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Emerald ash borer biocontrol in ash saplings: The potential for early stage recovery of North American ash trees

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ABSTRACT

In many parts of North America, ash (*Fraxinus*) stands have been reduced by the emerald ash borer (*Agrilus planipennis*) invasion to a few surviving mature trees, saplings, basal sprouts, and seedlings. Without a soil seed bank for *Fraxinus* spp., tree recovery will require survival and maturation of these younger cohorts to reproductive age. Here we report and analyze the population dynamics of emerald ash borer and its associated natural enemies in ash saplings (2.5–5.8 cm DBH) in six deciduous forest stands in southern Michigan. At these sites, the outbreak population of the pest collapsed during the study, and a biocontrol agent introduced from China, the larval parasitoid *Tetrastichus planipennisi*, became widely established and increased in rates of parasitism. To assess the potential for ash recovery in these stands, we also quantified the abundance and crown condition of the ash saplings and surviving ash trees at the study sites. We found that *T. planipennisi* was the dominant biotic mortality factor in saplings, killing 36–85% of the late instar borer larvae. Neither woodpecker predation nor native parasitoids caused more than minor levels (<20%) of borer mortality in saplings. Life table analyses of these data further showed that the net population growth rate of the pest in saplings was near or under replacement levels, and that the introduced biocontrol agent reduced the pest's net population growth rate in saplings at our study sites by over 50%. In addition, stand inventories found that healthy ash saplings (4–16 per 100 m^2) and smaller (pole size) trees (2–9 per 100 m^2) remained in the six study sites, despite an early high density population of the pest at the sites. These findings indicate that the introduced biocontrol agent *T. planipennisi* is providing significant biocontrol services, enhancing ash survival and promoting recovery of the ash in southern Michigan.

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1. Introduction

North American forests are frequently invaded by non-native insects due to increasing global travel of people and expanding international trade (Liebhold et al., 1995; Brockerhoff et al., 2006; Aukema et al., 2010, 2011). Some of these invasive insects severely damage North American forest ecosystems (Aukema et al., 2010, 2011; Van Driesche and Reardon, 2014). An understanding of the population dynamics of such invasive forest pests is needed when restoration efforts are initiated after the invasion (Lockwood et al., 2007).

The emerald ash borer, *Agrilus planipennis* Fairmaire, a buprestid beetle native to northeastern Asia, was discovered in North America as the cause of widespread ash tree (*Fraxinus* spp.) mortality in southeast Michigan and nearby Ontario in 2002 (Haack et al., 2002; Cappaert et al., 2005; Poland and McCullough, 2006). Since then, this invasive beetle has spread throughout much of the eastern United States and Canada, where it has killed hundreds of millions of ash trees (Emerald Ash Borer Information, 2017). In Michigan and Ohio, near the epicenter of the invasion, researchers found 99% mortality of healthy overstory ash trees within six years of detection of emerald ash borer (Smith, 2006; Knight et al., 2013; Klooster et al., 2014). The ecological impacts of such a rapid reduction in ash abundance include changes in forest succession, species composition, and hydrologic processes (Flower et al., 2013; Slesak et al., 2014; Nisbet et al., 2015), losses in biodiversity of ash-dependent species (Gandhi et al., 2014; Wagner and Todd, 2016; Jennings et al., 2016a), and alterations in nutrient and carbon cycles (Ulyshen et al., 2011, 2012; Stephens et al., 2013; Flower et al., 2014).

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Despite predictions that *Fraxinus* could be functionally extirpated from North American forests (Herms and McCullough, 2014), research shows that tree mortality is moderated by several factors including ash species and genotype (Liu et al., 2003; Rebek et al., 2008; Koch et al., 2015); ash tree age, vigor, and stand density (Siegert et al., 2010; Kashian and Witter, 2011; Mercader et al., 2011; Knight et al., 2013; Kashian, 2016); pest population outbreak stages (Burr and McCullough, 2014); climatic factors (Wu et al., 2007; Crosthwaite et al., 2011; DeSantis et al., 2013); and natural enemies (Liu et al., 2003, 2007; Lindell et al., 2008; Duan et al., 2010, 2012a, 2013a, 2015; Bauer et al., 2015; Jennings et al., 2016b, 2016c; Murphy, 2017). Moreover, a recent five-year study of green ash (*F. pennsylvanica* Marsh) regeneration in the aftermath forests of southeast Michigan revealed seed production in small ash trees and basal ash sprouts in 2011 and subsequent seedling recruitment throughout the region (Kashian, 2016). These findings suggest that green ash will likely persist in the presence of emerald ash borer and may remain an important forest species, although its stature and population densities may be greatly diminished on the landscape (Kashian, 2016).

The natural enemy release hypothesis states that some non-native species achieve pest status because they are accidentally separated from their specialized natural enemies when they arrive to new locations and local species are unable to suppress them (e.g., Keane and Crawley, 2002; Mitchell and Power, 2003; Murphy et al., 2014). Although this hypothesis has been criticized for lack of direct experimental evidence in some cases (e.g., Berdegue et al., 1996; Colautti et al., 2004), many dramatic successes in biological control have resulted from the re-association of such invasive pests with their co-evolved natural enemies from the pests' native ranges (e.g., Embree, 1966; see case reviews in Clausen, 1978; van den Bosch et al., 1982; Van Driesche et al., 2010; Van Driesche and Reardon, 2014).

Biological control of emerald ash borer was initiated by the United States Department of Agriculture (USDA) shortly after the beetle was detected in North America (Bauer et al., 2008, 2015). Following regulatory review and approval, USDA issued permits in 2007 for the environmental release of three emerald ash borer parasitoids from northeast China into the United States: the solitary egg parasitoid *Oobius agrili* Zhang & Huang (Hymenoptera: Encyrtidae) and the two gregarious larval parasitoids *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae) and *Spathius agrili* Yang (Hymenoptera: Braconidae) (Federal Register, 2007). *Tetrastichus planipennisi* is an endoparasitoid attacking older emerald ash borer larvae (third and fourth instars) (Liu et al., 2003, 2007; Ulyshen et al., 2010), while *S. agrili* is an ectoparasitoid of the same stages (Yang et al., 2005). Another larval ectoparasitoid, *Spathius galinae* Belokobylskij & Strazanac (Braconidae), from the Russian Far East, was approved for release in 2015 in the U.S. (Belokobylskij et al., 2012; Duan et al., 2012b; Federal Register, 2015). Release of *T. planipennisi* and *O. agrili* continues in emerald ash borer-infested regions of the United States (to date, in 26 of the 31 infested states) and Canada (two provinces). These two species have been consistently recovered more than one year after their release and are considered established in northern regions (Duan et al., 2013a; Abell et al., 2014; Bauer et al., 2015; Mapbiocontrol, 2017). Release of *S. agrili*, however, is now limited to regions south of the 40th parallel due to lack of establishment in northern regions, while *S. galinae* has been approved since 2015 for release in regions north of the 40th parallel (USDA-APHIS/ARS/FS, 2016).

Since the start of biocontrol releases in 2007, field studies in different regions of North America have monitored emerald ash borer parasitoid populations for their establishment and prevalence (Duan et al., 2013a, 2014, 2015; Abell et al., 2014, 2016; Bauer et al., 2015; Davidson and Rieske, 2016; Parisio et al., 2017; Mapbiocontrol.org, 2017). As the pest infestation continues to expand in ash stands in North America, predation of emerald ash borer larvae and pupae by woodpeckers and other bark-foraging birds, and larval parasitism by native parasitoids via new species associations, are regularly observed both in the invasion's epicenter in Michigan (Lindell et al., 2008; Cappaert and McCullough, 2009; Duan et al., 2010, 2014; Jennings et al., 2016c) and at its expanding edges (e.g., Colorado, Texas, New England, Ontario, and Quebec) (Kula et al., 2010; Duan et al., 2013b; Jennings et al., 2013, 2016b, 2016c; Flower et al., 2014; Roscoe et al., 2016).

A seven-year field study (2008–2014) in southern Michigan, following release of the three Chinese parasitoids, showed that parasitism by *T. planipennisi* and *O. agrili* contributed significantly to the reduction of net population growth rate (R_0) of emerald ash borers infesting small to medium ash trees (averaging 8.7–12.1 cm diameter at breast height [DBH]) four years after their initial release (Duan et al., 2013a, 2015; Abell et al., 2014). These biocontrol agents, together with woodpeckers and native parasitoids, primarily *Atanycolus* spp., caused target pest densities in infested ash to decline ~90% (Duan et al., 2015). However, studies are lacking on the impact of introduced and native natural enemies on emerald ash borers attacking ash saplings. Saplings are a critical bridge cohort, whose survival is essential as new ash trees develop from understory seedlings, after the loss of overstory trees (Kashian, 2016).

Here we report results of a three-year study (2013–2015) on the impact of natural enemies on emerald ash borer population dynamics in saplings (2.5–5.8 cm DBH) at six deciduous forest stands in southern Michigan, where *O. agrili*, *T. planipennisi*, and *S. agrili* were released from 2007 to 2010 and where *O. agrili* and *T. planipennisi* became widely established (Duan et al., 2010, 2013a; Abell et al., 2014). For emerald ash borer life stages found in ash saplings, we constructed lifetables and estimated population growth rates using methods previously applied in larger ash trees at the same sites from 2008 to 2014 (Duan et al., 2014, 2015). Lifetables for the emerald ash borer in saplings allowed estimation of pest population growth rates with and without larval parasitism and the contribution to pest reduction due to *T. planipennisi*. To provide insights into the potential future survival and recovery of ash in North American forests, we also assessed ash abundance and crown condition for four size-class ash trees at our study sites.

2. Methods

2.1. Site description

Our study on saplings was conducted in six forested sites in three southern Michigan counties: Ingham Co. (three sites), Gratiot Co. (two sites), and Shiawassee Co. (one site), with 10–60 km between sites. These sites were primarily early successional, second-growth northern deciduous forests dominated by green (*F. pennsylvanica*) and white ash (*F. americana* L.). Less abundant trees species in these forests were black ash (*F. nigra* Marsh), red maple (*Acer rubrum* L.), boxelder (*A. negundo* L.), oaks (*Quercus* spp.), black cherry (*Prunus serotina* Ehrh.), aspen (*Populus tremuloides* Michx), eastern cottonwood (*Populus deltoides* Bartr. ex Marsh), black walnut (*Juglans nigra* L.), American basswood (*Tilia america* L.), and some pine (*Pinus*) species. The location of these sites is described in Duan et al. (2013a).

2.2. Biological control agents released

Each forest site was divided into two plots (each 10–20 ha and separated by 1–6 km), which were randomly designated as either parasitoid-release or non-release control at each location. From