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Facilitation between invasive herbivores: hemlock woolly adelgid increases gypsy moth preference for and performance on eastern hemlock

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2

16 **Abstract.**

17 1. Interactions between invertebrate herbivores with different feeding modes are common on

18 long-lived woody plants. In cases where one herbivore facilitates the success of another, the

19 consequences for their shared host plant may be severe. Eastern hemlock (*Tsuga canadensis*), a

20 canopy-dominant conifer native to the eastern U.S., is currently threatened with extirpation by

21 the invasive stylet-feeding hemlock woolly adelgid (*Adelges tsugae*). The effect of adelgid on

22 invasive hemlock-feeding folivores remains unknown.

23 2. We evaluated the impact of feeding by hemlock woolly adelgid on gypsy moth (*Lymantria*

24 *dispar*) larval preference for, and performance on, eastern hemlock. To assess preference, we

25 surveyed 245 field-grown hemlocks for gypsy moth herbivory damage and conducted laboratory

26 paired-choice bioassays. To assess performance, gypsy moth larvae were reared to pupation on

27 adelgid-infested or uninfested hemlock foliage and pupal weight, proportional weight gain, and

28 larval period were analyzed.

29 3. Adelgid-infested hemlocks experienced more gypsy moth herbivory than uninfested control

30 trees, and laboratory tests confirmed that gypsy moth larvae preferentially feed on adelgid-

31 infested hemlock foliage. Gypsy moth larvae reared to pupation on adelgid-infested foliage

32 gained more weight than larvae reared on uninfested control foliage.

33 4. Our results suggest that the synergistic effect of adelgid and gypsy moth poses an additional

34 threat to eastern hemlock that may increase extirpation risk and ecological impact throughout

35 most of its range.

36

37 **Key words.** Facilitation, herbivores, *Adelges tsugae*, *Lymantria dispar*, invasional meltdown

38 **Introduction**

39   Many interactions between co-occurring insect herbivores are mediated by their impact

40 on the shared host plant (Kaplan & Denno, 2007). Feeding by one insect may cause alterations in

41 plant quality, such as the induction of toxic secondary metabolites or changes to various leaf

42 structural traits, which can affect simultaneously- or sequentially-feeding competitors (Nykänen

43 & Koricheva, 2004). Although many such changes negatively impact the other species, they can

44 also be facilitative (Kaplan & Denno, 2007; Ohgushi, 2008). Sap feeding by the aphid

45 *Brevicoryne brassicae*, for example, improves the performance of folivorous *Pieris brassicae*

46 larvae by attenuating chemical defense induction in *Brassica oleracea* (Li *et al.*, 2014).

47   Understanding herbivore-herbivore interactions is especially important in cases where

48 one or both herbivores can substantially affect plant growth and fitness. One such species is

49 hemlock woolly adelgid (*Adelges tsugae*; 'adelgid' hereafter), a destructive pest that has caused

50 widespread mortality and decline of an ecologically significant conifer, eastern hemlock (*Tsuga*

51 *canadensis*; 'hemlock' hereafter), in eastern U.S. forests. Adelgid feeds by inserting its stylet

52 bundle into the xylem ray parenchyma cells at the base of a hemlock needle (Shields *et al.*,

53 1995). This feeding reduces the production of new foliage (Gonda-King *et al.*, 2014; McClure,

54 1991), alters wood morphology (Domec *et al.*, 2013; Gonda-King *et al.*, 2012), and substantially

55 impacts plant physiology. Adelgid-infested hemlocks have elevated tissue levels of salicylic acid

56 (SA) and emissions of its methylated form, methyl salicylate (Pezet *et al.*, 2013; Pezet &

57 Elkinton, 2014). SA is a phytohormone that plays a critical role in plant response to abiotic

58 stresses and biotrophic pathogens; it has also been shown to accumulate following stylet-feeding

59 insect infestations (Walling, 2000). SA accumulation and subsequent monomerization of NPR1,

60 a transcriptional regulator that promotes the expression of SA-responsive genes, can interfere

61   with the biosynthesis of jasmonic acid (JA)/ethylene-dependent defenses that help protect against

62   leaf-chewing herbivores (Walling, 2008; Zarate *et al.*, 2007). Adelgid feeding has also been

63   shown to increase nitrogen (Gonda-King *et al.*, 2014) and total amino acid content (Gomez *et al.*,

64   2012) in hemlock needles. Because nitrogen is critical to insect growth (Awmack & Leather,

65   2002; Kerslake *et al.*, 1998), such adelgid-mediated increases may enhance host plant quality for

66   folivorous herbivores.

67   Recent work in the hemlock system suggests that adelgid-induced phytochemical changes

68   may influence interactions between hemlock and other herbivores (Rigsby *et al.*, 2019; Schaeffer

69   *et al.*, 2018; Wilson *et al.*, 2018). Larvae of the native hemlock looper (*Lambdina fiscellaria*) had

70   higher survival and enhanced larval development when reared on adelgid-infested versus

71   uninfested hemlock foliage (Wilson *et al.*, 2016). This work led us to explore whether similar

72   interactions might be occurring between the adelgid and more commonly-occurring folivores.

73   We focused our attention on gypsy moth (*Lymantria dispar*), an invasive folivore that has

74   devastated eastern U.S. forests. Since its introduction in 1890, periodic gypsy moth outbreaks

75   have defoliated millions of acres and altered forest structure and composition (Gandhi & Herms,

76   2010; Lovett *et al.*, 2006). Gypsy moth can feed on eastern hemlock (Lovett *et al.*, 2006) and

77   although it and hemlock woolly adelgid co-occur in their introduced range, their interactions

78   have not been considered.

79   We report the results of work assessing the impact of adelgid infestation on gypsy moth-

80   hemlock interactions. We surveyed hemlocks planted into a deciduous forest understory for

81   gypsy moth herbivory and conducted two laboratory experiments to measure gypsy moth

82   preference for, and performance on, adelgid-infested hemlock foliage. Because the adelgid

83   inhibits hemlock anti-folivore defense pathways and increases the nutritional value of its needles,

84   we hypothesized that gypsy moth larvae would both prefer (consume more of) and do better

85   (pupate at higher weights) on adelgid-infested foliage. The 'invasional meltdown hypothesis'

86   suggests that much of the damage caused by introduced species may result from positive

87   interactions between invaders that can facilitate their establishment and increase their ecological

88   impact (Simberloff & Von Holle, 1999). Our findings illustrate the potential for such facilitation

89   between two invasive herbivores and highlight the threat this may pose to their shared host and

90   its associated ecosystem.

91   **Materials and Methods**

92   *Field preference survey*: Our field preference survey took advantage of a 2016 gypsy

93   moth outbreak to assess their impacts on field-grown eastern hemlock. The trees in this survey

94   were planted in 2014 for use in an unrelated experiment. Briefly, 1-1.2 m-tall hemlock saplings

95   were purchased from Van Pines Nursery (West Olive, MI) in spring 2014, planted, and grown

96   for two years in the understory of a mixed hardwood stand at the Kingston Wildlife Research

97   Station (South Kingstown, RI). Hemlocks were planted in five 64-tree blocks, with each tree

98   spaced 1-1.5 m apart. Trees were protected from herbivory and cross-contamination of

99   treatments with chicken-wire cages covered by mesh bags (Agribon-15, Johnny's Selected

100 Seeds, Waterville, ME, USA; 90% light transmission. Sixteen trees in each block were randomly

101 assigned one of the following two treatments: infestation with adelgid or another invasive

102 herbivore (*Fiorinia externa*; elongate hemlock scale, 'scale' hereafter). The remaining 32 trees in

103 each block were maintained as controls. Trees in the adelgid and scale infestation treatments

104 were inoculated in the spring of 2014, 2015, 2016, and 2017 with infested foliage collected from

105 nearby adelgid-infested and scale-infested hemlocks, respectively; trees in the control treatment

106 had herbivore-free hemlock foliage placed on them to control for disturbance.

107   In spring 2016, a gypsy moth outbreak occurred at our field site. Late-instar gypsy moth

108   larvae were regularly seen roaming on the ground, where they could crawl under the mesh bags

109   enclosing our trees. Over a short (2-3 week) time period, we observed that many of our trees

110   received substantial damage from gypsy moth larvae. In late June 2016, 69 trees in the adelgid-

111   infested treatment group, 69 trees in the scale-infested treatment group, and 107 trees in the

112   control treatment group were assessed for gypsy moth herbivory damage, for a total of 245 trees.

113   All branches emerging from the main stem of each tree were surveyed, and each tree was given a

114   combined damage score of 0-3 (0=0-25% foliage loss, 1=26-50%, 2=51-75%, 3=76-100%). An

115   annual, early spring survey confirmed that trees did not experience foliage loss prior to the gypsy

116   moth outbreak. During the survey, gypsy moth larvae were confirmed to be the only folivores

117   present on trees.

118   *Laboratory preference assay:* Hemlock foliage used in the laboratory preference assay

119   came from 0.5-0.7m hemlock saplings purchased from Vans Pines Nursery (West Olive, MI) in

120   spring 2016. In late spring 2016, we inoculated half of the trees with adelgid-infested foliage

121   from nearby trees; we attached adelgid-free hemlock foliage to the other trees (the control group)

122   to control for disturbance. All trees were covered in mesh (Agribon-15, Johnny's Selected Seeds,

123   Waterville, ME, USA; 90% light transmission) to prevent cross-contamination between

124   treatments and grown in 1-gallon pots outside of the greenhouse complex at the University of

125   Rhode Island (URI; Kingston, RI). Adelgid densities on each tree were assessed in late fall 2016

126   and early spring 2017. Five secondary branches on each tree were randomly selected, and all

127   adelgid present on the branches were counted. We used this data to ensure that both the trees and

128   specific branches used in this experiment had similar adelgid densities (0.8-1 adelgid/cm).

129   In late spring 2017, we collected 40 gypsy moth larvae from a mixed-hardwood forest

130   located adjacent to the URI greenhouses. We collected 4th-5th instar larvae found wandering on

131   the ground or on tree trunks; all larvae were similarly-sized and highly active throughout the

132   experiment. To assess gypsy moth preference for adelgid-infested hemlock, we collected 40

133   ~10cm terminal branches: one branch from each of 20 adelgid-infested trees, and one branch

134   from each of 20 uninfested trees. Each branch was weighed; analysis *via* two-tailed Welch's

135   unequal variances t-test confirmed there was no significant difference in the mean branch weight

136   experienced by larvae in each treatment group (t_{36} = -0.72, P = 0.4731). Following weighing, the

137   branches were inserted into individual blocks of water-saturated floral foam (Oasis brand, Kent,

138   OH). Two pieces of foliage (one adelgid-infested and one control) were then put in a 6L

139   polypropylene bin (Sterilite brand, Townsend, MA). The pieces of foliage were placed at the

140   25% and 75% marks between the left and right sides of the bin; treatment placement was

141   alternated between left and right. After two similarly-sized gypsy moth larvae were weighed,

142   they were both added to the center of each bin. Each bin was then covered with metal mesh held

143   in place by a rubber band. There were a total of 20 bins in the experiment. After one day, the

144   mesh was removed and the larvae and foliage (including any dropped needles) were weighed; the

145   adelgid-infested and uninfested foliage were weighed separately to calculate larval consumption

146   for each treatment.

147   *Laboratory performance assay:* Hemlock foliage used in the laboratory performance

148   assay came from the common garden planting described in the field preference survey. In late

149   spring 2018, 3rd-instar gypsy moth larvae were obtained from the USDA-APHIS Laboratory in

150   Buzzards Bay, MA. These larvae originated from the New Jersey Standard Strain-APHIS

151   substrain, a laboratory colony which has been in cultivation for >60 generations. Larvae were

152   reared on an artificial diet (Frontier Agricultural Sciences, USDA Hamden Formula) until they

153   reached the fourth instar, at which point each larva was weighed and placed individually into one

154   of 50 473 ml glass mason jars (Ball brand, Broomfield CO). Fourth-instar larvae were used in

155   this experiment because younger stages have trouble consuming hemlock foliage, likely because

156   their undeveloped mouthparts cannot penetrate lignified needles. By contrast, larvae in the fourth

157   instar and above readily consume hemlock.

158   Half of the jars contained foliage from adelgid-infested hemlocks, while the other half of

159   the jars contained foliage from uninfested hemlocks, for a total of 25 replicates per treatment.

160   The foliage in each jar consisted of a single ~17cm sprig of foliage kept upright in hydrated

161   floral foam (Oasis brand, Kent, OH); foliage was checked every day and replaced if >50% of the

162   needles had been consumed. The top of each jar was covered with nylon mesh and all jars were

163   kept in a growth chamber (15:9 L:D, 24° C, 60-70% RH). Larvae were checked every two days

164   and the position of the jars rotated within the growth chamber; the date of and weight at pupation

165   was recorded for each individual.

166   *Statistical analysis:* All data were inspected for normality (Shapiro-Wilk test) and

167   homoscedasticity (Bartlett's test) prior to analysis; data were log-transformed where necessary to

168   meet assumptions. Damage scores were tabulated by treatment group and analyzed *via* Pearson's

169   chi-squared test. Data from the laboratory preference assay were analyzed *via* two-tailed Welch's

170   unequal variances t-test. Percent weight gain, pupal weight and larval period were analyzed

171   separately *via* three-way analysis of covariance (ANCOVA), with foliage type and sex as the

172   predictors, initial larval weight as a covariate, and all two-way interactions. We classified larvae

173   as male or female because the sexes differ substantially in their time to and weight at pupation

174   (Myers et al., 1998); this allowed us to analyze percent weight gain, pupal weight, and larval

175   period of the two sexes separately for both foliage treatment groups. Tukey's test was used to

176   separate the mean response of the two sexes in either foliage treatment group. Figures were

177   created using *ggplot2* (Wickham, 2016). R software v. 3.5.0 was used for all statistical analyses

178   (R Development Core Team, 2018).

179

180   **Results**

181   *Field preference survey*: Adelgid-infested hemlocks experienced significantly more

182   gypsy moth herbivory damage than scale-infested or control trees ($X^2 = 48.96$, $P < 0.0001$; Fig.

183   1). Nearly 40% of adelgid-infested trees lost more than half of their foliage to gypsy moth

184   herbivory, while fewer than 10% of scale-infested trees and 5% of control trees experienced

185   similar levels of damage. Conversely, 84% of both control and scale-infested trees experienced

186   minimal (0-25% foliage loss) herbivory.

187   *Laboratory preference assay*: When allowed to choose between adelgid-infested and

188   control foliage, larvae consumed an average of 37% more adelgid-infested foliage than control

189   foliage (0.36 g +/- 0.054 SE and 0.22 g +/- 0.034 SE, respectively; $t_{31} = -2.17$, $P = 0.0380$).

190   *Laboratory performance assay:* Larvae reared to pupation on adelgid-infested hemlock

191   foliage gained more weight, and pupated at a higher weight, than larvae reared on uninfested

192   foliage (both $P < 0.05$; Fig. 2 A, B). Female larvae gained more weight, pupated at a higher

193   weight, and took longer to pupate than male larvae (all $P < 0.05$; Fig. 2 A, B, C). Initial larval

194   weight affected larval weight gain and weight at pupation, but not larval period.

195   Female larvae reared on adelgid-infested foliage gained 256% of their initial weight,

196   while those fed control foliage gained 120% of their initial weight ($P < 0.001$; Fig. 2 A). Male

197   larvae reared on adelgid-infested and uninfested foliage gained 115% and 67% of their initial

198   weight, respectively (P < 0.001; Fig. 2 A).

199   Female larvae reared on adelgid-infested foliage pupated at weights 25% greater than

200   those reared on uninfested foliage ($F_{1,36}$ = 12.5, P = 0.0011; Fig. 2 B). Conversely, male larvae

201   reared on adelgid-infested and control foliage pupated at similar weights (P = 0.88; Fig. 2 B).

202   Larval period was not affected by treatment or initial weight (both P > 0.4; Fig. 2 C),

203   although female larvae reared on adelgid-infested hemlock foliage had a larval period five days

204   longer than that of male larvae reared on uninfested foliage (P = 0.0249; Fig. 2 C).

205

206   **Discussion**

207   Here we present evidence that one destructive forest pest, hemlock woolly adelgid,

208   facilitates the development of the invasive gypsy moth. We found that gypsy moth larvae prefer

209   hemlock foliage infested with hemlock woolly adelgid (Fig. 1), and that feeding on this infested

210   foliage facilitates gypsy moth larval development. Female larvae reared on adelgid-infested

211   hemlock foliage gained more than twice as much of their initial weight (Fig. 2 A) and pupated at

212   25% higher weights (Fig. 2 B) than larvae reared on uninfested foliage. Male larvae reared to

213   pupation on adelgid-infested foliage also gained 48% more weight than those fed uninfested

214   foliage (Fig. 2 A) but pupated similar weights (Fig. 2 B). Additionally, gypsy moth larvae

215   exhibited a preference for adelgid-infested foliage over uninfested foliage, and in a natural

216   setting, adelgid-infested hemlocks experienced substantially more gypsy moth herbivory than

217   uninfested trees. Our results are consistent with findings from previous studies documenting a

218   facilitative effect of hemlock woolly adelgid on other leaf-chewing herbivores.

219   The enhanced performance of gypsy moth larvae reared on adelgid-infested foliage may

220   result from adelgid-induced changes to hemlock defenses. Adelgid infestation of hemlock

221   increases foliar emissions of methyl salicylic acid (Pezet *et al.*, 2013; Pezet & Elkinton, 2014)

222   and triggers salicylic acid (SA) accumulation in needles (Schaeffer *et al.*, 2018; Rigsby *et al.*,

223   2019), activating SA-linked stress responses in hemlock. The accumulation of SA, and

224   subsequent monomerization of NPR1, has been shown to inhibit jasmonic acid (JA) biosynthesis

225   and JA-responsive gene expression (Zarate *et al.*, 2007). Plant defense against leaf-chewing

226   herbivores is primarily mediated by JA (Gilbert & Liebhold, 2010; Kroes *et al.*, 2014), and

227   blocking the induction of JA-related defenses may make the foliage of adelgid-infested hemlocks

228   more digestible and/or easily converted into body mass by gypsy moth larvae. This interpretation

229   is supported by work on other systems where negative cross-talk between these pathways has

230   been shown to improve the performance of a later-arriving herbivore (reviewed in Stam *et al*.,

231   2014).

232   The improved performance of gypsy moth may also be driven by enhanced foliar

233   nutritional quality in adelgid-infested hemlocks. Hemlock needles on adelgid-infested stems are

234   higher in nitrogen, suggesting that hemlock woolly adelgid may turn needles into nitrogen-rich

235   sinks. For instance, amino acid content in adelgid-infested hemlock foliage has been measured at

236   levels 3.3-fold greater than uninfested foliage (Gomez *et al.*, 2012). Nitrogen plays a key role in

237   the development and fecundity of herbivorous insects (Awmack & Leather, 2002; Kerslake *et*

238   *al.*, 1998). High concentrations of dietary nitrogen have been shown to increase gypsy moth

239   larval survival and pupal weights (Lindroth *et al.*, 1997), and gypsy moth fecundity has been

240   positively correlated with host plant foliar nitrogen content (Hough & Pimentel, 1978). This is

241   consistent with prior work in this system by Wilson *et al.* (2016) that found hemlock looper

242 larvae reared on adelgid-infested foliage had higher early-instar survival and attained higher

243 pupal weights than larvae reared on uninfested foliage.

244   Adelgid-infested hemlocks in our common garden planting experienced significantly

245 higher rates of defoliation compared to both control (herbivore-free) and scale-infested trees

246 (Fig. 1). Laboratory choice-assays confirmed that gypsy moth larvae preferentially feed on

247 adelgid-infested hemlock foliage. In addition to documenting increased overall nitrogen and

248 amino acid concentrations in adelgid-infested hemlocks, Gomez *et al.* (2012) reported substantial

249 increases in levels of the amino acid proline. Proline can act as an indicator of plant stress

250 (Mattson & Haack, 1987), and is an important source of stored energy for insects (Gäde &

251 Auerswald, 2002). In this case, elevated proline content in adelgid-infested hemlocks may act as

252 a phagostimulatory signal of vulnerability and elevated nutrient content. This pattern has been

253 documented in other plant-insect systems, particularly for various Hemiptera, Lepidoptera,

254 Orthoptera and mite species (Mattson & Haack, 1987).

255   The fact that adelgid feeding enhances gypsy moth preference for, and performance on,

256 eastern hemlock, makes it likely that their co-occurrence on hemlock can additively stress and

257 further threaten this important conifer. In southern New England, adelgid infestation has caused

258 extensive mortality of overstory hemlocks (Eschtruth *et al.*, 2006; Orwig *et al.*, 2002; Preisser *et*

259 *al.*, 2008), altering understory conditions that put hemlock seedlings at a competitive

260 disadvantage (Orwig *et al.*, 2013; Orwig *et al.*, 2008). Hemlocks are adapted to cool

261 microclimates and low light levels (Hadley, 2000), and increased light exposure due to crown

262 thinning and mortality of mature trees inhibits recruitment of hemlock seedlings and favors

263 establishment of black birch (*Betula lenta*) and other deciduous trees (Ingwell *et al.*, 2012; Orwig

264 & Foster, 1998; Orwig *et al.*, 2002). Preferential feeding by gypsy moth larvae on adelgid-

265 infested overstory hemlocks may exacerbate this effect, reducing the likelihood of new hemlock

266 recruits eventually repopulating devastated hemlock forests. The damage inflicted by gypsy

267 moths on adelgid-infested hemlock saplings may further compromise regeneration. Over a four-

268 year period, hemlock regeneration in adelgid-infested forests declined by 46% (Preisser *et al.*,

269 2011). Feeding by both species may accelerate this decline, if inhibited seedling recruitment is

270 coupled with significant mortality of juvenile hemlock saplings.

271   Enhanced performance of gypsy moth larvae on adelgid-infested hemlock may also have

272 a cascading effect on other plant taxa that grow with hemlock in forests of the eastern U.S. Oaks

273 (*Quercus* spp.) are a preferred host of gypsy moth (Barbosa *et al.*, 1979; Hough & Pimentel,

274 1978), and feeding by gypsy moth larvae has caused extensive mortality and decline of overstory

275 oaks throughout this region (Gandhi & Herms, 2010). Total basal area of overstory oaks has

276 decreased due to gypsy moth herbivory, and mortality of white oak (*Quercus alba*), northern red

277 oak (*Quercus rubra*), and chestnut oak (*Quercus montana*) specifically has increased by 40%

278 (Fajvan & Wood, 1976). Gypsy moth herbivory in southern New England forests has increased

279 oak mortality and reduced the growth of surviving canopy trees by as much as 65% (Gottschalk

280 *et al.*, 1990). It is plausible that the enhanced growth of female gypsy moth larvae on adelgid-

281 infested hemlock may translate to greater fecundity, which could increase gypsy moth population

282 densities in southern New England forests. Since tree mortality increases as the intensity and

283 frequency of gypsy moth defoliation increases (Davidson *et al.*, 1999), larger gypsy moth

284 populations here could speed oak decline.

285   It is important to realize that ecological traits of the gypsy moth larvae used in the

286 laboratory performance assay may not be comparable with those of wild gypsy moth larvae.

287 Larvae used in the laboratory performance assay were part of the New Jersey Standard Strain-

14

288 APHIS substrain, a mass-reared colony of gypsy moth larvae that has been in cultivation for >60

289 generations. Because this colony is intended for research, certain selective regimes and control

290 measures have been enacted upon it to maximize the survival and fecundity of the gypsy moths.

291 These include laboratory selection for higher survival and fecundity, and an artificial diet

292 (Frontier Agricultural Sciences, USDA Hamden Formula), which may incidentally select for

293 genotypes that show reduced performance on a natural diet (Grayson *et al*., 2015). However, a

294 comparison of development between gypsy moth larvae from the New Jersey Standard Strain-

295 APHIS substrain, -FS substrain, and three wild populations all reared on a natural diet, found no

296 population-level differences in male and female pupal weights (Grayson *et al*., 2015).

297 Additionally, our observation of substantial wild gypsy moth larval herbivory damage to adelgid-

298 infested field-grown eastern hemlocks, as well as a confirmed wild gypsy moth larval preference

299 for adelgid-infested hemlocks, mirror results from the laboratory performance assay and further

300 support their ecological relevance.

301   Adelgid-induced hemlock mortality has severely affected ecosystem dynamics in eastern

302 U.S. forests. Hemlock supports critical habitat for unique vertebrate and invertebrate

303 communities (Ellison *et al.*, 2010), and dramatic shifts in understory vegetation, soil nutrient

304 cycling and hydrological regimes may have long-lasting changes that compromise these areas

305 (Orwig *et al.*, 2008). Future work should evaluate the extent to which adelgid and gypsy moth

306 act synergistically to speed the decline of eastern hemlock and other canopy-dominant species,

307 and the impact this could have on hemlock-associated ecosystems.

308

309 **Acknowledgments**

320

Contribution of Authors

322   IGK, ELP, CMR, and CMO were responsible for project design. IGK, AKB, ERW, SKS, EES,

323   and ELP were responsible for data collection and analysis. IGK, ELP, AKB, CMR, and CMO

324   were responsible for paper writing.

325

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458 **Figure Legends**

459   **Figure 1**. Gypsy moth larval herbivory damage to eastern hemlocks in adelgid (*Adelges*

460 *tsugae*)-infested, uninfested control, and scale (*Fiorinia externa*)-infested treatment groups.

461 Damage was quantified on a scale of 0-3, representing % foliage loss of trees in each treatment

462 group (0=0-25% foliage loss, 1=26-50%, 2=51-75%, 3=76-100%).

463   **Figure 2**. Percent weight gain (A), pupal weight (B), and larval period (C) of gypsy moth

464 larvae reared on either adelgid-infested or uninfested control hemlock foliage. Bars represent

465 means +/- 1 SE; F = female larvae, M = male larvae. Capital letters denote significant treatment-

466 level differences (P < 0.05).
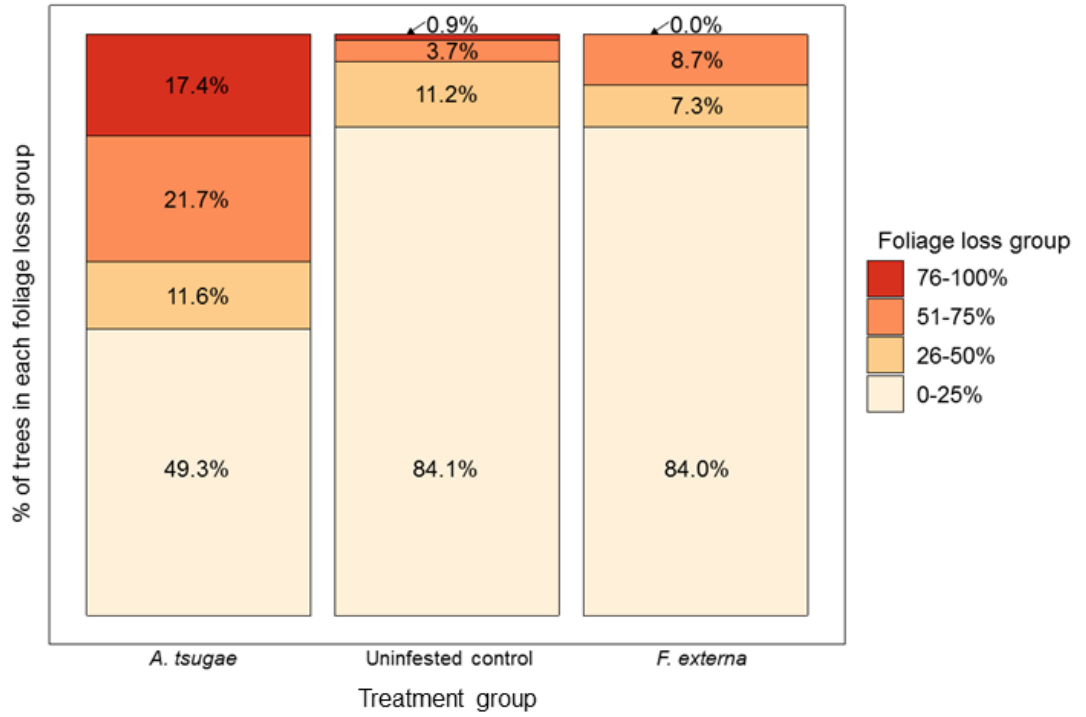
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478   **Figure 1.**

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