Chapter 22 Progress Toward Successful Biological Control of the Invasive Emerald Ash Borer in the United States

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NON-TECHNICAL SUMMARY

Emerald ash borer (EAB), *Agrilus planipennis* (Coleoptera: Buprestidae), was first detected infesting ash (*Fraxinus* spp.) trees in southeastern Michigan and nearby Ontario in 2002. Shortly after the discovery of EAB in North America, researchers began foreign exploration for natural enemies of this destructive beetle in northeastern Asia, where it is native. This activity led to development of a classical biological control program in 2003. In 2007, North American regulatory agencies approved the first environmental releases of three EAB hymenopteran parasitoid species from China to EAB-infested forests in southeastern Michigan: *Oobius agrili* (Encyrtidae), *Tetrastichus planipennisi* (Eulophidae), and *Spathius agrili* (Braconidae). *Oobius agrili* parasitizes EAB eggs, whereas the two other species parasitize EAB larvae. In 2015, a fourth EAB parasitoid, *Spathius galinae* (Braconidae) from the Russian Far East, was approved for release in northern states. To date, one or more of these introduced parasitoid species has been released in over 350 counties in 30 EAB-infested states and Washington, D.C. in the United States, and four provinces of Canada. Recent studies in Michigan and several northeastern states, where parasitoids were released five or more years ago, indicate that two larval parasitoids (*T. planipennisi* and *S. galinae*) have established co-existing populations in EAB infesting different size-class ash trees; there they complement each other by partitioning host resources, and they play a significant role in suppressing EAB populations. The egg parasitoid *O. agrili* has also established and spread in EAB-infested forests. It is still too early to determine if biological control will result in significant improvement in ash recovery and regeneration. However, the results from long-term field studies in Michigan and several states in the northeastern United States reveal that ash saplings and pole-size ash trees now experience low EAB densities, which are regulated by established populations of the three introduced biocontrol agents. Researchers and land managers are hopeful that surviving North American ash trees will be protected from EAB and ultimately become overstory trees after successful

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areawide suppression of EAB populations by these introduced natural enemies. Monitoring over the next 10–20 years is required to evaluate survival of the different ash tree species impacted by EAB.

HISTORY OF INVASION AND NATURE OF PROBLEM

The Species Invasion

The emerald ash borer (EAB), *Agrilus planipennis* (Coleoptera: Buprestidae), was first identified as the sole factor causing ash (*Fraxinus* spp., family Oleaceae) tree mortality in southeastern Michigan and nearby Ontario in 2002 (**Fig. 1**). During the next 20 years, the spread and establishment of EAB has been confirmed in 35 states and Washington, D.C. in the United States and five Canadian provinces (CIFA, 2022; Emerald Ash Borer Information, 2022). Dendrochronological examination of infested (dead) ash trees in the epicenter of the EAB invasion in Michigan and genetic analyses of beetles collected from different geographic regions of North America and Asia strongly suggest that this beetle arrived in southeastern Michigan in the early to mid-1990s, probably in solid wood-packaging materials and dunnage used in cargo ships originating in northern China (Bray et al., 2011; Keever et al., 2013; Siegert et al., 2014). After EAB's accidental introduction, it presumably established and spread throughout the forests of southeastern Michigan and nearby Ontario where ash trees were once abundant (Haack et al., 2002, 2015; Poland and McCullough, 2006; Pugh et al., 2011; Herms and McCullough, 2014). Emerald ash borer is a strong flier and can disperse more than 10 miles (16 km) per year; however, its long-range spread occurs primarily through movement of firewood and other ash products that contain live stages of EAB (Haack et al., 2010; Prasad et al., 2010; Taylor et al., 2010; Kashian and Witter, 2011; Haack and Petrice, 2021).

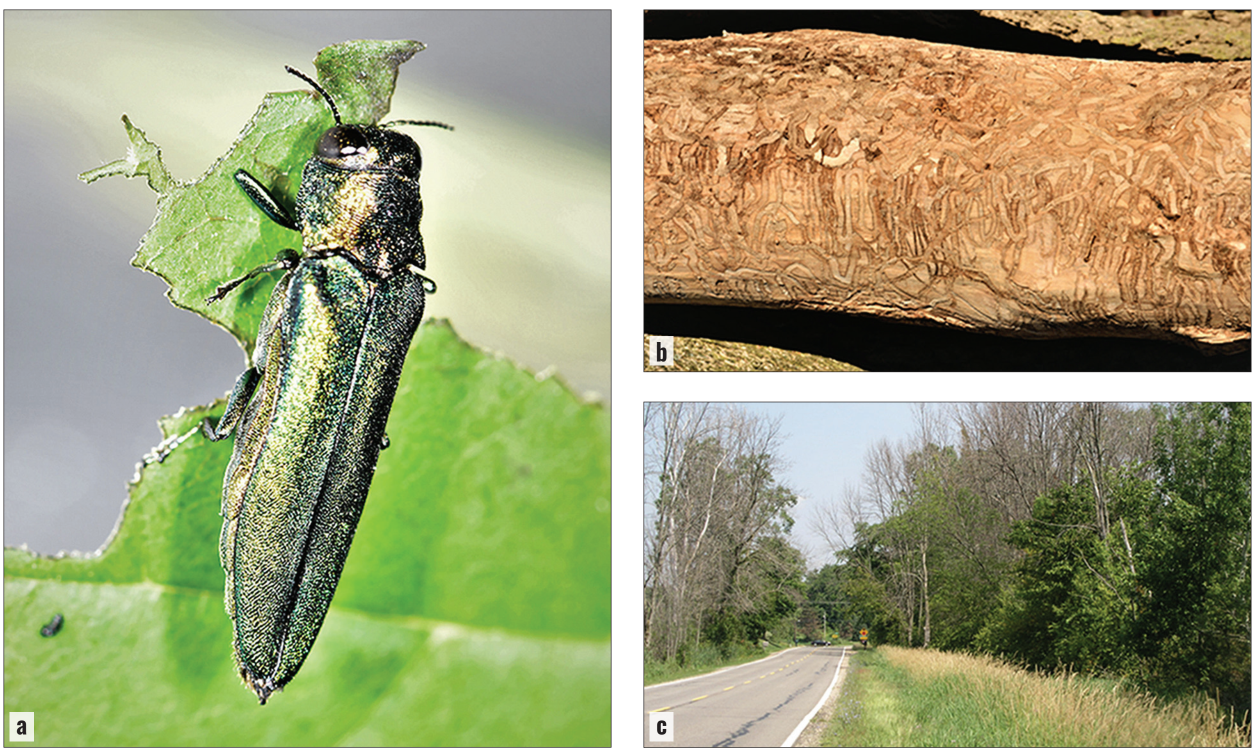

Figure 1. Emerald ash borer (*Agrilus planipennis*, EAB) and its damage to North American ash trees: (a) EAB adult beetle feeding on an ash leaf; (b) feeding galleries of EAB larvae in the phloem and cambium (under the bark) of an ash tree; and (c) widespread and extensive mortality of ash trees caused by EAB ca. 5 years after its initial detection in East Lansing, Michigan. (2009) (J. Duan, USDA-ARS)

Ash species native to North America are highly susceptible to EAB, and even healthy North American trees are quickly killed by EAB (Rebek et al., 2008; Rigsby et al., 2015; Villari et al., 2016). After North American ash trees were introduced to China for reforestation and widely planted in plantations and as landscape trees, their high susceptibility to EAB became increasingly evident, starting in the 1990s (Yu et al., 1992; Liu et al., 2003, 2007; Wei et al., 2004, 2007; Zhao et al., 2005; Wang et al., 2010; Duan et al., 2012a, Straw et al., 2013; Haack et al., 2015; Dang et al., 2021). In the invaded region of North America, EAB populations dispersed quickly in both urban and natural areas due to the abundance of native ash trees in forests, the widespread planting of susceptible North American ash species for landscaping, and movement of EAB-infested materials through human activities (see review in Herms and McCullough, 2014).

Nature of the Problem

Although susceptibility to EAB varies among ash species (e.g., Rebek et al., 2008; Tanis and McCullough, 2012, 2015), all ash species native to North America are known to be susceptible to mortality from EAB, including the most common species—green (*Fraxinus pennsylvanica*), white (*Fraxinus americana*), and black (*Fraxinus nigra*)—as well as the less widespread blue (*Fraxinus quadrangulata*) and pumpkin ash (*Fraxinus profunda*). The potential economic costs associated with the EAB invasion were estimated to be $1 billion per year from 2009 to 2019 (Kovacs et al., 2010), and the ecological impacts on North American forests are already severe and widespread. Emerald ash borer killed 99% of healthy ash trees in some forests infested early in the EAB invasion, and it has the potential to functionally extirpate ash trees from the continent (Klooster et al., 2014; Herms and McCullough, 2014). The loss of ash diversity and abundance in natural forests in earlier invaded regions (e.g., Midwestern and Mid-Atlantic states) has damaged biodiversity and ecosystem processes such as nutrient cycling (Gandhi et al., 2010, 2014; Pugh et al., 2011; Kashian and Witter, 2011; Ulyshen et al., 2011, 2012; Flower et al., 2013; Stephens et al., 2013; Jennings et al., 2017; Morin et al., 2017; Engelken et al., 2020; Jacobsen, 2020).

More recently, EAB was observed attacking the white fringetree (*Chionanthus virginicus*, a species in the same family as ash that is native in the southeastern United States) when it was planted as an ornamental near heavily infested ash trees in Ohio and nearby states (Cipollini, 2015; Peterson and Cipollini, 2020). Because EAB was not confirmed to attack host plants other than ash (Anulewicz et al., 2008), its successful development in *C. virginicus* represents a host range expansion and suggests other woody plants in Oleaceae planted in North America may be susceptible to EAB attack (e.g., forsythia, lilac, privet). In a recent laboratory study, EAB completed development on European olive tree, *Olea europaea* (Oleaceae), suggesting EAB may become an economic pest of olive crops in the United States (Cipollini et al., 2017).

WHY CONTROL THIS INVASIVE SPECIES?

Initial efforts to control EAB focused on containment and eradication of newly detected EAB populations by destroying every ash tree within a 0.5-mile (0.8-km) radius of an EAB-infested ash, as well as restricting the movements of ash materials (e.g., nursery trees and firewood) from the quarantined areas to non-infested areas (Federal Register, 2003; Cappaert et al., 2005; Sawyer, 2007; Taylor et al., 2010). Eradication efforts were abandoned by 2009 because EAB populations in many infested areas (such as Michigan, Ohio, and Maryland) were already too high and too widespread, and EAB-detection methods were inadequate to locate new infestations (GAO, 2006; Poland and McCullough, 2006; Herms and McCullough, 2014). Subsequently, efforts shifted toward slowing the spread of EAB to new areas through regulatory restrictions on the movement of EAB-infested wood or plant materials, insecticide treatment of susceptible trees (either artificially girdled or naturally stressed) as trap trees (e.g., Mercader et al., 2015; Sadof et al., 2021), and classical biological control via the introduction of natural enemies originating in EAB's native range. By 2021, federal quarantine rules restricting the movement of this pest and infested plant materials were discontinued in the United States (Federal Register, 2020), although some state and regional restrictions remain. Thus, protection of North American ash tree species against EAB now relies on sustainable management strategies. Because it is neither environmentally safe nor economically feasible to protect all ash trees in natural forests against EAB using insecticides, classical biological control is currently the only sustainable option available (Bauer et al., 2014, 2015; Duan et al., 2018; USDA-APHIS, 2020; USDA-APHIS/ARS/FS, 2021).

Evidence from field observations in the Russian Far East and northeastern China strongly suggests that several specialized egg and larval parasitoids have protected the more susceptible North American ash species in parts of EAB's native range (Liu et al., 2003, 2007; Duan et al., 2012a; J. Duan, unpub. data). This protection against EAB by specialized natural enemies may occur at two different phases of EAB attack. First, saplings and young susceptible North American ash trees in Asia might be initially colonized by EAB at only low levels because there are few available beetles migrating from resistant Asian ash species. Second, the relatively higher abundance of natural enemies specialized to attack EAB in the pest's native range, notably several species of egg and larval parasitoids, may allow parasitoid populations to increase more rapidly via numerical and functional responses and attack incipient infestations of EAB on susceptible ash species. Both processes may suppress EAB to low densities by slowing its population growth rate.

THE ECOLOGY OF THE PROBLEM

EAB is a beetle that feeds on phloem and neighboring tissues (sapwood and cambium), hereafter referred to only by 'phloem', and it specializes on ash (*Fraxinus* spp.) trees (Yu, 1992; Haack et al., 2002). It has a relatively long lifecycle, requiring one or two years per generation, and a female beetle can lay over 100 eggs (Rutledge and Keena, 2012; Haack et al., 2015; Duan et al., 2020a; Petrice et al., 2021a). Adult beetles normally emerge from infested ash trees from late spring through early summer and feed on ash foliage for about two weeks before mating and oviposition (Rutledge and Keena, 2012; Jennings et al., 2014). Feeding on ash foliage by adult beetles rarely causes significant damage to ash trees. However, tunnelling by the larval stages (1^{st}–4^{th} instars) in the phloem effectively girdles host trees, severely disrupting water and nutrient movement in the trunk, branches, and stems (>0.4 in or 1 cm in diameter).

Generally, infested mature ash trees die 3–5 years following initial EAB attack, even with only moderate larval densities (Knight et al., 2013). In ash-dominant forests, the EAB invasion process can be described as having three phases: the cusp, crest, and core (Burr and McCullough, 2014). The initial infestation, or cusp phase, occurs during the first few years at newly infested sites, while EAB populations slowly build, followed by the crest phase when EAB numbers increase rapidly, causing widespread ash mortality. The core phase follows and lasts 5–10 years after the initial infestation, by which time most larger ash trees have died and the EAB population has collapsed (Burr et al., 2018).

In North America, it is not feasible to attempt to immediately protect susceptible overstory ash trees against EAB in a newly invaded area through the introduction and establishment of specialized natural enemies from Asia because methods to detect early EAB infestations (cusp phase of invasion) are lacking. Moreover, the EAB biocontrol agents are expensive and difficult to rear, and the release a few thousand parasitoid wasps against hundreds of thousands of EAB beetles will not control the invasive EAB populations in time to protect the large ash trees. Susceptible North American ash species are abundant and widespread, and invasive EAB populations grow rapidly in the newly invaded forests (crest phase), making it difficult to suppress EAB outbreaks before mature ash trees suffer substantial mortality. In the post-EAB invaded (core phase) hardwood forests of North America, ash trees are typically scarcer than in the pre-invaded forests, and EAB populations are greatly reduced. Establishment of the introduced EAB parasitoids in the post-invaded forests may effectively protect younger surviving ash trees, saplings, and seedlings by moderating the frequency and amplitude of future EAB outbreaks, as in EAB's native Northeastern Asian range. Subsequently, ash density and size are expected to increase, resulting in a partial return to pre-invasion conditions. Tree regrowth is a slow process, which could allow adequate time for populations of the introduced parasitoids to expand to levels needed to suppress EAB populations below a tolerance threshold for *Fraxinus* spp.

PROJECT HISTORY THROUGH BIOCONTROL AGENT ESTABLISHMENT

Foreign Exploration for Natural Enemies

Shortly after EAB was detected in Michigan, the United States Department of Agriculture (USDA) initiated research to develop a classical biocontrol program for EAB. Exploration started in 2003 for EAB natural enemies in regions of northeastern Asia where it is native, including the Chinese provinces of Hebei, Heilongjiang, Jilin, Liaoning, and Shandong, and the cities of Beijing and Tianjin (Liu et al., 2003). Three major hymenopteran natural enemies of EAB were discovered: the egg parasitoid *Oobius agrili* (Encyrtidae) and two larval parasitoids, *Tetrastichus planipennisi* (Eulophidae) and *Spathius agrili* (Braconidae) (Liu et al., 2003, 2007; Zhang et al., 2005; Yang et al., 2005, 2006). Since then, several other minor species were found in China, including a larval-pupal parasitoid, *Sclerodermus pupariae* (Bethylidae) (Wang et al., 2010; Yang et al., 2012; Wang et al., 2016). Foreign exploration for EAB natural enemies in both Japan and Mongolia was unsuccessful due to the lack of observable EAB populations. However, exploration in the Russian Far East in EAB-infested North American ash planted as landscape trees as well as artificially stressed Asian ash in natural forests resulted in the discovery of three hymenopteran EAB natural enemies: the egg parasitoid *Oobius primorskyensis* (Encyrtidae) and the larval parasitoids *Spathius galinae* and *Atanycolus nigriventris* (Braconidae) (Belokobylskij et al., 2012; Duan et al., 2012a, 2019a; Yao et al., 2016). In addition, foreign exploration in South Korea identified low densities of EAB populations infesting Asian ash trees, and three natural enemy species were found: *S. galinae*, *Tetrastichus telon* (Eulophidae), and a parasitic beetle *Teneroides maculicollis* (Cleridae) (Williams et al., 2010; Gould et al., 2015).

Selection of Potential Agents and Regulatory Permission for Release

The selection of Asian EAB natural enemies for introduction to North America was based on field surveys of natural enemies and their impacts on EAB populations in Asia, combined with generally accepted characteristics of potentially successful biological control agents (e.g., Doutt and DeBach, 1964; Kimberling, 2004). Attributes of candidate natural enemies include but are not limited to (1) high degree of host specificity, (2) high searching ability, (3) high reproductive rate, (4) good spatial and temporal synchrony with the host, and (5) adaptability to a wide range of ecological conditions. For example, *S. pupariae* did not meet several of these criteria as a potential EAB biological control agent because (1) species in this genus are known to sting humans (Gordh and Moczar, 1990), (2) its hosts include a broad range of wood-boring insects (Tang et al., 2012), and (3) the parasitism of EAB in China is low (Yang et al., 2012). Another braconid species, *A. nigriventris*, from the Russian Far East seemed promising, but scientists were unable to successfully rear it in the laboratory. The remaining two egg parasitoids (*O. agrili* and *O. primorskyensis*) and three larval parasitoids (*T. planipennisi*, *S. agrili*, and *S. galinae*) were all considered promising candidates as biological control agents and were imported into quarantine in the United States for further testing shortly after their discovery (for reviews see Bauer et al., 2014, 2015; Duan et al., 2018). The safety and host specificity of Asian parasitoids were assessed for environmental release in North America using data collected from field surveys of other wood-boring insects in China and the Russian Far East and laboratory testing of Asian and North American wood-boring insects. Host specificity of these parasitoids was found to be highly constrained by the close phylogenetic relatedness of potential nontarget hosts to EAB (Federal Register, 2007, 2015; Yang et al., 2008; Bauer et al., 2008, 2014; Duan et al., 2015a). Field data from China and the Russian Far East showed that these parasitoids do not attack other wood-boring insects in ash, such as bark beetles (Curculionidae: Scolytinae) or longhorned beetles (Cerambycidae) (Yang et al., 2008; Duan et al., 2015a). Host specificity studies in the laboratory found that EAB was the only host of *T. planipennisi*, whereas the other four potential biocontrol agents (*O. agrili*, *O. primorskyensis*, *S. agrili*, and *S. galinae*) attacked some other Asian or North American *Agrilus* species (**Table 1**). In contrast to the high rates of parasitism by these parasitoids in EAB, rates in non-target species were consistently much lower, even under laboratory conditions, which promotes maximum parasitism (Federal Register, 2007, 2015; Yang et al., 2008; Bauer et al., 2014; Duan et al., 2015a, 2019a). Based on both laboratory and field host-range studies, the predicted non-target impact from introduction of these Asian parasitoids for EAB biocontrol was low levels of parasitism of some North American *Agrilus* species.

Table 1. Number of non-target insect taxa tested with EAB parasitoids from China and the Russian Far East petitioned to the North American Plant Protection Organization for first environmental releases in North America as EAB biocontrol agents. (modified from Duan et al., 2018)

Parasitoid Species	Orders tested	Families tested	Species tested	*Agrilus* spp. tested	*Agrilus* spp. attacked
Oobius agrili [1]	2	6	18	6	3
Tetrastichus planipennisi [1]	3	6	14	5	0
Spathius agrili [1]	2	6	18	9	5
Spathius galinae [2]	3	6	15	6	1
Oobius primorskyensis [3]	3	6	30	10	7

[1] Data compiled from Federal Register, 2007; Yang et al., 2008; Bauer et al., 2014
[2] Data compiled from Federal Register, 2015; Duan et al., 2015a
[3] Data compiled from Duan et al., 2019a

Release and Establishment of EAB Natural Enemies in North America

In 2007, after completion of extensive field and laboratory studies, the three EAB parasitoid species from China (*O. agrili*, *T. planipennisi*, and *S. agrili* [**Fig. 2a–f**]) were approved for release in the United States (Federal Register, 2007; Bauer et al., 2008, 2014, 2015). In Canada, releases of *T. planipennisi* were approved in 2013 and *O. agrili* in 2015 (Duan et al., 2018). *Spathius galinae* (**Fig. 2g,h**) from the Russian Far East was subsequently approved for release in the United States in 2015 (Federal Register, 2015) and in Canada in 2017 (CFIA, 2018). However, *O. primorskyensis* was not approved for release in the United States, and its release will not be reconsidered until the petition is revised and resubmitted with additional justification and research (Gould and Duan, 2018; J. Duan and J. Gould, unpub. data).

In the summer and fall of 2007, adults of *O. agrili*, *T. planipennisi*, and *S. agrili* were released in small numbers in EAB-infested ash stands in two counties in southern Michigan (Bauer et al., 2014, 2015; Gould et al., 2015; Duan et al., 2018). Field studies in the spring of 2008 revealed successful reproduction

Figure 2. (next page) *Oobius agrili*, a solitary and parthenogenic egg parasitoid of emerald ash borer EAB, (a) adult female wasp laying an egg inside an EAB egg and (b) EAB eggs parasitized by *O. agrili*. *Tetrastichus planipennisi*, a gregarious eulophid larval endoparasitoid of EAB, (c) adult wasp drilling through ash bark to oviposit in an EAB larva and (d) a parasitized EAB larva being consumed internally by a brood of *T. planipennisi* larvae. *Spathius agrili*, a gregarious braconid larval ectoparasitoid of EAB, (e) adult female wasp drilling through ash bark to oviposit on an EAB larva and (f) a brood of parasitoid larvae pupating in their cocoons after consuming and developing on an EAB larva in its gallery under the bark of an ash tree. *Spathius galinae*, a gregarious braconid larval ectoparasitoid of EAB, (g) adult female wasp drilling through ash bark to oviposit on an EAB larva and (h) a brood of parasitoid larvae, pupating in their cocoons, after consuming and developing on an EAB larva in its gallery under the bark of an ash tree. (a, c-h: J. Duan, USDA-ARS; b: L. Bauer, US Forest Service)

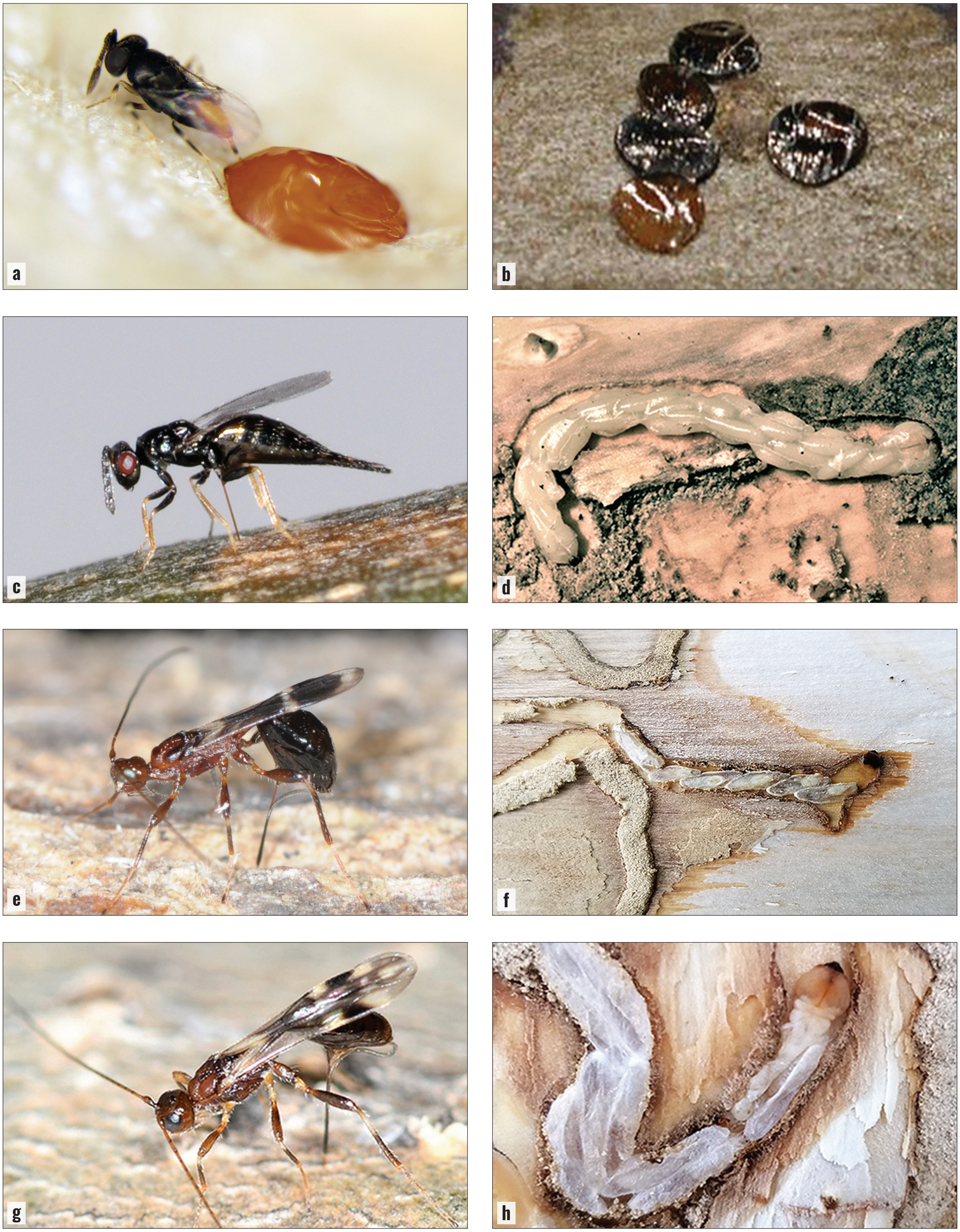

Figure 2. Emerald ash borer parasitoid species approved for release in the United States (explanation of images given on previous page).

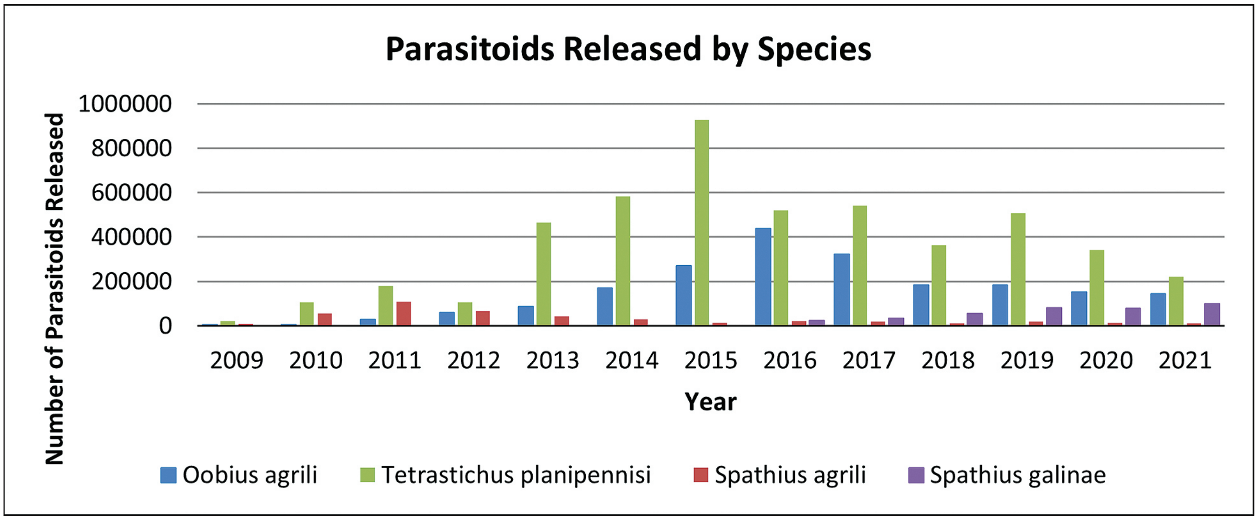

Figure 3. Total number of the Asian parasitoids released for biocontrol of emerald ash borer in the United States from 2009 to 2021. (B. Slager and J. Gould unpub. data, USDA-APHIS Brighton Biocontrol rearing facility)

and overwintering of all three parasitoids species in Michigan, and additional releases were made at EAB-infested forests in Ohio and Indiana, as well as additional locations in Michigan (Bauer et al., 2014, 2015; Duan et al., 2018). In 2009, USDA constructed a rearing facility in Brighton, Michigan for mass-rearing the three EAB parasitoid species, which greatly increased production and field releases of these biocontrol agents (**Fig. 3**). As rearing methods progressively improved, parasitoid production of the three Chinese species, and later *S. galinae* from Russia, increased in the years that followed. However, production of *S. agrili* was purposely reduced because its release in northern states was discontinued by 2013 due to lack of establishment (Duan et al., 2018; Jones et al., 2020). As of the fall of 2021, at least one parasitoid species has been released in more than 350 counties in 30 of the 35 EAB-infested states and Washington D.C. in the United States and in four of the five EAB-infested provinces in Canada (**Fig. 4**) (MapBiocontrol, 2021).

To assess establishment of introduced EAB biocontrol agents, various recovery and sampling methods have been developed and tested, such as tree-cutting and rearing parasitoids from bolts, field-debarking to look for parasitized larvae, outer bark sampling for recovery of EAB eggs and egg parasitism, use of sentinel host larvae or eggs, and deployment of yellow pan traps (e.g., Duan et al., 2012b, 2012c, 2013; Jennings et al., 2018; Petrice et al., 2021b; Rutledge et al., 2021; USDA–APHIS/ARS/FS, 2021; Quinn et al., 2022a,b). Although all three EAB biocontrol agents from China were recovered from EAB larvae or eggs one year after their first release in several northern states, only *O. agrili* and *T. planipennisi* have been consistently recovered for two or more years after final release. These two species are now considered widely established and spreading naturally beyond their initial release sites. More than a decade since its first release in 2007 in Michigan, establishment of *S. agrili* remains unconfirmed in the northern United States and most of the Mid-Atlantic region. However, its parasitism of EAB larvae has been found sporadically at some sites south of the 40th parallel, where this species continues to be released (e.g., Hooie et al., 2015; Aker et al., 2022). Recent field work on *S. galinae*, which was released between 2015 and 2021 in Michigan, Maryland, Colorado, Connecticut, Illinois, Massachusetts, New York, Rhode Island, and Tennessee in the United States, has found it to be establishing and spreading in nearly all release areas and beyond (Duan et al., 2019b, 2020; Aker et al., 2022; J. Gould, pers. obs.).

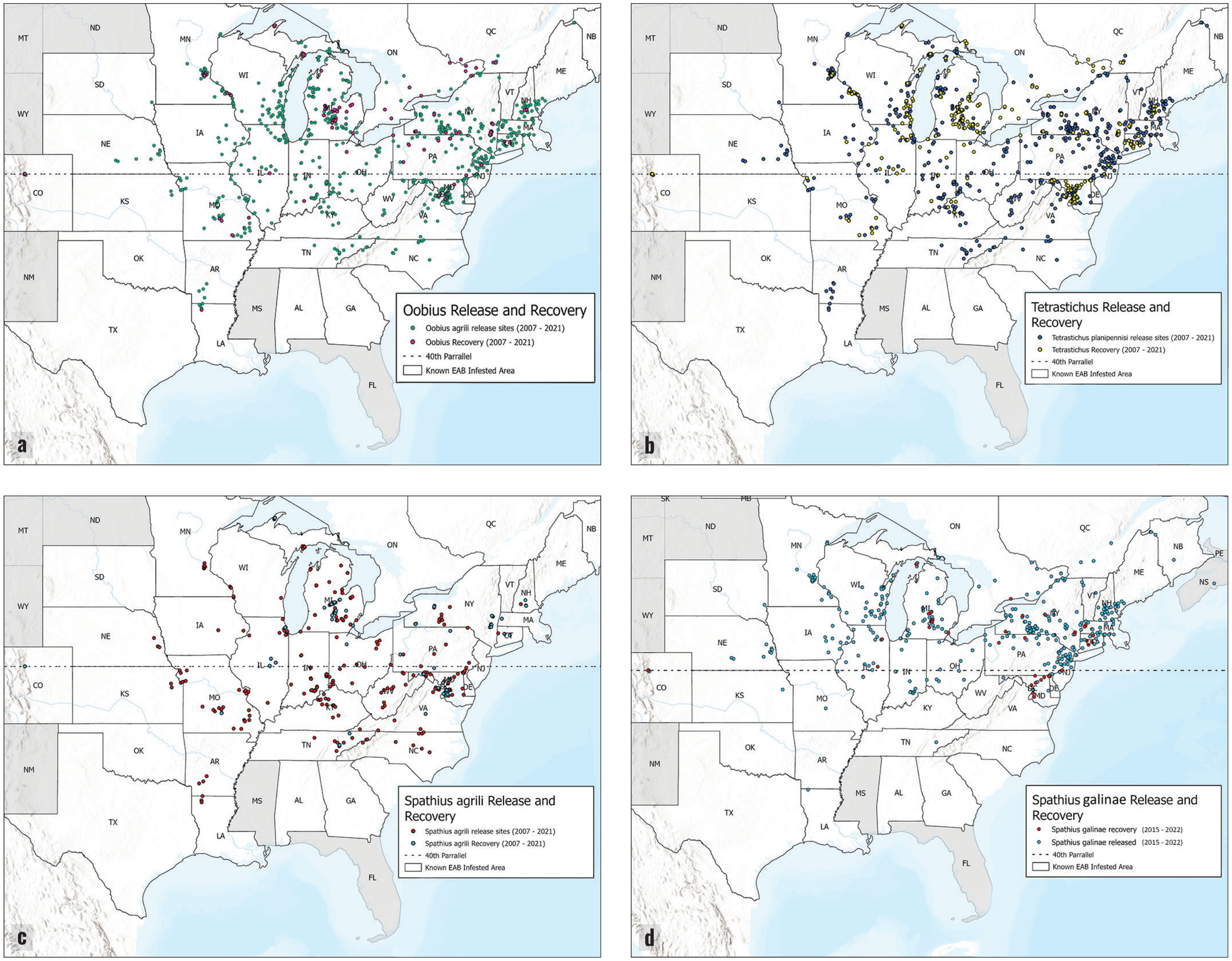

Figure 4. Maps showing known regions of North America invaded by emerald ash borer (EAB), and the release and recovery sites for biocontrol agents introduced from Northeast Asia into North America from 2007 to 2021 for classical biological control of EAB, as reported on the EAB biocontrol geospatial database (mapbiocontrol.org 2021): (a) *Oobius agrili*; (b) *Tetrastichus planipennisi*; (c) *Spathius agrili*; and (d) *Spathius galinae*. In the United States, releases of *O. agrili*, *T. planipennisi*, and *S. agrili* began in 2007, and releases of *S. galinae* began in 2015, thus there are fewer release and recovery sites for *S. galinae* than for the other three biocontrol agents. In Canada, *T. planipennisi* releases began in 2013, *O. agrili* in 2015, and *S. galinae* in 2017. Note: some release and recovery sites are not visible due to the close geographic proximity of many sites at the scale of these maps, especially in states with many release and recovery sites.

HOW WELL DID BIOLOGICAL CONTROL WORK?

To evaluate establishment, spread, and impacts of the biocontrol agents on EAB population dynamics and ash tree health, six long-term study sites were established in southern Michigan between 2007 and 2010, and each was comprised of paired release and non-release control plots. At each release plot, 1,000–3,000 females of *O. agrili*, *S. agrili*, and *T. planipennisi* were released. In subsequent years, infested ash trees were sampled to estimate EAB egg and larval parasitism and other causes of larval mortality (Duan et al., 2013; Abell et al., 2014). During the first five years after release of the three Chinese parasitoids at these Michigan sites (2008–2011), average EAB egg parasitism by *O. agrili* was 1 to 4%, but by 2014 it increased to ~28% in release and control plots (Duan et al., 2012b, 2013, 2015b). Spread of *O. agrili* from the release plots to the control plots, however, was slow (Abell et al., 2014). Overall, the impact of *O. agrili* in suppressing EAB population growth, as well as the natural spread of this biocontrol agent, has yet to be determined because sampling EAB eggs from ash bark layers and crevices is labor-intensive and difficult to standardize (Duan et al., 2011; Abell et al., 2014; Jennings et al., 2018; Petrice et al., 2021b). Moreover, parasitism of EAB eggs by *O. agrili* is patchy, and therefore, relatively more intensive sampling is needed to recover it and quantify its impact on EAB population dynamics (Petrice et al., 2021b).

For *T. planipennisi*, larval parasitism ranged from 1 to 6% from 2008 to 2011, but by 2014, it increased to ~ 30% in both the release and control plots (Duan et al., 2012b, 2013, 2015b). Moreover, the results from recent studies found that *T. planipennisi* can spread rapidly across EAB-infested forests surrounding release sites (e.g., Jones et al., 2019; Rutledge et al., 2021; Quinn et al., 2022a). Life table analyses, including seven years of data from the six Michigan study sites, revealed that *T. planipennisi* also contributed significantly to the reduction of net EAB population growth rates in the aftermath of the EAB invasion outbreak within approximately four years of its initial release (Duan et al., 2014, 2015b). Although local generalist natural enemies, such as *Atanycolus* spp. and woodpeckers, played a significant role in reducing invasive EAB populations during its outbreak phase, the introduced specialist *T. planipennisi* has since become the dominant mortality factor of EAB larvae in the aftermath of the EAB invasion in Michigan (**Fig. 5**).

Results from field surveys in China, the Russian Far East, and the United States showed that EAB larval parasitism by *T. planipennisi* is concentrated in smaller-diameter ash trees (Liu et al., 2007; Abell et al., 2012; Duan et al., 2012a; Jennings et al., 2016). A recent study of randomly

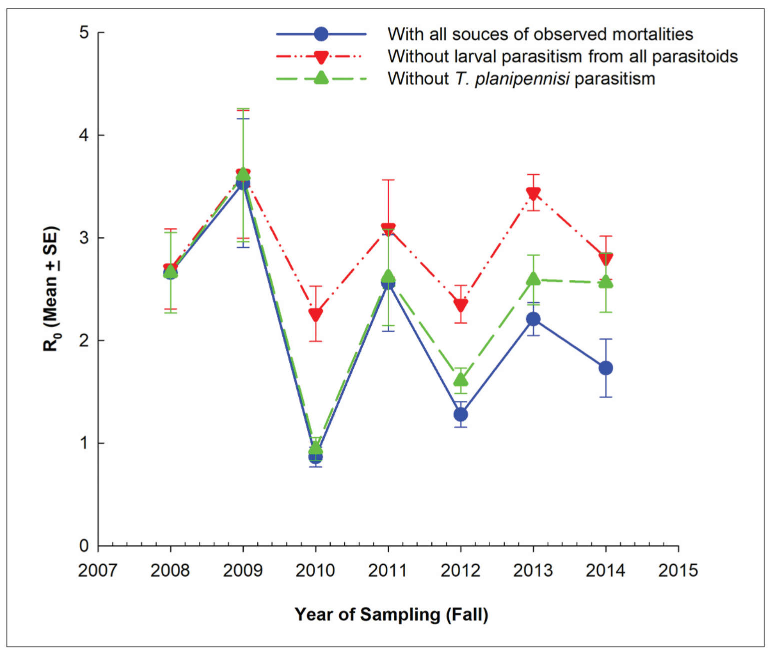

Figure 5. Net population growth rates (R_0) of emerald ash borers infesting young ash trees (DBH = 7 – 21 cm) across six different study sites in southern Lower Michigan, where the larval parasitoid *T. planipennisi* was released between 2007 and 2010. Blue solid line represents R0 estimated using life table analysis by including all sources of the observed larval mortalities. Red-dotted line represents R_0 estimated using the same lifetable analysis after excluding larval parasitism from all larval parasitoids including both the native North American parasitoids (primarily *Atanycolus* spp.) and the introduced larval parasitoid *T. planipennisi*. Green-dashed line represents R_0 estimated using the same lifetable analysis after excluding only *T. planipennisi* from the life table, assuming mortality rates from other factors would not change due to increases in EAB densities. (modified from Duan et al., 2015)

sampled ash saplings (2–6 cm or 0.8–2.4 in DBH [Diameter at Breast Height]) at the six study sites in Michigan found that *T. planipennisi* was the dominant mortality factor, causing 36–85% parasitism of older EAB larvae (3rd and 4th instar), thereby reducing EAB damage in young ash (Duan et al., 2017a). Studies in regenerating ash in eastern and western New York showed similar results, with avian predators (primarily woodpeckers) and *T. planipennisi* reducing EAB population growth to zero at six sites in western New York (Gould et al., 2022). As suspected, the ability of *T. planipennisi* to parasitize EAB in larger ash trees, which have thick bark (>3.2 mm or 0.125 in thick), is limited by its short ovipositor that ranges from 1.9 to 2.6 mm (0.07–0.1 in) long (Abell et al., 2012; Duan et al., 2020b). Consequently, *T. planipennisi* does not attack EAB larvae feeding under thick bark on the lower boles of larger ash trees (>12 cm or 4.7 in DBH) (Abell et al., 2012).

To achieve parasitism of EAB larvae attacking larger-diameter overstory ash trees, and perhaps to reduce widespread ash mortality, EAB biocontrol efforts are now focused on introducing and establishing species of *Spathius,* which have longer ovipositors in EAB-infested regions of North America, presumably with *S. agrili* in the southern states and *S. galinae* in the north (Jones et al., 2020; Aker et al., 2022). However, the lack of consistent recovery of *S. agrili* from many previous release sites in Michigan (Duan et al., 2013, 2015b), New York, Maryland (Jennings et al., 2016), Tennessee (Hooie et al., 2015), and Kentucky (Davison and Rieske, 2016) suggests that this species may not be well suited for EAB biocontrol in the eastern deciduous forests of North America.

Releases of *S. galinae* began in the summer of 2015 after its approval for field release in Michigan and several northeastern and Mid-Atlantic states including Connecticut, Massachusetts, New York, and Maryland. The ovipositor of *S. galinae* averages 4–6 mm (0.16–0.24 in), more than twice the length of *T. planipennisi*'s ovipositor. Consequently, *S. galinae* can attack EAB larvae feeding in ash trees up to 30 cm (12 in) DBH (Duan et al., 2012a; Murphy et al., 2017). Recent field studies from both Michigan and the northeastern states showed that *S. galinae* has established self-sustaining populations in areas where *T. planipennis* was previously released (Duan et al., 2021a, b). Further lifetable analyses showed that *S. galinae* alone contributed a 31–57% reduction of invasive EAB populations during the outbreak (crest) phase (Duan et al., 2021b). Alongside the local generalist natural enemies (e.g., avian predators and some native parasitoids), *T. planipennisi* and *S. galinae* are now the dominate parasitoid species, reducing average densities of live EAB larvae to a low density (<7 live larvae per m^2 [<0.65 live larvae/ft^2] of tree phloem) between 2015 and 2020. This EAB larval density is expected to provide an opportunity for ash recovery and regeneration in the aftermath of the EAB invasion (**Fig. 6**).

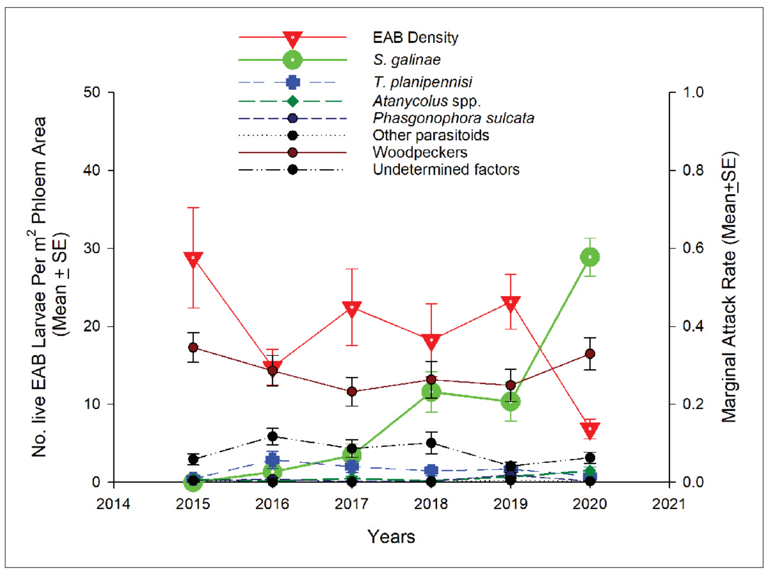

Figure 6. Mean (± SE) EAB (*Agrilus planipennis*) density and mean (± SE) marginal attack rates by different groups of parasitoids, woodpeckers and other avian predators, and undetermined factors observed across the five different study sites in northeastern United States (Connecticut, Massachusetts, and New York) where the three introduced biocontrol agents (*Spathius galinae, Tetrastichus planipennisi,* and *Oobius agrili*) were released from 2015 to 2017. Note: Parasitism by the egg parasitoid (*O. agrili*) is not presented in this study. (modified from Duan et al., 2021b)

BENEFITS OF BIOLOGICAL CONTROL OF EAB

In the eastern and midwestern United States and Canada, EAB's invasion caused 95–100% mortality of the overstory ash trees in many invaded areas within a relatively short period (5–10 years) following its first local detection (e.g., Kashian and Witter, 2011; Klooster et al., 2014). The classical biological control program against EAB in the United States is showing considerable potential for this pest's sustainable management by reducing population densities to a sufficiently low level to allow recovery of ash saplings and young trees, allowing them to fill in forest gaps, successfully reproduce, and reach the canopy over time. Recovery and regeneration of ash trees due to the success in EAB biocontrol could eventually lead to restoration of ash-dominated hardwood forest ecosystems, as well as provide opportunities for recovery of the ash nursery and timber industries. In addition, benefits of ash recovery resulting from EAB biocontrol are likely to accrue without additional costs because the established biocontrol agents are self-sustaining and may effectively maintain EAB population densities at low levels and moderate outbreak amplitude and frequency in the aftermath forests.

Figure 7. Healthy green ash (*Fraxinus pennsylvanica*) trees (left and center) observed in 2018 recovering from initial EAB (*Agrilus planipennis*) invasion, at one of the emerald ash borer biocontrol study sites in southern Michigan, established between 2007 and 2010, where earlier EAB attack killed many trees (right). (J. Duan, USDA-ARS)

In southern Michigan, where the establishment and spread of *T. planipennisi* and *O. agrili* have been confirmed since they were first introduced in 2007, densities of ash were higher in forests closer to sites where more parasitoids were released (Margulies et al., 2017). In these EAB biocontrol sites, researchers also found that healthy ash saplings (4–16 per 100 m^2 [0.4–1.5/100 ft^2) and pole-size young trees (2–9 per 100 m^2 [0.2–0.8/100 ft^2]) have persisted (**Fig. 7**) despite formerly high EAB densities that had resulted in loss of most of the original overstory ash trees by 2010 (Duan et al., 2017ab; J. Duan and T. Petrice, unpub. data). With the most recent establishment of *S. galinae*, it is very likely that the parasitoids released by the EAB biological control program will provide significant services by enhancing the survival, recovery, and growth of large-diameter ash trees, thereby promoting forest recovery in North America (Duan et al., 2017ab; Margulies et al., 2017; Kashian et al., 2018; Duan et al., 2020b). However, recovery of mature North American ash trees, following successful suppression of EAB with biological control, will take time due to the long lifespan of *Fraxinus* spp. The nature of tree regrowth and regeneration will likely take more than a decade to develop an overstory ash canopy (Kashian and Witter, 2011; Kashian, 2016).

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REFERENCES

Abell, K. J., J. J. Duan, L. S. Bauer, J. P. Lelito, and R. G. Van Driesche. 2012. The effect of bark thickness on the effectiveness of *Tetrastichus planipennisi* (Hymen: Eulophidae) and *Atanycolus* spp. (Hymen: Braconidae) two parasitoids of emerald ash borer (Coleop: Buprestidae). *Biological Control* 63: 320–325.

Abell, K. J., L. S. Bauer, J. J. Duan, and R. G. Van Driesche. 2014. Long-term monitoring of the introduced emerald ash borer (Coleoptera: Buprestidae) egg parasitoid, *Oobius agrili* (Hymenoptera: Encyrtidae), in Michigan, USA and evaluation of a newly developed monitoring technique. *Biological Control* 79: 36–42.

Aker, S. A., R. B. de Andrade, J. J. Duan, and D.S. Gruner. 2022. Rapid spread of an introduced parasitoid for biological control of emerald ash borer (Coleoptera: Buprestidae) in Maryland. *Journal of Economic Entomology* 115(1): 381–386. https://doi.org/10.1093/jee/toab248

Anulewicz, A.C., McCullough, D.G., Cappaert, D.L., Poland, T.M., 2008. Host range of the emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) in North America: results of multiple-choice field experiments. *Environmental Entomology* 37: 230–241.

Bauer, L. S., H. P. Liu, D. L. Miller, and J. Gould. 2008. Developing a classical biological control program for *Agrilus planipennis* (Coleoptera: Buprestidae), an invasive ash pest in North America. *Newsletter of the Michigan Entomological Society* 53: 38–39. https://www.fs.usda.gov/treesearch/pubs/11439

Bauer, L.S., J. J. Duan, and J. R. Gould. 2014. Emerald ash borer *Agrilus planipennis* Fairmaire Coleoptera: Buprestidae, pp. 189–209. *In:* Van Driesche, R. and R. Reardon (eds.). *The Use of Classical Biological Control to Preserve Forests in North America.* FHTET-2013-2, USDA Forest Service, Morgantown, West Virginia, USA. https://www.fs.usda.gov/treesearch/pubs/48051

Bauer, L.S., J. J. Duan, J. R. Gould, and R. G. Van Driesche. 2015. Progress in the classical biological control of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America. *The Canadian Entomologist* 147: 300–317. https://www.fs.usda.gov/treesearch/pubs/48338

Belokobylskij, S. A., G. I. Yurchenko, J. S. Strazanac, A. L. Zaldi'var-Riveron, and V. Mastro. 2012. A new emerald ash borer (Coleoptera: Buprestidae) parasitoid species of *Spathius* Nees (Hymenoptera: Braconidae: Doryctinae) from the Russian Far East and South Korea. *Annales of the Entomological Society of America* 105: 165–178.

Bray, A.M., L. S. Bauer, T. M. Poland, R. A. Haack, A. I. Cognato, and J. J. Smith. 2011. Genetic analysis of emerald ash borer (*Agrilus planipennis* Fairmaire) populations in Asia and North America. *Biological Invasions* 13: 2869–2887.

Burr, S. J. and D. G. McCullough. 2014. Condition of green ash (*Fraxinus pennsylvanica*) overstory and regeneration at three stages of the emerald ash borer invasion wave. *Canadian Journal of Forest Research* 44: 768–776.

Burr, S. J., D. G. McCullough, and T. M. Poland. 2018. Density of emerald ash borer (Coleoptera: Buprestidae) adults and larvae at three stages of the invasion wave. *Environmental Entomology* 47: 121–132

Cappaert, D. L., D. G. McCullough, T. M. Poland, and N. W. Siegert. 2005. Emerald ash borer in North America: A research and regulatory challenge. *American Entomologist* 51: 152–165.

CFIA (Canadian Food Inspection Agency). 2018. Emerald Ash Borer. https://inspection.canada.ca/plant-health/invasive-species/insects/emerald-ash-borer/eng/1337273882117/1337273975030

Cipollini, D. 2015. White fringe tree as a novel larval host for emerald ash borer. *Journal of Economic Entomology* 108: 370–375. https://doi.org/10.1093/jee/tou026

Cipollini, D., C. M. Rigsby, and D. L. Peterson. 2017. Feeding and development of emerald ash borer (Coleoptera: Buprestidae) on cultivated olive, *Olea europaea*. *Journal of Economic Entomology* 110: 1935–1937.

Dang, Y., K. Wei, X. Y. Wang, J. J. Duan, D. E. Jennings, and T. M. Poland. 2021. Introduced plants induce outbreaks of a native pest and facilitate invasion in the plants' native range: Evidence from the emerald ash borer. *Journal of Ecology*: https://doi.org/10.1111/1365-2745.13822

Davidson, D. and L. K. Rieske. 2016. Establishment of classical biological control targeting emerald ash borer is facilitated by use of insecticides, with little effect on native arthropod communities. *Biological Control* 101: 78–86.

Doutt, R. L. and P. DeBach. 1964. Some biological control concepts and questions, pp.118–142. *In:* DeBach, P. (ed.). *Biological Control of Insect Pests and Weeds.* Rheinhold, New York.

Duan, J. J., L. S. Bauer, M. D. Ulyshen, J. R. Gould, and R. G. Van Driesche. 2011. Development of methods for the field evaluation of *Oobius agrili* (Hymenoptera: Encyrtidae) in North America, a newly introduced egg parasitoid of the emerald ash borer (Coleoptera: Buprestidae). *Biological Control* 56: 170–174

Duan, J. J., G. Yurchenko, and R. W. Fuester. 2012a. Occurrence of emerald ash borer (Coleoptera: Buprestidae) and biotic factors affecting its immature stages in the Russian Far East. *Environmental Entomology* 41: 245–254.

Duan, J. J., L. S. Bauer, K. J. Abell, and R. G. Van Driesche. 2012b. Population responses of hymenopteran parasitoids to the emerald ash borer (Coleoptera: Buprestidae) in recently invaded areas in north central United States. *BioControl* 57: 199–209.

Duan, J. J., L. S. Bauer, J. A. Hansen, K. J. Abell, and R. G. Van Driesche. 2012c. An improved method for monitoring parasitism and establishment of *Oobius agrili* (Hymenoptera: Encyrtidae), an egg parasitoid introduced for biological control of the emerald ash borer (Coleoptera: Buprestidae) in North America. *Biological Control* 60: 255–261

Duan, J. J., L. S. Bauer, K.J. Abell, J. P. Lelito, and R. G. Van Driesche. 2013. Establishment and abundance of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) in Michigan: Potential for success in classical biocontrol of the invasive emerald ash borer (Coleoptera: Buprestidae). *Journal of Economic Entomology* 106: 1145–1154.

Duan, J. J., L.S. Bauer, K. J. Abell, and R. G. Van Driesche. 2014. Natural enemies implicated in the regulations of an invasive pest: a life table analysis of the population dynamics of the invasive emerald ash borer. *Agricultural and Forest Entomology* 16: 406–416.

Duan, J. J., J. R. Gould, and R. W. Fuester. 2015a. Evaluation of the host specificity of *Spathius galinae* (Hymenoptera: Braconidae), a larval parasitoid of the emerald ash borer (Coleoptera: Buprestidae) in Northeast Asia. *Biological Control* 89: 91–97.

Duan, J. J., L.S. Bauer, K. J. Abell, M. D. Ulyshen, and R. G. Van Driesche. 2015b. Population dynamics of an invasive forest insect and associated natural enemies in the aftermath of invasion: implications for biological control. *Journal of Applied Ecology* 52: 1246–1254.

Duan, J. J., L. S. Bauer, and R. G. Van Driesche. 2017a. Emerald ash borer biocontrol in ash saplings: the potential for early-stage recovery of North American ash trees. *Forest Ecology and Management* 394: 64–72.

Duan, J. J., R. G. Van Driesche, L. S. Bauer, R. Reardon, J. Gould, and J. S. Elkinton. 2017b. *The Role of Biocontrol of Emerald Ash Borer in Protecting Ash Regeneration after Invasion.* FHAAST-2017-02. USDA Forest Service.: Morgantown, West Virginia, USA.

Duan, J. J., L. S. Bauer, R. G. Van Driesche, and J. R. Gould. 2018. Progress and challenges of protecting North American ash trees from the emerald ash borer using biological control. *Forests* 9: 1–17. https://www.mdpi.com/1999-4907/9/3/142

Duan, J. J., J. M. Schmude, K. M. Larson, R. W. Fuester, J. R. Gould, and M. D. Ulyshen. 2019a. Field parasitism and host specificity of *Oobius primorskyensis* (Hymenoptera: Encyrtidae), an egg parasitoid of the emerald ash borer (Coleoptera: Buprestidae) in the Russian Far East. *Biological Control* 10: 44–50.

Duan J. J., R. G. Van Driesche, R. S. Crandall, J. M. Schmude, C. E. Rutledge, B. H. Slager, J. R. Gould, and J. S. Elkinton. 2019b. Establishment and early impact of *Spathius galinae* (Hymenoptera: Braconidae) on emerald ash borer (Coleoptera: Buprestidae) in the Northeastern United States. *Journal of Economic Entomology* 112: 2121–2130.

Duan, J. J., J. M. Schmude, and K.M. Larson. 2020a. Effects of low temperature exposure on diapause, development, and reproductive fitness of the emerald ash borer (Coleoptera: Buprestidae): implications for voltinism and laboratory rearing. *Journal of Economic Entomology* 114: 201–208. https:/doi.org/10.1093/jee/toaa252

Duan, J. J., L. S. Bauer, R. G. Van Driesche, J. M. Schmude, T. Petrice, J. L. Chandler, and J. Elkinton. 2020. Effects of extreme low winter temperatures on the overwintering survival of the introduced larval parasitoids *Spathius galinae* and *Tetrastichus planipennisi*: Implications for biological control of emerald ash borer in North America. *Journal of Economic Entomology* 113: 1145–1151. https://doi.org/10.1093/jee/toaa048

Duan, J. J., R. G. Van Driesche, J. M. Schmude, N. F. Quinn, T. R. Petrice, C. E. Rutledge, T. M. Poland, L. S. Bauer, and J. S. Elkinton. 2021a. Niche partitioning and coexistence of parasitoids of the same feeding guild introduced for biological control of an invasive forest pest. *Biological Control* 160: https://doi.org/10.1016/j.biocontrol.2021.104698

Duan, J. J., R. G. Van Driesche, J. M. Schmude, R. Crandall, C. E. Rutlege, N. F. Quinn, B. H. Slager, J. R. Gould, and J. E. Elkinton 2021b. Significant suppression of invasive emerald ash borer by introduced parasitoids: potential for North American ash recovery. *Journal of Pest Science*: https://doi.org/10.1007/s10340-021-01441-9

Emerald Ash Borer Information. 2022. Emerald Ash Borer Information Network. http://www.emeraldashborer.info/ [accessed on 5 Jan 2022].

Engelken, P., M. E. Benbow, and D. G. McCullough. 2020. Legacy effects of emerald ash borer on riparian forest vegetation and structure. *Forest Ecology and Management* 457: 117684. https://doi.org/10.1016/j.foreco.2019.117684

Federal Register. 2003. Emerald Ash Borer; Quarantine and Regulations. Fed. Regist. 2003, 7 CFR Part 301 [docket Number 02-125-1]. https://www.federalregister.gov/documents/2003/10/14/03-25881/emerald-ash-borer-quarantine-and-regulations

Federal Register. 2007. Availability of an environmental assessment for the proposed release of three parasitoids for the biological control of the emerald ash borer *Agrilus planipennis* in the Continental United States. Federal Register 2007, 72, 28947–28948, [docket number APHIS14 -2007-006]. https://www.regulations.gov/document/APHIS-2007-0060-0044

Federal Register. 2015. Availability of an environmental assessment for field release of the parasitoid *Spathius galinae* for the biological control of the emerald ash borer (*Agrilus planipennis*) in the contiguous United States. Federal Register 2015, 80, 7827-7828, [docket number APHIS–2014–0094]. https://www.regulations.gov/document/APHIS-2014-0094-0014

Federal Register. 2020. Removal of emerald ash borer domestic quarantine regulations. Fed. Regist. 2020, 85-FR-81085, [Docket No. APHIS-2017-0056]. https://www.federalregister.gov/documents/2020/12/15/2020-26734/removal-of-emerald-ash-borer-domestic-quarantine-regulations

Flower, C. E., K. S. Knight, and M. A. Gonzalez-Meler. 2013. Impacts of the emerald ash borer (*Agrilus planipennis*) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. *Biological Invasions* 15: 931–944.

GAO. 2006. Invasive forest pests: lessons learned from three recent infestations may aid in managing future efforts. Report of the United States Government Accounting Office., GAO-06-353. https://www.gao.gov/assets/gao-06-353.pdf

Gandhi, K. J. K. and D. A. Herms. 2010 North American arthropods at risk due to widespread *Fraxinus* mortality caused by the alien emerald ash borer. *Biological Invasions* 12: 1839–1846.

Gandhi, K. J. K., A. Smith, D. M. Hartzler, and D. A. Herms. 2014. Indirect effects of emerald ash borer-induced ash mortality and canopy gap formation on epigaeic beetles. *Environmental Entomology* 43: 546–555.

Gordh, G. and L. Moczar. 1990. *A Catalog of the World Bethylidae (Hymenoptera: Aculeata).* American Entomological Institute, Gainesville, Florida, USA.

Gould, J.R, M. Hickin, and M. M. Fierke, M.K. 2022. Mortality of emerald ash borer larvae in small regenerating ash in New York Forests. *Journal of Economic Entomology* (in press).

Gould, J. R., and J. J. Duan. 2018. Petition for Release of an Exotic Parasitoid, *Oobius primorskyensis* Yao & Duan, for the Biological Control of the Emerald Ash Borer, *Agrilus planipennis* Fairmaire. Submitted to NAPPO Biocontrol Review Committee.

Gould, J. R., L. S. Bauer, J. J. Duan, D. Williams, and H. P. Liu. 2015. History of emerald ash borer biological control, pp 83–95. *In:* Van Driesche, R. G. and R. Reardon (eds). *Biology and Control of Emerald Ash Borer.* FHTET-2014-09. USDA Forest Service, Morgantown, West Virginia, USA. https://www.fs.usda.gov/treesearch/pubs/49321

Haack, R. A., E. Jendek, H. P. Liu, K, R. Marchant, T. R. Petrice, T. M. Poland, and H. Ye. 2002. The emerald ash borer: A new exotic pest in North America. *Newsletter of the Michigan Entomological Society* 47: 1–5. https://www.fs.usda.gov/treesearch/pubs/11858

Haack, R. A., Y. Baranchikov, L. S. Bauer, and T. M. Poland. 2015. Emerald ash borer biology and invasion history, pp. 1–13. *In:* Van Driesche, R. G. and R. C. Reardon (eds.). *Biology and Control of Emerald Ash Borer.* FHTET-2014-09. USDA, Forest Service, Morgantown, West Virginia, USA. https://www.fs.usda.gov/treesearch/pubs/49254

Haack, R. A., T. R. Petrice, and A. C. Wiedenhoeft. 2010. Incidence of bark- and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. *Journal of Economic Entomolology* 103: 1682–1692.

Haack, R. A., and T. R. Petrice 2021. Public transport of firewood across the Mackinac Bridge in Michigan, United States of America: origin, destination, woody taxa, and reasons for transporting firewood. *The Canadian Entomologis* 153: 586–597.

Herms, D. A. and D. G. McCullough. 2014. Emerald ash borer invasion of North America: History, biology, ecology, impact, and management. *Annual Review of Entomology* 59: 13–30.

Hooie, N. A., G. J. Wiggins, P. L. Lambdin, J. F. Grant, S. D. Powell, and J. P. Lelito. 2015. Native parasitoids and recovery of *Spathius agrili* from areas of release against emerald ash borer in eastern Tennessee, USA. *Biocontrol Science and Technology* 25: 345–351. https://doi.org/10.1080/09583157.2014.971712

Jennings, D. E., P. Taylor, and J. J. Duan. 2014. The mating and oviposition behavior of the invasive emerald ash borer (*Agrilus planipennis*), with reference to the influence of host tree condition. *Journal of Pest Science* 87: 71–78.

Jacobsen, A. 2020. Emerald Ash Borer in the Ash (*Fraxinus*)-dominated tidal swamps of the lower Patuxent River, Maryland. *Northeastern Naturalist* 27: 817–840.

Jennings, D. E., J. J. Duan, D. Bean, J. R. Gould, A. P. Kimberly, and P. M. Shrewsbury. 2016. Monitoring the establishment and abundance of introduced parasitoids of emerald ash borer larvae in Maryland, U.S.A. *Biological Control* 101: 138–144.

Jennings, D. E., J. J. Duan, D. Bean, A. R. Kimberly, G. L. Williams, S. K. Bells, A. S. Shurtleff, and P. M. Shrewsbury. 2017. Effects of the emerald ash borer invasion on the community composition of arthropods associated with ash tree boles in Maryland, U.S.A. *Agricultural and Forest Entomology* 19: 122–129. https://doi.org/10.1111/afe.12186

Jennings, D. E, J. J. Duan, and P. M. Shrewsbury. 2018. Comparing methods for monitoring establishment of the emerald ash borer (*Agrilus planipennis*, Coleoptera: Buprestidae) egg parasitoid *Oobius agrili* (Hymenoptera: Encyrtidae) in Maryland, USA. *Forests* 9: 1–9. https://doi.org/10.3390/f9100659

Jones, M. I, J. R. Gould, M. L. Warden, and M. K. Fierke. 2019. Dispersal of emerald ash borer (Coleoptera: Buprestidae) parasitoids along an ash corridor in western New York. *Biological Control* 128: 94–101.

Jones, M. I., J. R. Gould, H. J. Mahon, and M. K. Fierke. 2020. Phenology of emerald ash borer (Coleoptera: Buprestidae) and its introduced larval parasitoids in the northeastern United States. *Journal of Economic Entomology* 113: 622–632.

Kimberling, D. N. 2004. Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. *Biological Invasions* 6: 301–318.

Kashian, D.M. 2016. Sprouting and seed production may promote persistence of green ash in the presence of the emerald ash borer. *Ecosphere* 7: 1–15.

Kashian, D. M. and J. A. Witter. 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. *Forest Ecology and Management* 261: 480–488.

Kashian, D. M., L. S. Bauer, B. Spei, J. J. Duan, and J. Gould. 2018. Potential impacts of emerald ash borer biocontrol on ash health and recovery in southern Michigan. *Forests* 9: 296. https://doi.org/10.3390/f9060296

Keever, C. C., C. Nieman, L. Ramsay, C. E. Ritland, L. S. Bauer, D. B. Lyons, and J. S. Cory. 2013. Microsatellite population genetics of the emerald ash borer (*Agrilus planipennis* Fairmaire): comparisons between Asian and North American populations. *Biological Invasions* 15: 1537–1559.

Knight, K.S., J. P. Brown, and R. P. Long. 2013. Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (*Agrilus planipennis*). *Biological Invasions* 15: 371–383.

Kovacs, F. K., R. G. Haight, D. G. McCullough, R. J. Mercader, N. W. Siegert, and A. M. Leibhold. 2010. Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. *Ecological Economics* 69: 569–578.

Klooster, W. S., D. A. Herms, K. S. Knight, C. P. Herms, D. G. McCullough, A. S. Smith, K. J. K. Gandhi, and J. Cardina. 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological Invasions* 16: 859–873. https://doi.org/10.1007/s10530-013-0543-7

Liu, H. P., L. S. Bauer, R. T. Gao, T. H. Zhao, T. R. Petrice, and R. A. Haack. 2003. Exploratory survey for the emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae), and its natural enemies in China. *Great Lakes Entomologist* 36: 191–204. https://www.fs.usda.gov/treesearch/pubs/12798

Liu, H. P., L. S. Bauer, D. L. Miller, T.H. Zhao, R.T. Gao, L. Song, Q. Luan, R. Jin, and C. Gao. 2007. Seasonal abundance of *Agrilus planipennis* (Coleoptera: Buprestidae) and its natural enemies *Oobius agrili* (Hymenoptera: Encyrtidae) and *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) in China. *Biological Control* 42: 61–71. https://doi.org/10.1016/j.biocontrol.2007.03.011

Liu, H. P. 2017. Under siege: ash management in the wake of the emerald ash borer. *Journal of Integrated Pest Management* 9: 1–16. https://doi.org/10.1093/jipm/pmx029

MapBioControl.org. 2021. Agent release tracking and data management for federal, state, and researchers releasing biocontrol agents for management of the emerald ash borer. https://www.mapbiocontrol.org/ [accessed on 4 March 2022].

Mercader, R. J., D. G. McCullough, A. J. Storer, J. Bedford, T. M. Poland, and S. Katovich. 2015. Evaluation of the potential use of a systemic insecticide and girdled trees in area wide management of the emerald ash borer. *Forest Ecology and Management* 350: 70–80.

Margulies, E., L. S. Bauer, and I. Ibanez. 2017. Buying time: preliminary assessment of biocontrol in the recovery of native forest vegetation in the aftermath of the invasive emerald ash borer. *Forests* 8: 369. https://doi.org/10.3390/f8100369

Morin, R. S., A. M. Liebhold, S. A. Pugh, and S. J. Crocker. 2017. Regional assessment of emerald ash borer, *Agrilus planipennis*, impacts in forests of the eastern United States. *Biological Invasions* 19: 703–711.

Murphy, T. C., R. G. Van Driesche, J. R. Gould, and J. S. Elkinton. 2017. Can *Spathius galinae* attack emerald ash borer larvae feeding in large ash trees? *Biological Control* 114: 8–13.

Poland, T. M. and D. G. McCullough. 2006. Emerald ash borer: Invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry* 104: 118–124.

Peterson, D. L and D. Cipollini. 2020. Larval performance of a major forest pest on novel hosts and the effect of stressors. *Environmental Entomology* 49: 482–488. https://doi.org/10.1093/ee/nvz160

Pugh, S. A., A. M. Liebhold, and R. S. Morin. 2011. Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. *Canadian Journal of Forest Research* 41: 2165–2175

Prasad, A. A., L. R. Iverson, M. P. Peters, J. M. Bossenbroek, S. M. Matthews, T. D. Sydnor, and M. W. Schwartz. 2010. Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. *Landscape Ecology* 25: 353–369.

Petrice, T.R., L.S. Bauer, D. L. Miller, T. M. Poland, and F. W. Ravlin. 2021a. A phenology model for simulating *Oobius agrili* (Hymenoptera: Encyrtidae) seasonal voltinism and synchrony with emerald ash borer oviposition. *Environmental Entomology* 50: 280–292.

Petrice, T. R., L.S. Bauer, D. L. Miller, J. S. Stonovick, T. M. Poland, and F. W. Ravlin. 2021b. Monitoring field establishment of the emerald ash borer biocontrol agent *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae): Sampling methods, sample size, and phenology. *Biological Control* 156: https://doi.org/10.1016/j.biocontrol.2021.104535

Quinn, N. F., J. R. Gould, C. E. Rutledge, A. Fassler, J. S. Elkinton, and J. J. Duan. 2022a. Spread and phenology of *Spathius galinae* and *Tetrastichus planipennisi*, recently introduced for biocontrol of emerald ash borer (Coleoptera: Buprestidae) in the northeastern United States. *Biological Control* 165: https://doi.org/10.1016/j.biocontrol.2021.104794

Quinn, N. F., J. J. Duan, and J. S. Elkinton. 2022b. Monitoring the impact of introduced emerald ash borer biocontrol agents: Factors affecting *Oobius agrili* dispersal and parasitization of sentinel host eggs. *BioControl* (in press).

Rebek, E.J., D. A. Herms, and D. R. Smitley. 2008. Interspecific variation in resistance to emerald ash borer (Coleoptera: Buprestidae) among North American and Asian ash (*Fraxinus* spp.). *Environmental Entomology* 37: 242–246.

Rigsby, C. M., D. N. Showalter, D. A. Herms, J. L. Koch, P. Bonello, and D. Cipollini. 2015. Physiological responses of emerald ash borer larvae to feeding on different ash species reveal putative resistance mechanisms and insect counter-adaptations. *Journal of Insect Physiology* 78: 47–54.

Rutledge, C. E., R. G. Van Driesche, and J. J. Duan. 2021. Comparative efficacy of three techniques for monitoring the establishment and spread of larval parasitoids recently introduced for biological control of emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae). *Biological Control* 161: https://doi.org/10.1016/j.biocontrol.2021.104704

Rutledge, C. E. and M. A. Keena. 2012. Mating frequency and fecundity in the emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae). *Annals of the Entomological Society of America* 105: 66–72.

Sawyer, A. J. 2007. Defining the “edge” of isolated emerald ash borer infestations: simulation results and implications for survey and host removal, pp. 16–18. *In:* Mastro, V., D. Lance, R. Reardon, and G. Parra (eds). *Proceedings of 2006 Emerald Ash Borer and Asian Longhorned Beetle Research and Technology Development Meeting, Cincinnati, OH.* FHTET-2007-04. USDA Forest Service, Morgantown, West Virginia, USA. http://www.emeraldashborer.info/documents/EAB_ALB_2006.pdf

Siegert, N.W., D. G. McCullough, A. M. Liebhold, and F.W. Telewski. 2014. Dendrochronological reconstruction of the epicenter and early spread of emerald ash borer in North America. *Diversity and Distributions* 20: 847–858.

Sadof, C.S., L. Mockus, and M. D. Ginzel. 2021. Factors influencing efficacy of an area-wide pest management program in three urban forests. *Urban Forestry and Urban Greening* 58: 126965. https://doi.org/10.1016/j.ufug.2020.126965

Stephens, J. P., K. A. Berven, and S. D. Tiegs. 2013. Anthropogenic changes to leaf litter input affect the fitness of a larval amphibian. *Freshwater Biology* 58: 1631–1646.

Straw, A. N., D. T. Williams, O. Kulinich, and Y. I. Gninenko. 2013. Distribution, impact, and rate of spread of emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae) in the Moscow region of Russia. *Forestry* 86: 515–522. https://doi.org/10.1093/forestry/cpt031

Tang, Y-L., X-Y. Wang, Z-Q. Yang, J. Jiang, X-H. Wang, and J. Lu. 2012. Alternative hosts of *Sclerodermus pupariae* (Hymenoptera: Bethylidae), a larval parasitoid of the longhorn beetle *Massicus raddei* (Coleoptera: Cerambycidae). *Acta Entomologca Sinica* 55: 55–62.

Tanis, S. R. and D. G. McCullough. 2012. Differential persistence of blue ash (*Fraxinus quadrangulata*) and white ash (*Fraxinus americana*) following emerald ash borer (*Agrilus planipennis*) invasion. *Canadian Journal of Forest Research* 42: 1542–1550.

Tanis, S.R. and D. G. McCullough. 2015. Host resistance of five *Fraxinus* species to *Agrilus planipennis* (Coleoptera: Buprestidae) and effects of paclobutrazol and fertilization. *Environmental Entomology* 41: 287–299.

Taylor, R. A. J., L. S. Bauer, T. M. Poland, and K. Windell. 2010. Flight performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight. *Journal of Insect Behavior* 23: 128–148.

Ulyshen, M. D., W. S. Klooster, W. T. Barrington, and D. A. Herms. 2011. Impacts of emerald ash borer-induced tree mortality on leaf litter arthropods and exotic earthworms. *Pedobiologia* 54: 261–265.

Ulyshen, M. D., W. T. Barrington, E. R. Hoebeke, and D. A Herms. 2012. Vertically stratified ash-limb beetle fauna in northern Ohio. *Psyche:* 215891. https://doi.org/10.1155/2012/215891

USDA-APHIS. 2020. Emerald Ash Borer Program Manual *Agrilus planipennis* (Fairmaire). TOC-1, 2nd Edition. https://www.aphis.usda.gov/import_export/plants/manuals/domestic/downloads/eab-manual.pdf

USDA-APHIS/ARS/FS. 2021. USDA–Animal Plant Health Inspection Service–Agricultural Research Service–Forest Service. Emerald Ash Borer Biological Control Release and Recovery Guidelines. https://www.aphis.usda.gov/plant_health/plant_pest_info/emerald_ash_b/downloads/eab-field-release-guidelines.pdf

Villari, C., D. A. Herms, J. G. Whitehill, D. Cipollini, D., and P. Bonello. 2016. Progress and gaps in understanding mechanisms of ash tree resistance to emerald ash borer, a model for wood-boring insects that kill angiosperms. *New Phytologist* 209: 63–79. https://doi.org/10.1111/nph.13604

Wei, X., R. Reardon, Y. Wu, and J. J. Sun. 2004. Emerald ash borer, *Agrilus planipennis*, in China: a review and distribution survey. *Acta Entomologica Sinica* 47: 679–685.

Wei, X., Y. Wu, R. Reardon, T. H. Sun, M. Lu, and J. H. Sun. 2007. Biology and damage traits of emerald ash borer (*Agrilus planipennis* Fairmaire) in China. *Insect Science*14: 367–373.

Wang, X.Y, Z. Q. Yang, J. R. Gould, Y. N. Zhang, and G. J. Liu. 2010. The biology and ecology of the emerald ash borer, *Agrilus planipennis*, in China. *Journal of Insect Science* 10: 1–23.

Wang, X. Y., L. M. Cao, Z. Q. Yang, J. J. Duan, J. R. Gould, and L. S. Bauer. 2016. Natural enemies of emerald ash borer (Coleoptera: Buprestidae) in northeast China, with notes on two species of parasitic Coleoptera. *The Canadian Entomologist* 148: 329–342.

Williams, D., H-P Lee, Y-S Jo, G. Yurchenko, and V. C. Mastro. 2010 Exploration for EAB and its natural enemies in South Korea and Eastern Russia in 2004– 2009, pp. 94–95. *In:* Mastro, V. and R. Reardon (eds). *Emerald Ash Borer Research and Development Meeting, Pittsburgh, Pennyslvania, October 20–21, 2009.* FHTET-2010-01. USDA Forest Service and APHIS, Morgantown, West Virginia, USA.

Yang, Z. Q., C. V. Achterberg, W. Y. Choi, and P. M. Marsh. 2005. First recorded parasitoid from China of *Agrilus planipennis*: a new species of *Spathius* (Hymenoptera: Braconidae: Doryctinae). *Annals of the Entomological Society of America* 98: 636–642.

Yang, Z. Q., Y. X. Yao, and X. Y. Wang. 2006. A new species of emerald ash borer parasitoid from China belonging to the genus *Tetrastichus* (Hymneoptera: Eulophidae). *Proceedings of the Entomological Society of Washington* 108: 550–558.

Yang, Z. Q., X. Y. Wang, J. R. Gould, and H. Wu. 2008. Host specificity of *Spathius agrili* Yang (Hymenoptera: Braconidae), an important parasitoid of the emerald ash borer. *Biological Control* 47: 216–221.

Yang, Z.Q., X. Y. Wang, Y. X. Yao, J. R. Gould, and L. M. Cao. 2012. A new species of *Sclerodermus* (Hymenoptera: Bethylidae) parasitizing *Agrilus planipennis* (Coleoptera: Buprestidae) from China, with a key to Chinese species in the genus. *Annals of the Entomological Society of America* 105: 619–627.

Yao, Y. X., J. J. Duan, K. R. Hopper, J. L. Mottern, and M. W. Gates. 2016. A new species of *Oobius* Trjapitzin (Hymenoptera: Encyrtidae) from the Russian Far East that parasitizes eggs of emerald ash borer (Coleoptera: Buprestidae). *Annals of the Entomological Society of America* 106: 629–638.

Yu, C. M. 1992. *Agrilus* marcopoli Obenberger (Coleoptera: Buprestidae), pp. 400–401. *In:* Xiao, G. (ed.). *Forest Insects of China, 2nd edition.* China Forestry Publishing House, Beijing.

Zhang, Y. Z., D. W. Huang, T. H. Zhao, H. P. Liu, and L. S. Bauer. 2005 Two new species of egg parasitoids (Hymenoptera: Encyrtidae) of wood-boring beetle pests from China. *Phytoparasitica* 53: 253–260.

Zhao, T. H., R. T. Gao, H. P. Liu, L. S. Bauer, and L. Q. Sun. 2005. Host range of emerald ash borer, *Agrilus planipennis* Fairmaire, its damage and the countermeasures. *Acta Entomologica Sinica* 48: 594–59.