney 2006). While noticeable hemlock mortality and decline continues, however, the
176 initial predictions of complete mortality of Eastern and Carolina Hemlock have not been realized
177 (Preisser et al. 2008). Especially in the northeastern US, a substantial number of infested trees
178 continue to persist: a long-term study in Delaware Water Gap National Park (located on the NJ-
179 PA border) found that 73% of hemlocks survived for longer than ten years (Eschtruth et al.,
180 2013). A recently-published analysis of Forest Inventory Analysis (FIA) data for 432 US
181 counties made a similar point (Trotter et al., 2013). It found little evidence for large-scale decline

182 and a slight increase in median live hemlock basal area between 1985 and 2005, a fact it
183 attributed to the positive effects of reforestation and regeneration overwhelming the more recent
184 negative impacts of the adelgid.

185 Even if Eastern and Carolina Hemlock persist in eastern US ecosystems, the large losses
186 caused by adelgid infestation will substantially alter eastern forest ecosystems. Hemlocks are a
187 shade-tolerant 'foundation' species that shade and cool headwater streams that are home to trout
188 and a wide variety of aquatic invertebrates (reviewed in Ellison et al. 2005, Orwig and Foster
189 2000). They also assist in soil stabilization and controlling hydrologic regimes (Ford and Vose
190 2007). Over a nine-year period, adelgid-induced hemlock decline in the Delaware Water Gap
191 National Recreational Area (NJ) more than doubled understory light levels, increased vascular
192 plant cover nearly fourfold, and led to invasive plants colonizing 35% of the surveyed plots
193 (Eschtruth et al. 2006). Hemlock stands are also critical habitat for a number of bird species
194 (Rabenold et al. 1998), and the loss of hemlocks can substantially affect invertebrate community
195 composition (Adkins and Rieske 2013, Dilling et al. 2007, Ingwell et al. 2012).

196 There are 274 cultivars of eastern hemlock, “making it one of the most cultured and
197 cultivated landscape tree species” (Quimby 1996, Swartley 1984) that is often used as a hedge
198 because of its response to shearing (Swartley 1984). It is also desired for its color, graceful habit,
199 and, until recently, its freedom from disease and insects. According to 1995 nursery inventories
200 in Tennessee and North Carolina, the value of eastern hemlock was approximately \$34 million
201 (J.R. Rhea, personal communication, cited in Bentz et al. 2002). The invasion of the adelgid has
202 reduced the importance of native hemlocks for ornamental use and will likely also affect the
203 more than 4 million cubic feet of timber produced in the region annually (Rhea 1995, Woodsen
204 2001). Land values also deteriorate as a result of adelgid infestations. A study in residential New

205 Jersey found that 25-50% hemlock defoliation by the Hemlock Woolly Adelgid led nearby
206 property values to decline by an average of more than \$7,000.00 (Holmes et al. 2005). The future
207 use of hemlocks as ornamentals relies in part on the ability to effectively manage the adelgid.

208 **Management methods**

209 *Chemical control.* Management of the Hemlock Woolly Adelgid is largely focused on
210 biological control and chemical control (McClure 2001, McClure and Cheah 1999, Montgomery
211 1999, also see Onken and Reardon 2011). Chemical control is currently the most effective
212 method and is widely used in ornamental and landscape settings, but it is generally impractical in
213 forest settings due to prohibitive costs and the potential environmental impacts of wide-scale use
214 (Cowles 2009, McClure 1992). The biggest limiting factor is cost. Trees must be treated
215 individually, often leading managers to target a series of 'high value' trees for treatment.
216 Because chemicals degrade over time, they must be periodically re-applied to ensure continued
217 control; in addition, there is the potential for non-target environmental impacts. The water-
218 solubility of systemic insecticides allows for rapid uptake and internal transportation of the
219 chemical throughout the tree, but also allows them to impact aquatic organisms in nearby water
220 bodies. Imidacloprid, for example, has been detected in water at sites with low soil organic
221 matter (U.S. EPA 2003). The mode of chemical application may also affect hemlock forest-
222 associated fauna. Soil injections of imidacloprid, for example, can cause significant declines in
223 the abundance and richness of soil-dwelling springtails and other non-target organisms
224 (Reynolds 2008). Forest applications may be limited due to geographical and logistical
225 constraints such as difficulties in bringing equipment into a forest (Cowles et al. 2006). Lastly,
226 pesticides are not a fail-proof method. In Joyce Kilmer Memorial Forest (NC), for example,
227 pesticide applications appear relatively ineffective in reducing adelgid populations (Bompey

228 11/08/2010). Despite these concerns, research into chemical treatment options has decreased
229 their environmental impacts while increasing their efficacy (e.g., Cowles 2009). While chemicals
230 are often the best option in ornamental settings, they are generally impractical in forests as a
231 stand-alone management tool. Sustainable long-term adelgid management in forest settings will
232 likely require an integrated pest management program incorporating multiple management
233 techniques (Bentz et al. 2002, Del Tredici and Kitajima 2004, McClure and Cheah 1999).

234 *Biological control.* There appear to be no predators native to the invaded range capable of
235 consistently lowering adelgid densities sufficiently to prevent tree decline and death
236 (Montgomery and Lyon 1996, Wallace and Hain 2000, Havill et al. 2012). Researchers searching
237 for effective adelgid predators began to explore Asia and northwestern North America, the native
238 range of the Hemlock Woolly Adelgid, for organisms useful in a classical biological control
239 program. Since the 1990s, biological control has been a major focus of adelgid research and
240 management (McClure and Cheah 2002, Onken and Reardon 2011), an effort that expanded
241 considerably with the development of the Hemlock Woolly Adelgid Initiative in 2003. The
242 current program includes 28 federal and state agencies, 24 universities, seven institutions in
243 China and Japan, and numerous private industries (Onken and Reardon 2011).

244 Several beetle species have been released in hopes of controlling the Hemlock Woolly
245 Adelgid. The first was a coccinellid beetle, *Sasajiscymnus tsugae* Sasaji and McClure, that is
246 native to Japan and was first released in 1995 (Cheah 2008, 2011; Cheah and McClure 1998).
247 Since then, there have been more than two million *S. tsugae* released on more than 400 sites in
248 16 states (Cheah 2011, Grant et al. 2010, Salom et al. 2008). It successfully reproduces and
249 disperses following release, and is capable of surviving extreme climatic events (Cheah 2011).

250 Between 2004 and 2011, more than 61,000 individuals of *Scymnus sinuanodulus* Yu and
251 Yao, another coccinellid beetle native to China, have been released (Montgomery and Keena
252 2011). Because research suggests that this species is most climatically suited to the southern
253 portion of the hemlock range in the eastern US (Salom et al. 2008), most of these releases have
254 occurred in Georgia, North Carolina, and Tennessee. When released in these areas, the species
255 does not seem to require additional efforts to assist in its establishment (Montgomery and Keena
256 2011). Other beetles in the same genus have also been (*S. ningshanensis* Yu and Yao) or are
257 currently being pursued (*S. coniferarum* Crotch and *S. camptodromus* Yu and Liu) as biological
258 control agents. Native to western North America, the beetle *S. coniferarum* seems especially
259 promising since its feeding habits temporally complement that of *Laricobius nigrinus* Fender
260 (discussed in the next paragraph). Releases of *S. coniferarum* have begun, and research and
261 efficacy trials continue (Montgomery et al. 2011). Initial problems in rearing *S. camptodromus*
262 slowed this species' evaluation, but it is still being pursued because it diapauses at the same time
263 as the adelgid, has a broad geographic distribution, and is active during a critical period in the
264 adelgid life cycle (Montgomery and Keena 2011).

265 *Laricobius nigrinus* (Coleoptera: Derodontidae), a specialist adelgid predator native to
266 Oregon and Washington (Kohler et al. 2008), shows particular promise as a biological control
267 agent. Since its initial release in 2003, more than 380,000 beetles have been released throughout
268 the eastern US (Mausel et al. 2011, Salom et al. 2008). While its role as a biological control
269 agent seems promising given its field recovery success and ability to reduce adelgid populations,
270 it is hybridizing with a native beetle, *L. rubidus* LeConte (Klein et al. 2010), with unknown
271 consequences (Havill et al. 2012). This native beetle, which feeds primarily on *Pineus strobi*
272 Hartig (Pine Bark Adelgid), can be found feeding on Hemlock Woolly Adelgid in areas where

273 white pine and hemlock co-occur (Montgomery and Lyon 1996, Wallace and Hain 2000). The
274 fact that *L. nigrinus* feeds exclusively on spring-generation eggs and nymphs (Kohler et al. 2008,
275 Zilahi-Balogh et al. 2002) suggests that it will be most effective as part of a suite of predators.
276 Another beetle in the same genus that is native to Japan, *L. osakensis* Montgomery and Shuyake,
277 is also being researched and released. This beetle is especially important since is native to the
278 region where the invasive lineage of the adelgid also occurs (Havill et al. 2006, Lamb et al.
279 2011). In 2012, 2000 *L. osakensis* were released (K. Mooneyham, pers. comm.) and research and
280 releases continue.

281 A number of other organisms also have potential as biological control agents. *Leucopis* spp.
282 flies (Diptera: Chamaemyiidae) prey on Hemlock Woolly Adelgid in northwestern North
283 America, but a lack of rearing methods and difficulty in species identification have slowed their
284 development as control agents (Ross et al. 2010). A fungal agent, *Lecanicillium muscarium* Zare
285 and Gams, is also under investigation (Salom et al. 2008). It is commercially available as
286 Mycotal, a biopesticide. Some formulations of this fungal agent, which has been approved for
287 use in the US and can already be found in eastern US hemlock forests, can reduce adelgid
288 populations by up to 75%; research into the challenges posed by harsh abiotic conditions and the
289 need for mass deployment is ongoing (Costa 2010, 2011).

290 While biological control agents may help manage Hemlock Woolly Adelgid populations, the
291 high susceptibility of Eastern and Carolina Hemlock to the adelgid means that these agents must
292 cause extremely high adelgid mortality in order to be successful (McClure 1996). This level of
293 adelgid suppression will likely require a suite of predators (Cheah et al. 2004, Montgomery and
294 Lyon 1996); biological control agents may ultimately be most successful when incorporated into
295 a well-rounded integrated pest management program.

296 *Host-plant resistance.* When grown in the eastern US and experimentally infested with the
297 Hemlock Woolly Adelgid, hemlock species native to Asia and the Pacific Northwest are tolerant
298 of and/or resistant to this pest (Bentz et al. 2002, 2007; Del Tredici and Kitajima 2004; Jetton et
299 al. 2008; Oten 2011). This suggests that host-plant factors may play a role, perhaps in concert
300 with natural enemies and the scattered distribution of hemlocks, in keeping adelgid densities low
301 in the native range (Montgomery and Lyon 1996).

302 Interspecific variation in hemlock resistance to the Hemlock Woolly Adelgid is well-
303 documented and continues to be pursued as a key component in a long-term, integrated approach
304 to adelgid management. Hybrid crosses between adelgid-resistant *T. chinensis* (Franch.) Pritzl
305 ex Diels and the adelgid-susceptible Carolina Hemlock produce progeny that are more adelgid-
306 resistant than Carolina Hemlocks (Montgomery et al. 2009). Similar hybridization attempts with
307 Eastern Hemlock have been unsuccessful (Bentz et al. 2002, Pooler et al. 2002), but advances in
308 hybridization methodology may assist in overcoming this obstacle.

309 There have also been reports of a few Eastern Hemlocks growing in heavily adelgid-
310 damaged regions that appear to have remained healthy and vigorous. Their existence and
311 continued vigor, despite coexisting with the Hemlock Woolly Adelgid for more than 20 years,
312 suggests the potential for some degree of adelgid resistance/tolerance in Eastern and Carolina
313 Hemlocks (Caswell et al. 2008). When cuttings from these putatively-resistant trees were grown
314 and evaluated in conjunction with cuttings from known adelgid-susceptible trees, the putatively-
315 resistant cuttings had lower adelgid settlement and higher adelgid mortality than did control
316 cuttings (Ingwell and Preisser 2011).

317 While the development of resistant hemlocks suitable for forest restoration in the eastern US
318 is a long process, initial investigations look somewhat promising. A long-term and sustainable

319 approach to adelgid management will likely incorporate chemical control, biological control, and
320 host-plant resistance into an integrated management program.

321 **Conclusion**

322 The past decades have seen substantial progress towards a better understanding of adelgid
323 ecology and management. These accomplishments notwithstanding, we have yet to develop a
324 long-term and cost-effective management strategy for the Hemlock Woolly Adelgid. It is our
325 hope that the articles contained in this special feature move us closer to this goal, and to the
326 preservation of our native hemlock trees.

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329 **Literature Cited**

- 330 Abell, K., and R. Van Driesche. 2012. Impact of latitude on synchrony of a scale (*Fiorinia*
331 *externa*) (Hemiptera: Diaspididae) and its parasitoid (*Encarsia citrina*) (Hymenoptera:
332 Aphelinidae) in the Eastern United States. *Biological Control* 63:339-347.
- 333 Adkins, J.K., and L.K. Rieske. 2013. Loss of a foundation forest species due to an exotic invader
334 impacts terrestrial arthropod communities. *Forest Ecology and Management* 295:126-135.
- 335 Annand, P. 1924. A new species of *Adelges* (Hemiptera: Phylloxeridae). *Pan-Pacific*
336 *Entomologist* 1:79-82.
- 337 Bentz, S.E., L. Riedel, M.R. Pooler, and A.M. Townsend. 2002. Hybridization and self-
338 compatibility in controlled pollinations of eastern North American and Asian hemlock
339 (*Tsuga*) species. *Journal of Arboriculture* 28:200-205.
- 340 Bentz, S.E., R.J. Griesbach, M.R. Pooler, and A.M. Townsend. 2007. *Tsuga chinensis* as a
341 source of host resistance to the hemlock woolly adelgid. Pp. 24-25, *In* K.W. Gottschalk (Ed.).

- 342 Proceedings: 17th U.S. Department of Agriculture Interagency Research Forum on Gypsy
343 Moth and other Invasive Species. US Forest Service, Morgantown WV.
- 344 Bompey, N. 11/08/2010. US Forest Service increases efforts to save hemlocks in Asheville area.
345 Page 2 Asheville Citizen Times, Asheville NC.
- 346 Butin, E., A.M. Porter, and J.S. Elkinton. 2005. Adaptation during biological invasions and the
347 case of *Adelges tsugae*. *Evolutionary Ecology Research* 87:887-900.
- 348 Caswell, T., R. Casagrande, B. Maynard, and E.L. Preisser. 2008. Production and evaluation of
349 eastern hemlocks potentially resistant to the hemlock woolly adelgid. Pp. 124-134, *In* B.
350 Onken and R.C. Reardon (Eds.). Fourth Symposium on Hemlock Woolly Adelgid in the
351 Eastern United States. US Forest Service, Hartford, CT.
- 352 Cheah, C. 2008. The case for *Sasajiscymnus tsugae*: Biological control has helped save
353 Connecticut's hemlocks. Pp. 279-280, *In* B. Onken and R.C. Reardon (Eds.). Fourth
354 Symposium on Hemlock Woolly Adelgid in the Eastern United States. US Forest Service,
355 Hartford, CT.
- 356 Cheah, C. 2011. *Sasajiscymnus* (= *Pseudoscymnus*) *tsugae*, a ladybeetle from Japan. Pp. 43-52,
357 *In* B. Onken and R.C. Reardon (Eds.). Implementation and Status of Biological Control of
358 the Hemlock Woolly Adelgid. U.S. Forest Service, Morgantown, WV. 230 pp.
- 359 Cheah, C. and M. McClure. 1998. Life history and development of *Pseudoscymnus tsugae*
360 (Coleoptera: Coccinellidae), a new predator of the hemlock woolly adelgid (Homoptera:
361 Adelgidae). *Environmental Entomology* 27:1531-1536.
- 362 Cheah, C., M.E. Montgomery, S.M. Salom, B.L. Parker, S.D. Costa, and M. Skinner. 2004.
363 Biological control of hemlock woolly adelgid. Reardon, R.C., and B. Onken (tech. coords.).
364 US Forest Service, Morgantown WV. 22 pp.

- 365 Costa, S.D. 2010. Hemlock woolly adelgid suppression with aerial application of mycotal fungus
366 in a microfactory formulation: can it work? Pp. 36-42, *In* B. Onken and R.C. Reardon (Eds.).
367 Fifth Symposium on Hemlock Woolly Adelgid in the Eastern United States. US Forest
368 Service, Asheville NC.
- 369 Costa, S.D. 2011. Insect-killing fungi for HWA management: Current status. Pp. 107-115, *In* B.
370 Onken and R. Reardon (Eds.). Implementation and Status of Biological Control of the
371 Hemlock Woolly Adelgid. U.S. Forest Service, Morgantown, WV.
- 372 Cota Vieira, L., A.S. Lamb, S. Shiyake, S. M. Salom, and L. T. Kok. 2013. Seasonal abundance
373 and synchrony between *Laricobius osakensis* (Coleoptera: Derodontidae) and its prey,
374 *Adelges tsugae* (Hemiptera: Adelgidae), in Japan. *Annals of the Entomological Society of*
375 *America* 106:249-257.
- 376 Cowles, R., M.E. Montgomery, and C. Cheah. 2006. Activity and residues of imidacloprid
377 applied to soil and tree trunks to control hemlock woolly adelgid (Hemiptera: Adelgidae) in
378 forests. *Journal of Economic Entomology* 99:1258-1267.
- 379 Cowles, R. 2009. Optimizing dosage and preventing leaching of imidacloprid for management of
380 hemlock woolly adelgid in forests. *Forest Ecology and Management* 257: 1026-1033.
- 381 Del Tredici, P. and A. Kitajima. 2004. Introduction and cultivation of Chinese hemlock (*Tsuga*
382 *chinensis*) and its resistance to hemlock woolly adelgid (*Adelges tsugae*). *Journal of*
383 *Arboriculture* 30:282-286.
- 384 Dilling, C., P. Lambdin, J. Grant, and L. Buck. 2007. Insect guild structure associated with
385 eastern hemlock in the southern Appalachians. *Environmental Entomology* 36:1408-1414.
- 386 Domec, J.-C., L.N. Rivera, J.S. King, I. Peszlen, F.P. Hain, B. Smith, and J. Frampton. 2013.
387 Hemlock woolly adelgid (*Adelges tsugae*) infestation affects water and carbon relations of

- 388 eastern hemlock (*Tsuga canadensis*) and Carolina hemlock (*Tsuga caroliniana*). New
389 Phytologist 199:452-463.
- 390 Ellison, A., M. Bank, B. Clinton, E. Colburn, K. Elliott, C. Ford, D. Foster, B. Kloeppel, J.
391 Knoepp, G. Lovett, J. Mohan, D. Orwig, N. Rodenhouse, W. Sobczak, K. Stinson, J. Stone,
392 C. Swan, J. Thompson, B. Von Holle, and J. Webster. 2005. Loss of foundation species:
393 consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology*
394 *and the Environment* 3:479-486.
- 395 Eschtruth, A.K., N. Cleavitt, J.J. Battles, R.A. Evans, and T. Fahey. 2006. Vegetation dynamics
396 in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid
397 infestation. *Canadian Journal of Forest Research* 36:1435-1450.
- 398 Eschtruth, A.K., R.A. Evans, and J.J. Battles. 2013. Patterns and predictors of survival in *Tsuga*
399 *canadensis* populations infested by the exotic pest *Adelges tsugae*: 20 years of monitoring.
400 *Forest Ecology and Management* 305:195-203.
- 401 Farjon, A. 2013. *Tsuga canadensis*. In: IUCN 2013. IUCN Red List of Threatened Species.
402 Version 2013.1. <www.iucnredlist.org>. Downloaded on 14 October 2013.
- 403 Fernandes, G. 1990. Hypersensitivity: a neglected plant resistance mechanism against insect
404 herbivores. *Environmental Entomology* 19:1173-1182.
- 405 Fernandes, G., and D. Negreiros. 2001. The occurrence and effectiveness of hypersensitive
406 reaction against galling herbivores across host taxa. *Ecological Entomology* 26:46-55.
- 407 Ford, C.R., and J.M. Vose. 2007. *Tsuga canadensis* (L.) Carr. mortality will impact hydrological
408 processes in southern Appalachian forest ecosystems. *Ecological Applications* 17: 1156-
409 1167.

- 410 Gomez, S., L. Gonda-King, C.M. Orians, and E.L. Preisser. 2014. Competitor avoidance drives
411 within-host feeding site selection in a passively-dispersed herbivore. *Ecological Entomology*
412 39:10-16.
- 413 Gómez, S., C.M. Orians, and E.L. Preisser. 2012. Exotic herbivores on a shared native host:
414 tissue quality after individual, simultaneous, and sequential attack. *Oecologia* 169:1015-
415 1024.
- 416 Gonda-King, L., L. Radville, and E.L. Preisser. 2012. False ring formation in eastern hemlock
417 branches: impacts of hemlock woolly adelgid and elongate hemlock scale. *Environmental*
418 *Entomology* 41:523-531.
- 419 Grant, J., A. Hakeem, J.R. Rhea, G. Wiggins, P. Lambdin, and G. Taylor. 2010. Recovery and
420 establishment of introduced predators of hemlock woolly adelgid in the southern
421 Appalachians. Pp. 21-23, *In* B. Onken and R.C. Reardon (Eds.). Fifth Symposium on
422 Hemlock Woolly Adelgid in the Eastern United States. US Forest Service, Asheville NC.
- 423 Hakeem, A., J. Grant, G. Wiggins, P. Lambdin, and J.R. Rhea. 2011. Establishment and
424 coexistence of two predators, *Laricobius nigrinus* and *Sasajiscymnus tsugae*, introduced
425 against hemlock woolly adelgid on eastern hemlock. *Biocontrol Science and Technology*
426 21:687-691.
- 427 Havill, N., G. Davis, D.L. Mausel, J. Klein, R. McDonald, C. Jones, M. Fischer, S.M. Salom,
428 and A. Caccone. 2012. Hybridization between a native and introduced predator of Adelgidae:
429 An unintended result of classical biological control. *Biological Control* 63:359-369.
- 430 Havill, N. and R. Foottit. 2007. Biology and evolution of Adelgidae. *Annual Review of*
431 *Entomology* 52:325-349.

- 432 Havill, N., M.E. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006. Mitochondrial DNA
433 from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and
434 pinpoints the source of the introduction to eastern North America. *Annals of the*
435 *Entomological Society of America* 99:195-203.
- 436 Holmes, T., E. Murphy, and D. Royle. 2005. The economic impacts of hemlock woolly adelgid
437 on residential landscape values: Sparta, New Jersey case study. Pp. 15-24, *In* B. Onken and
438 R.C. Reardon (Eds.). *Third Symposium on the Hemlock Woolly Adelgid in the Eastern*
439 *United States*. US Forest Service, Asheville, NC.
- 440 Ingwell, L.L., and E.L. Preisser. 2011. Using citizen science programs to identify host resistance
441 in pest-invaded forests. *Conservation Biology* 25:182–188.
- 442 Ingwell, L., M. Miller-Pierce, R.T. Trotter III, and E.L. Preisser. 2012. Vegetation and
443 invertebrate community response to eastern hemlock decline in southern New England.
444 *Northeastern Naturalist* 19:541-558.
- 445 Jetton, R.M., F.P. Hain, W.S. Dvorak, and J. Frampton. 2008. Infestation rate of hemlock woolly
446 adelgid (Hemiptera: Adelgidae) among three North American hemlock (*Tsuga*) species
447 following artificial inoculation. *Journal of Entomological Science* 43:438–442.
- 448 Klein, J.L., A. Caccone, and N. Havill. 2010. Polymorphic microsatellite loci for *Laricobius*
449 *nigrinus* and *L. rubidus* (Coleoptera: Derodontidae), predators of the hemlock woolly
450 adelgid. *Molecular Ecology Resources* 10: 751–754.
- 451 Kohler, G.R., V.L. Stiefel, K.F. Wallin, and D.W. Ross. 2008. Predators associated with the
452 hemlock woolly adelgid (Hemiptera: Adelgidae) in the Pacific Northwest. *Environmental*
453 *Entomology* 37: 494-505.

- 454 Lamb, A., M.E. Montgomery, L. Cota Vieira, S. Shiyake, and S.M. Salom. 2011. *Laricobius*
455 *osakensis*, a hemlock woolly adelgid predator from Japan. Pp. 90-96, *In* B. Onken and R.C.
456 Reardon (Eds.). Implementation and Status of Biological Control of the Hemlock Woolly
457 Adelgid. U.S. Forest Service, Publication FHTET-2011-04, Morgantown, WV. 230 pp.
- 458 Mausel, D.L., G.A. Davis, A.B. Lamb, G.M.G. Zilahi-Balogh, L.T. Kok, and S.M. Salom. 2011.
459 *Laricobius nigrinus* Fender (Coleoptera: Derodontidae). Pp. 77-89, *In* B. Onken and R.C.
460 Reardon (Eds.). Implementation and Status of Biological Control of the Hemlock Woolly
461 Adelgid. U.S. Forest Service, Publication FHTET-2011-04, Morgantown, WV. 230 pp.
- 462 McClure, M.S. 1978. Seasonal development of *Fiorinia externa*, *Tsugaspidotus tsugae*
463 (Homoptera: Diaspididae), and their parasite, *Aspidiotiphagus citrinus* (Hymenoptera:
464 Aphelinidae): Importance of parasite-host synchronism to the population dynamics of two
465 scale pests of hemlock. *Environmental Entomology* 7:863-870.
- 466 McClure, M.S. 1987. Biology and control of hemlock woolly adelgid. Bulletin of the
467 Connecticut Agricultural Experiment Station 851.
- 468 McClure, M.S. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid
469 *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America*
470 82:50-54.
- 471 McClure, M.S. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly
472 adelgid (Homoptera: Adelgidae). *Environmental Entomology* 19:36-43.
- 473 McClure, M.S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae*
474 (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environmental Entomology* 20:258-264.

- 475 McClure, M.S. 1992. Effect of implanted and injected pesticides and fertilizers on the survival of
476 *Adelges tsugae* (Homoptera: Adelgidae) and on the growth of *Tsuga canadensis*. Journal of
477 Economic Entomology 85:468-472.
- 478 McClure, M.S. 1996. Biology of *Adelges tsugae* and its potential for spread in the northeastern
479 United States. Pp. 16-25, In S.M. Salom, T. Tigner, and R.C. Reardon (Eds.). First Hemlock
480 Woolly Adelgid Review. US Forest Service, Morgantown, WV.
- 481 McClure, M.S. 1997. Biological control in native and introduced habitats: Lessons learned from
482 the sap-feeding guilds on hemlock and pine. Pp 31-52, In D. Andow, D. Ragsdale, and R.
483 Nyvall, editors. Ecological Interactions and Biological Control. Westview Press, Boulder
484 CO.
- 485 McClure, M.S. 2001. Biological control of hemlock woolly adelgid in the eastern United States.
486 FHTET-2000-08. USDA Forest Service, Forest Health Technology Enterprise Team,
487 Morgantown, WV. 10 pp.
- 488 McClure, M.S., and C. Cheah. 1999. Reshaping the ecology of invading populations of hemlock
489 woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in Eastern North America.
490 Biological Invasions 1:241-254.
- 491 McClure, M.S., and C. Cheah. 2002. Important mortality factors in the life cycle of hemlock
492 woolly adelgid *Adelges tsugae* in the northeastern United States. Pp. 13-22, In Symposium
493 on the Hemlock Woolly Adelgid in Eastern North America. US Forest Service, New
494 Brunswick, NJ.
- 495 Miller-Pierce, M., D.A. Orwig, and E.L. Preisser. 2010. Effects of hemlock woolly adelgid and
496 elongate hemlock scale on eastern hemlock growth and foliar chemistry. Environmental
497 Entomology 39:513-519.

- 498 Miller-Pierce, M. and E.L. Preisser. 2012. Asymmetric priority effects influence the success of
499 invasive forest insects. *Ecological Entomology* 37:350-358.
- 500 Montgomery, M.E. 1999. Woolly adelgids in the southern Appalachians: Why they are harmful
501 and prospects for control. Pp. 47–57, *In* P. Gibson and C.R. Parker (Eds.). Proceedings of the
502 Southern Appalachian Biological Control Initiative Workshop, 26–27 September 1996.
503 FHTET-98-14. USDA Forest Service, Forest Health Technology Enterprise Team,
504 Morgantown, WV.
- 505 Montgomery, M.E., and M.A. Keena. 2011. *Scymnus* (*Neopullus*) lady beetles from China. Pp.
506 53-76, *In* B. Onken and R.C. Reardon (Eds.). Implementation and Status of Biological
507 Control of the Hemlock Woolly Adelgid. U.S. Forest Service, Publication FHTET-2011-04,
508 Morgantown, WV. 230 pp.
- 509 Montgomery, M.E., and S.M. Lyon. 1996. Natural enemies of adelgids in North America: Their
510 prospect for biological control of *Adelges tsugae* (Homoptera: Adelgidae). Pp. 89-102, *In*
511 S.M. Salom, T.C. Tigner, and R.C. Reardon (Eds.). Proceedings of the first Hemlock Woolly
512 Adelgid review; 1995 October 12; Charlottesville, VA. FHTET 96-10. Morgantown, WV:
513 U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team.
- 514 Montgomery, M., S. Bentz, and R. Olsen. 2009. Evaluation of hemlock (*Tsuga*) species and
515 hybrids for resistance to *Adelges tsugae* (Hemiptera: Adelgidae) using artificial infestation.
516 *Journal of Economic Entomology* 102:1247-1254.
- 517 Montgomery, M.E., T.J. McAvoy, and S.M. Salom. 2011. Other species considered. Pp. 116-
518 122, *In* B. Onken and R.C. Reardon (Eds.). Implementation and Status of Biological Control
519 of the Hemlock Woolly Adelgid. U.S. Forest Service, Publication FHTET-2011-04,
520 Morgantown, WV. 230 pp.

- 521 Mooneyham, K. 2013. Personal communication. 16 October 2013.
- 522 Onken, B., and R.C. Reardon (Eds.). 2011. Implementation and Status of Biological Control of
523 the Hemlock Woolly Adelgid. USDA FHTET-2011-04. 230 pp.
- 524 Orwig, D.A., and D. Foster. 2000. Stand, landscape, and ecosystem analyses of hemlock woolly
525 adelgid outbreaks in southern New England: an overview. Pp. 123-125, *In* Symposium on
526 Sustainable Management of Hemlock Ecosystems in Eastern North America. US Forest
527 Service, Newtown Square, PA.
- 528 Orwig, D.A., D. Foster, and D.L. Mausel. 2002. Landscape patterns of hemlock decline in New
529 England due to the introduced hemlock woolly adelgid. *Journal of Biogeography* 29:1475-
530 1487.
- 531 Oten, K.L.F. 2011. Host-plant selection by the hemlock woolly adelgid, *Adelges tsugae* Annand:
532 Sensory systems and feeding behavior in relation to physical and chemical host-plant
533 characteristics. Ph.D. Dissertation. North Carolina State University, Raleigh, N.C.
- 534 Oten, K.L.F., G.R. Bauchan, J. Frampton, and F.P. Hain. 2012. Biophysical characteristics of the
535 stem and petiole surface of six hemlock (*Tsuga*) species and a hybrid: implications for
536 resistance to *Adelges tsugae*. *Botany* 90:1170-1178.
- 537 Paradis, A. 2011. Population dynamics of the hemlock woolly adelgid (Hemiptera: Adelgidae).
538 Ph.D. Dissertation. University of Massachusetts, Amherst, Amherst.
- 539 Pooler, M.R., L.G.H. Riedel, S.E. Bentz, and A.M. Townsend. 2002. Molecular markers used to
540 verify interspecific hybridizations between hemlock (*Tsuga*) species. *Journal of the*
541 *American Society for Horticultural Science* 127(4):623–627.
- 542 Preisser, E.L., and J.S. Elkinton. 2008. Exploitative competition between invasive herbivores
543 benefits a native host plant. *Ecology* 89:2671-2677.

- 544 Preisser, E.L., A. Lodge, D.A. Orwig, and J.S. Elkinton. 2008. Range expansion and population
545 dynamics of co-occurring invasive herbivores. *Biological Invasions* 10:201-213.
- 546 Preisser, E.L., M. Miller-Pierce, J. Vansant, and D.A. Orwig. 2011. Eastern hemlock (*Tsuga*
547 *canadensis*) regeneration in the presence of hemlock woolly adelgid (*Adelges tsugae*) and
548 elongate hemlock scale (*Fiorinia externa*). *Canadian Journal of Forest Research* 41:2433-
549 2439.
- 550 Quimby, J.W. 1996. Value and importance of hemlock ecosystems in the eastern United States.
551 Pp. 1-8, *In* S.M. Salom, T. Tigner, and R.C. Reardon (Eds.). *First Hemlock Woolly Adelgid*
552 *Review*. US Forest Service, Morgantown, WV.
- 553 Rabenold, K.N., P.T. Fauth, B.W. Goodner, J.A. Sadowski, and P.G. Parker. 1998. Response of
554 avian communities to disturbance by an exotic insect in spruce-fir forests of the southern
555 Appalachians. *Conservation Biology* 12:177-189.
- 556 Radville, L., A. Chaves, and E.L. Preisser. 2011. Variation in plant defense against invasive
557 herbivores: evidence for a hypersensitive response in eastern hemlocks (*Tsuga canadensis*).
558 *Journal of Chemical Ecology* 37:592-597.
- 559 Reynolds, W.N. 2008. Imidacloprid insecticide treatments for hemlock woolly adelgid, *Adelges*
560 *tsugae* Annand (Hemiptera: Adelgidae), affect a non-target soil arthropod community
561 surrounding eastern hemlock, *Tsuga canadensis* Carriere. University of Tennessee,
562 Knoxville.
- 563 Rhea, J.R. 1995. Economic and environmental impacts of the hemlock woolly adelgid (*Adelges*
564 *tsugae*) on the hemlock resources of Eastern North America. *In Proceedings: International*
565 *Union of Forest Research Organizations, XX World Congress*.

- 566 Ross, D., S. Grubin, G. Kohler, and K.M. Wallin. 2010. Evaluation of *Leucopis* species (Diptera:
567 Chamaemyiidae) from the PNW as potential biological control for the hemlock woolly
568 adelgid. Pp. 32, *In* B. Onken and R.C. Reardon (Eds.). Fifth Symposium on Hemlock Woolly
569 Adelgid in the Eastern United States. US Forest Service, Asheville NC.
- 570 Salom, S.M., L.T. Kok, A.B. Lamb, C. Jubb, and B. Onken. 2008. Biological control of hemlock
571 woolly adelgid: What is it going to take to make it work? Pp. 11-18, *In* B. Onken and R.C.
572 Reardon (Eds.). Fourth Symposium on Hemlock Woolly Adelgid in the Eastern United
573 States. US Forest Service, Hartford, CT.
- 574 Sato, S. 1999. Galls on tiger-tail spruce made by *Aphrastasia tsugae* at Mt. Tsurugi. *Gensei* 73:1-
575 26.
- 576 Souto, D., T. Luther, and B. Chianese. 1996. Past and current status of hemlock woolly adelgid
577 in eastern and Carolina hemlock stands. Pp. 9-15, *In* S.M. Salom, T. Tigner, and R. Reardon
578 (Eds.). First Hemlock Woolly Adelgid Review. US Forest Service, Morgantown, WV.
- 579 Swartley, J.C. 1984. *The Cultivated Hemlocks*. Timber Press, Portland, OR.
- 580 Townsend, L. and L. Rieske-Kinney. 2006. ENTFACT-452: Meeting the threat of the hemlock
581 woolly adelgid. Pp. 1-8. UK Cooperative Extension Service, Lexington.
- 582 Trial, H. and M. Devine. 1995. The impact of the hemlock loopers, *Lambdina fiscellaria*
583 (Guenée) and *L. Athasaria* (Walker) on eastern hemlock and balsam fir in New England.
584 Bureau of Forestry, Orono ME.
- 585 Trotter III, R. T. and K. Shields. 2009. Variation in winter survival of the invasive hemlock
586 woolly adelgid (Hemiptera: Adelgidae) across the Eastern United States. *Environmental*
587 *Entomology* 38:577-587.

- 588 Trotter III, R.T., R.S. Morin, S.N. Oswald, and A.M. Liebhold. 2013. Changes in the regional
589 abundance of hemlock associated with the invasion of hemlock woolly adelgid. *Biological*
590 *Invasions* (2013): 1-13.
- 591 Turner, J., M. Fitzpatrick, and E.L. Preisser. 2011. Simulating the dispersal of hemlock woolly
592 adelgid in the temperate forest understory. *Entomologia Experimentalis et Applicata*
593 141:216-223.
- 594 U.S. Environmental Protection Agency, 2003. Imidacloprid; Pesticide tolerances. *Fed. Regist.*
595 68, 35303–35315 [online].[http://www.epa.gov/fedrgstr/EPA-PEST/2003/June/Day-](http://www.epa.gov/fedrgstr/EPA-PEST/2003/June/Day-13/p14880.htm)
596 [13/p14880.htm](http://www.epa.gov/fedrgstr/EPA-PEST/2003/June/Day-13/p14880.htm). U.S. EPA, Washington, DC.
- 597 USFS. 2012. Forest Health Protection - Hemlock Woolly Adelgid Distribution Map. Forest
598 Health Protection Service, Newtown Square PA.
- 599 Wallace, M. and F.P. Hain. 2000. Field surveys and evaluation of native and established
600 predators of the hemlock woolly adelgid (Homoptera: Adelgidae) in the southeastern United
601 States. *Environmental Entomology* 29:638-644.
- 602 Woodsen, M.M. 2001. Forest invaders-insects that invade hemlock trees. *American Forests* 4:
603 12-13.
- 604 Young, R., K. Shields, and G. Berlyn. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae):
605 stylet bundle insertion and feeding sites. *Annals of the Entomological Society of America*
606 88:827-835.
- 607 Zilahi-Balogh, G.M.G., L.T. Kok, and S.M. Salom. 2002. Host specificity of *Laricobius nigrinus*
608 Fender (Coleoptera: Derodontidae), a potential biological control agent of the hemlock
609 woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). *Biological Control* 24:
610 192-198.

611 **Figure 1:** Hemlock Woolly Adelgid life cycle. In Japan, the adelgid alternates between Hemlock
612 and Tigertail Spruce. Tigertail Spruce supports a sexual generation and gall formation. In the
613 eastern United States there are only two generations on Hemlock, because winged migrants do
614 not find suitable spruce species on which to complete the entire life cycle. The letters 'A' and 'B'
615 refer to where the cycle begins again. Vince D'Amico and Nathan Havill created the artwork for
616 this figure.

