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ORIGINAL PAPER

When one is not necessarily a lonely number: initial colonization dynamics of *Adelges tsugae* on eastern hemlock, *Tsuga canadensis*

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Abstract The ability to establish successfully in a new area can vary considerably among species. In addition to the well-recognized importance of propagule pressure in driving the rates of establishment of biological invaders, the life history strategy of a species can also affect establishment success, such as in the extent to which Allee effects (positive density-dependence), and environmental and demographic stochasticity manifest themselves. We quantified the establishment success of *Adelges tsugae*, a non-native insect currently invading North American hemlock. We inoculated eastern hemlock host trees with varying densities of this parthenogenetic insect, from 1 to >500 progrediens ovisacs. The number of settled sistens (the subsequent generation) was positively related to the initial density. More interesting, however, was that we recorded successful establishment from released progrediens ovisacs, and the subsequent initiation of the next generation (sistens), in ≈39 % of host trees inoculated with 1 ovisac. The observation that successful establishment can be accomplished by a single ovisac produced by a single individual has important implications in the invasion dynamics and management of *A. tsugae*.

Keywords Biological invasions · Establishment · Hemlock woolly adelgid · Invasion dynamics

This work is dedicated to our dear friend and colleague, Dan Snider, who tragically passed away prior to the completion of this paper.

Daniel A. Snider: Deceased.

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Introduction

A central question in invasion ecology is why establishment success in a new environment varies so markedly among and within species. In many low-density populations of invading species, such as those that could be typical in founder populations, establishment success can be affected by variety of factors, such as demographic and environmental stochasticity, the presence of suitable habitat and climates to which a new species arrives, and the presence of mutualists, competitors, and natural enemies (Lande 1993; Liebhold and Tobin 2008; Lockwood et al. 2007). Many low-density populations are also subject to Allee effects in which the per capita population growth rate increases with increasing population size (Allee 1938; Courchamp et al. 1999; Stephens et al. 1999; Tobin et al. 2011). Thus, in sparse populations,

individual fitness can be challenged due to, for example, difficulties in finding mates, saturating natural enemies, and exploiting food resources (Courchamp et al. 2008). Past research has highlighted the positive association between the number of individuals in a founder population and subsequent establishment success (Beirne 1975; Drake and Lodge 2006; Hopper and Roush 1993; Leung et al. 2004; Liebhold and Bascompte 2003; Lockwood et al. 2005; Simberloff 2009). Prior observations that suggest that only a minority of species that arrive to a new area establish successfully could reflect the importance of these various factors in limiting establishment success (Ludsin and Wolfe 2001; Simberloff 2009; Simberloff and Gibbons 2004; Williamson and Fitter 1996).

We were motivated by the life history of the hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae), in quantifying its establishment success at low densities. *Adelges tsugae* is parthenogenetic and is not known to engage in gregarious and cooperative behavioral strategies. It is also a species for which existing natural enemies have not been observed to play a significant role in the dynamics of *A. tsugae* (Wallace and Hain 2000), and that the importation and subsequent release of non-native natural enemies against *A. tsugae* populations in North America has been spatially limited to date (Onken and Reardon 2011). For these reasons, many of the documented causes of an Allee effect in insect populations (Liebhold and Tobin 2008) may not be relevant to *A. tsugae* invasion dynamics at present. Another cause of an Allee effect in insect populations is the inability to overcome induced host plant defenses at low densities (Raffa and Berryman 1983). It is not known if new *A. tsugae* populations are affected by plant defensive compounds when attacking North America *Tsuga* hosts. However, past work has reported changes in foliar chemistry after several years of infestation by *A. tsugae* (Stadler et al. 2005), which could ultimately affect subsequent establishment and per capita population growth rates. Low-density populations of *A. tsugae* could also be affected by demographic stochasticity, which can induce an Allee-like effect (Lande 1998). Understanding the potential roles, if any, of Allee effects and stochasticity in the establishment of new populations of *A. tsugae* has important ramifications in the invasion dynamics and management of *A. tsugae*.

Adelges tsugae was introduced from Japan to eastern North America (Havill et al. 2006) where it attacks and kills eastern, *Tsuga canadensis* (L.), and Carolina, *T. caroliniana* Engleman, hemlock (McClure 1989; Orwig et al. 2002). The polymorphic life cycle of *A. tsugae* also contains life stages, including winged adults, that in its native habitat in Japan reproduces sexually and produce galls on tigertail spruce, *Picea torano* (K. Koch) Koehne (Havill et al. 2011). It is believed that the *Picea* spp. in North America are not suitable hosts for this sexually reproducing life stage (McClure 1992). *Adelges tsugae* was first reported in Richmond, Virginia, in 1951 (Gouger 1971). It has since spread to over 182,000 km^2 in North America, which represents $\approx 1/4$ of the area believed to be susceptible to its invasion (Morin et al. 2005), and is estimated to be spreading at a rate of >8 km $year^{-1}$ (Evans and Gregoire 2007). There are two generations per year: an overwintering sistens generation and a spring-to-summer progrediens generation. Females are parthenogenetic and produce a single ovisac containing an average of 22 (for the progrediens generation) and 49–147 (for the sistens generation) individual eggs (McClure 1989; Paradis 2011). Upon hatching, the ambulatory crawlers locate a suitable feeding site at the base of the petiole of a hemlock needle, feed on the ray parenchyma cells, and develop into a sessile adult (Young et al. 1995). Longer-distance dispersal of life stages can be accomplished through the anthropogenic movement of infested host trees, atmospheric transport, and phoretically on other species such as birds and deer (McClure 1990).

Past work has indicated that cold winter temperatures can affect survivorship and thus be a constraint on its range expansion into the northern extent of *T. canadensis* (Paradis et al. 2008; Skinner et al. 2003; Trotter and Shields 2009). There has also been a management effort to release and establish natural enemies against *A. tsugae* populations (McClure and Cheah 1999; Onken and Reardon 2011), raising the possibility that predator-mediated Allee effects (Gascoigne and Lipcius 2004) could eventually arise in established *A. tsugae* populations. However, there remains little information regarding its invasion success at low population densities. We sought to quantify the relationship between initial colony size and subsequent establishment success, and provide evidence that successful establishment and reproduction can occur with an initial density of one ovisac that was produced by one individual.

Materials and methods

Tsuga canadensis trees, 1.2–2.0 m in height, were planted in 0.1 m^3 containers in 2009 and arranged in rows such that trees within a row, and rows, were separated by ≈1 m. Trees were placed under natural conditions on a 17 ha privately-owned commercial farm in Pentress, West Virginia (39.7083°N, 80.1708°W). This farm, situated in northwestern Monongalia County, was ideally located because although Monongalia County was considered to be infested by *A. tsugae*, infestations were primarily located in the eastern part of the county, >20 km away. Also, this site was chosen due to the lack of *Tsuga* spp. on or in the vicinity of the farm. Potted trees were enclosed with a deer fence, and each tree was equipped with a single drip irrigation line. In early spring of 2010 and 2011, trees were fertilized according to nursery recommendations. For studies conducted in 2010 and 2011, we used 48 and 64 trees, respectively. When additional trees were planted in autumn of 2010 (for studies in 2011), tree placement was re-randomized. Trees used in the second year were thoroughly inspected to ensure they were devoid of remaining *A. tsugae* life stages.

In March of 2010 (for studies conducted in 2010) and 2011 (for studies conducted in 2011), we collected branches infested with *A. tsugae* progrediens ovisacs from Rocky Gap State Park, Flintstone, Maryland (39.6974°N, 78.6667°W). Concurrently, we also collected an additional 195 and 101 progrediens ovisacs in 2010 and 2011, respectively, placed them individually into Petri dishes sealed with parafilm, and maintained them under laboratory conditions to monitor crawler emergence and to estimate the initial number of crawlers that hatched from each ovisac. Based upon preliminary work, we determined that our collections should occur at ≈90 degree days from January 1 (base threshold = 5 °C), and that trees should be inoculated with infested material at ≈100 to 110 degree days to ensure that our host trees were suitable for settlement of newly emerged progrediens crawlers. We inoculated trees on March 30, 2010 and April 5, 2011.

Each tree was randomly assigned to one of three (2010) or four (2011) treatments corresponding to initial progrediens ovisac density per tree, from one ovisac to 523 (Table 1; Fig. 1). The additional treatment group in 2011 was due to a lack of initial density greater than 1 but less than 50 ovisacs per tree in 2010. Depending on the treatment group, one or two infested branches were attached to the distal end of a single hemlock branch, approximately 10–15 cm from the tip of the branch. Infested branches were attached using twist ties according to the method of Butin et al. (2007). To maximize establishment and minimize predation, bags (38 cm wide × 45 cm long) were placed around the tree branches that we inoculated (Butin et al. 2007). Bags were constructed with Amber Lumite® screening (280 μg opening, BioQuip Products, Inc., Rancho Dominguez, CA) around a re-bar tie wire frame. For treatments in which only one branch was inoculated, we randomly chose a branch from either the north or west side of the tree. When two branches were inoculated, we randomly selected one branch from the north and one from the west side of the tree. Trees were pruned around the inoculated branches to allow for proper placement and attachment of the bags.

Approximately 1 month following inoculations, after which emerged crawlers had established or not, the bags were removed due to concerns of overheating within the bag. Preliminary work indicated that during June afternoon temperatures and when bags were unshaded, the temperature inside the bag often exceeded 40 °C, which was 10–15 °C greater than ambient temperatures. To alleviate overheating concerns, a shade fence was constructed on the southern and eastern side of the trees to reduce the heat from the morning sun. The location of our site had the advantage of an existing tree line on the western side of our trees, which reduced heat during the afternoon. To further reduce heating, we restricted our inoculations to the north and west side of the tree. After removing the bags, we also removed the initial infested branches to count number of initial ovisacs released per tree as a measure of initial population size per inoculated branch and tree. We also inspected the bags and counted any ovisacs that had fallen off the infested branches.

Adelges tsugae was allowed to complete the progrediens generation and develop ovisacs. Upon detecting newly emerged crawlers of the subsequent sistens generation, which occurred in mid-June at our location, branches (≈30 cm in length) were cut, placed into 1-gallon Ziploc® bags, and labeled by tree, treatment, and tree side (i.e., north or west). Trees were also inspected to ensure that *A. tsugae* was absent from additional branches from the tree that were not initially inoculated. Branches were allowed to remain at room temperature for ≈1 month, after which they

Table 1 Inoculating doses and number of trees by treatment in 2010 and 2011

Years	Treatment	Dose	Number of ovisacs/tree: mean (±SD); range	Number of trees
2010	Low	1 ovisac/tree	1 (0); 1–1	8
2010	Medium	2 infested branches/tree	200 (58); 99–288	20
2010	High	4 infested branches/tree	329 (79); 228–523	20
2011	Low	1 ovisac/tree	1 (0); 1–1	20
2011	Low-2	1 infested branch/tree	15 (8); 6–32	14
2011	Medium	2 infested branches/tree	118 (53); 57–236	15
2011	High	4 infested branches/tree	241 (87); 137–451	15

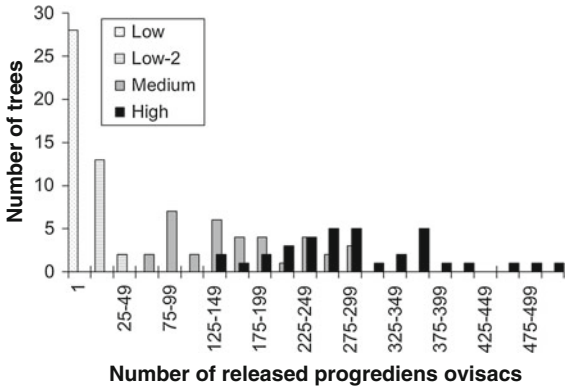

Fig. 1 Frequency distribution of the number of released progrediens ovisacs by treatment group across 2010 and 2011

were stored at −20 °C until they could be processed. Branches were microscopically examined to determine the number of settled sistens crawlers on both old and new hemlock growth, the latter of which would not have been available for colonization by newly hatched progrediens crawlers. We also counted the number of intact sistens ovisacs from the progrediens generation, which indicated successful establishment and development of progredientes but a failure to produce viable sistens offspring. When all branches were processed, we then initialized quality control procedures. Any branch that was part of the low treatment group (1 ovisac per tree) and any branch in which we did not detect any settled sistens crawlers were microscopically examined a second time by a different individual in a blind assay (i.e., the initial data recorded was hidden from the individual). In addition, 25 % of all remaining samples were randomly selected for this quality control procedure.

We tested the main effects of the number of released progrediens ovisacs and year (2010 or 2011), and their interaction, on the number of settled sistens in a general linear model. We also tested the main effects of the number of released progrediens ovisacs and growth type (old or new growth) on which settled sistens were observed, and their interaction, on the number of settled sistens, also in a general linear model. We used an *F* test for lack-of-fit to test the null hypothesis that a linear or quadratic regression model was statistically appropriate (Neter et al. 1990). We also examined the effect of the number of released progrediens ovisacs on the number of intact ovisacs from the progrediens generation (i.e., successful initial establishment and development, but a failure to produce viable sistens offspring) using a general linear model. All continuous variables were transformed using the $\log_{10}(+1)$ transformation to normalize the distribution. Statistical analyses were conducted in R (R Development Core Team 2012).

Results and discussion

From the subset of ovisacs maintained under laboratory conditions, we observed a mean (±SE) of 13.6 (2.0) and 10.8 (0.8) emerged crawlers per ovisac in 2010 and 2011, respectively. Of the 296 ovisacs we examined, only four failed to yield crawlers; otherwise, the range of crawlers per ovisac across both years was 1 to 44. Overwintering temperatures at Rocky Gap State Park were generally above supercooling points for *A. tsugae* and thus conducive to overwintering survival. Although supercooling points vary regionally and month-to-month, they generally range between −15 and −30 °C (Skinner et al. 2003). The minimum recorded temperature in January (when supercooling points are = −30 °C) at Rocky Gap

State was −13.9 and −16.5 °C in 2010 and 2011, respectively, while in March (when supercooling points are = −15 °C), the minimum recorded temperature was −2.8 and −8.3 °C in 2010 and 2011, respectively. The mean number of crawlers per ovisac were lower than previously reported (McClure 1989, 1990), but ideal for this study in which we sought to quantify invasion success specifically at low initial densities.

The number of settled sistens on old and new growth, and for studies conducted in 2010 and 2011, based upon the number of released progrediens ovisacs is presented in Fig. 2. The most significant variable in both cases was the number of released progrediens ovisacs ($P < 0.01$). In contrast, we did not observe a significant interaction effect between initial density and the rate of settling by sistens between old and new growth ($P = 0.34$), and between studies conducted in 2010 and 2011 when combining settled sistens on old and new growth ($P = 0.97$). At the time of branch cutting, new growth generally constituted <3 cm of the branch, which was ≈30 cm in length. Despite the fact that most of the available habitat for *A. tsugae* was on old growth, the lack of difference in settling rate between new and old growth could be due to several factors. For example, it is possible that stylet insertion by *A. tsugae* nymphs could be accomplished more easily in softer, new growth than older growth. Moreover, McClure (1991) reported that sistens crawlers preferred to settle on new growth, while Lagalante et al. (2006) suggested that both generations feed on foliage less than 14 months old. New growth could also be nutritionally superior to old growth (Miles 1990). We did notice anecdotally that crawlers that emerged from our released ovisacs tended to settle at the distal portion of the branch, which would place their progeny in closer proximity to new hemlock growth.

As expected, the number of settled sistens significantly increased with increasing initial densities ($P < 0.01$, Fig. 2). However, a particularly interesting aspect of our study is that despite the variation in establishment success at our lowest initial density (1 ovisac/tree), we observed successful establishment from released ovisacs, and the subsequent initiation of the next generation, in 2 of 8 trees in 2010, and 9 of 20 trees in 2011. Of these 11 trees, the number of settled sistens was greater than the mean number of emerged crawlers from our subset of progrediens ovisacs (13.6 and 10.8 in 2010 and 2011, respectively) in 4 cases, suggesting positive population growth. In 4 other cases, we observed 10–12 settled sistens, suggesting population replacement. Thus, our results suggest that new populations of *A. tsugae* could be initialized by a single individual producing a single ovisac.

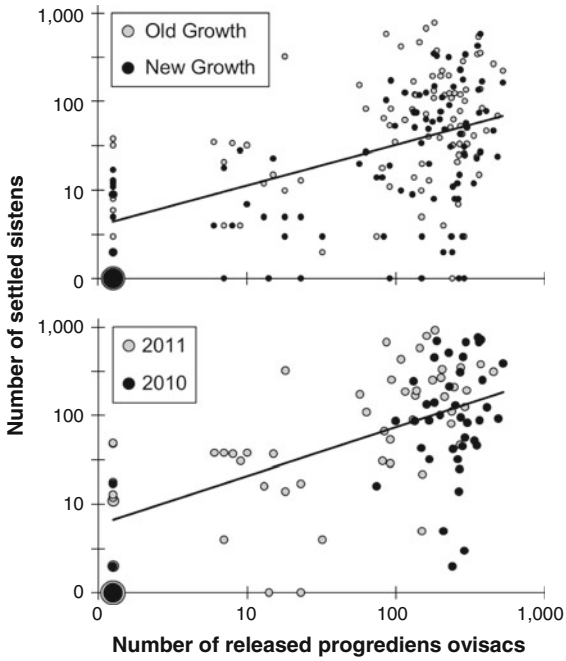

Fig. 2 The number of settled sistens on old and new hemlock growth (*top*), and in 2010 or 2011 (*bottom*), over the number of released progrediens ovisacs. In both cases, a common linear regression is shown given the lack of an interaction effect between initial density, and growth (old vs. new) or year (2010 vs. 2011). The *circle sizes* are proportional to the sample size

We observed a nonlinear relationship, based upon the *F* test for lack-of-fit, between the number of intact ovisacs from the progrediens generation (i.e., successful initial establishment and development, but a failure to produce viable offspring) and the number of ovisacs initially released (Fig. 3). Subsequent polynomial regression indicated that a quadratic equation provided the best fit based upon the *F* test for lack-of-fit. This curvilinear response could be indicative of positive-density dependence (i.e., an Allee effect, Stephens et al. 1999), which suggests a greater potential fitness cost at lower initial densities than at higher densities (Fig. 3). One explanation for the observed positive density-dependence could be due to interactions with host tree defenses. For example, past work has reported feeding by *A. tsugae* causes tree tissue to become more nutritious (Gómez et al. 2012),

analogous to the galling response induced by *A. tsugae* when feeding on spruce (Havill and Foottit 2007). This suggests that fitness could be enhanced in a positive density-dependent manner if feeding by *A. tsugae* increases the nutritional value of host trees in a positive density-dependent manner, thus giving rise to a potential Allee effect. These topics warrant additional study.

Non-native species continue to arrive and establish in new areas, and species can exhibit tremendous variation in their ability to establish. It is likely extremely rare for a single individual to successfully colonize a new area, especially for those that reproduce sexually. A single gravid female of the amphipod *Hyalella* was observed to successfully establish under experimental conditions (Wellborn and Capps 2012), but establishment success would be impossible in the absence of prior mating. Parthenogenetic species, such as *A. tsugae*, could have a particularly high invasion success rate if establishment success is not dependent upon the need to find mates given the importance of mate-finding failures in the biological invasion process (Gascoigne et al. 2009). Furthermore, many invading species spread through stratified dispersal, in which new colonies arrive and establish beyond the infested area, grow, and eventually coalesce with the expanding population front; the result is an accelerated spread rate relative to diffusive spread (Hastings et al. 2005; Hengeveld 1989; Shigesada and Kawasaki 1997). Consequently, the formation of new colonies can have a profound impact on the speed of invasion (Johnson et al. 2006; Suarez et al. 2001; Tobin et al. 2007). The finding that a single *A. tsugae* ovisac could initialize a new population thus has immediate implications to its invasion dynamics including the rate of *A. tsugae* spread.

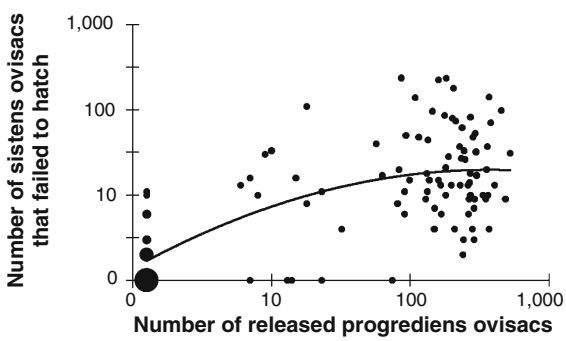

Fig. 3 The number of sistens ovisacs that successfully developed from released progrediens crawlers but failed to hatch based upon the initial number of released progrediens ovisacs. The *circle sizes* are proportional to the sample size

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