

Challenges, tactics and integrated management of emerald ash borer in North America

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Received 23 February 2019

Emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire), discovered in southeastern Michigan, USA in 2002, has become the most destructive and costly invasive forest insect in North America. This phloem-boring beetle has also invaded Moscow, Russia and continued spread of EAB potentially threatens European ash (*Fraxinus* spp.) species. This review summarizes EAB life history, including interspecific variation in host preference, invasion impacts and challenges of detecting new infestations and provides an overview of available management tactics. Advances in systemic insecticides, particularly emamectin benzoate products applied via trunk injection, have yielded effective and practical options both to protect individual trees and to slow EAB population growth and ash decline on an area-wide basis without disrupting natural enemies. Economic costs of treating ash are substantially lower than removal costs, retain ecosystem services provided by the trees, reduce sociocultural impacts and conserve genetic diversity in areas invaded by EAB. Girdled ash trees are highly attractive to EAB adults in low-density populations and debarking small girdled trees to locate larval galleries is the most effective EAB detection method. An array of woodpeckers, native larval parasitoids and introduced parasitoids attack EAB life stages but mortality is highly variable. Area-wide management strategies that integrate insecticide-treated trees, girdled ash trap trees and biological control can be adapted for local conditions to slow and reduce EAB impacts.

Introduction to emerald ash borer

Emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) has become the most destructive and economically costly forest insect to invade North America (Aukema *et al.*, 2011; Herms and McCullough, 2014). Dendrochronological evidence has shown this Asian beetle first became established in suburbs of Detroit in southeastern Michigan, USA by the early 1990s, if not earlier (Siegert *et al.*, 2014b). However, it was not discovered until ~10 years later, in 2002, when EAB was identified as the cause of declining and dying ash (*Fraxinus* spp.) trees in the greater Detroit area and in nearby Windsor, Ontario Canada (Cappaert *et al.*, 2005b; Poland and McCullough, 2006). Despite federal and state regulations designed to minimize the further anthropogenic spread of EAB in infested ash nursery trees, logs or firewood (Herms and McCullough, 2014; Siegert *et al.*, 2014b), the list of states and counties with EAB infestations has expanded every year since 2002. As of January 2019, EAB populations were established in 35 US states, along with five Canadian provinces (EAB.info, 2019). Hundreds of millions of ash (*Fraxinus* spp.) trees in forests, rural areas and landscapes have already been killed in the US (Herms and McCullough, 2014). More than 8.5 billion ash trees growing in forests in the continental US and millions of more ash

trees in US landscapes are threatened (US Federal Register, 2003; Poland and McCullough, 2006). In 2017, the International Union for Conservation of Nature added five major North American ash species to its 'red list' of critically endangered species. EAB has also invaded Moscow, Russia (Baranchicov *et al.*, 2008; Orlova-Bienkowskaja, 2014), resulting in widespread mortality of landscape ash trees. The continued spread of EAB from western Russia threatens three ash species native to Europe, eliciting concern and interest from European scientists in preparing for the eventual arrival of EAB.

It seems likely that EAB will continue to be a critically important forest pest in North America and the effects of EAB invasion could be similarly severe in many European countries. This review summarizes aspects of EAB behaviour that contribute to the challenges of detecting and managing this pest, along with an array of EAB impacts recorded in the US, and provides an overview of tactics available to manage EAB infestations. Since 2002, research has substantially advanced our understanding of EAB biology, life history, population dynamics and interactions between this pest, its host trees and natural enemies. There is increasing recognition that effective and economically viable tactics are available to protect individual ash trees. Efforts to evaluate the effects of systemic insecticides and girdled trees on EAB population growth and rates of ash decline are reviewed here,

primarily focusing on research conducted in Michigan. Developing management strategies tailored for specific areas could reduce ecological impacts and economic costs associated with the ongoing EAB invasion in North America and potentially in Europe.

Life history of EAB

In southern Michigan where EAB was first studied, adult beetles begin emerging in mid to late May and peak activity occurs from late June to mid-July (McCullough *et al.*, 2009a, 2009b; Poland *et al.*, 2011). Beetles feed on ash leaves for at least 5–7 days before mating begins and females feed 5–7 more days before eggs mature and oviposition begins (Cappaert *et al.*, 2005b; Poland and McCullough, 2006; Wang *et al.*, 2010). Adult EAB feeding is confined to leaf margins and results in negligible damage to trees regardless of EAB densities. Females deposit individual eggs in bark cracks, crevices or beneath bark flakes between bouts of leaf feeding and resting. Eggs hatch within 7–10 days and neonate larvae immediately chew through the outer bark and into the phloem.

Larvae feed on phloem and cambium in serpentine or winding galleries from mid-summer through early fall (Cappaert *et al.*, 2005b). Most larval galleries also score the outer sapwood, thus disrupting the transport of water, as well as nutrients, within ash trees, which are ring-porous (Kitin and Funada, 2016). Larvae complete four instars and most overwinter as J-shaped prepupae in individual chambers ~1 cm deep, either in thick outer bark on large trees or in the sapwood of thin-barked limbs or small trees. In trees stressed by high EAB larval densities, girdling, previous injury or poor site conditions, all or nearly all EAB develop in a single year. In healthy ash trees with low EAB larval densities, however, a high proportion of EAB larvae often overwinter as early instars, feed and overwinter again, then emerge the following summer, thus completing a 2-year life cycle (Cappaert *et al.*, 2005b; Siegert *et al.*, 2010; Tluczek *et al.*, 2011).

Impacts of EAB invasion

Although the number of *Fraxinus* species varies depending on taxonomic or phylogenetic assignments, at least 16 native ash species grow in forests in the continental US (Hinsinger *et al.* 2013, MacFarlane and Meyer, 2005, Nesom, 2014, Wallander, 2008). Ash trees are common and often abundant in eastern US forests where EAB is established, although much of the species diversity is endemic to southwestern states (USDA NRCS, 2019; Wallander, 2008). Green ash (*Fraxinus pennsylvanica*) and white ash (*F. americana*) are the most widely distributed *Fraxinus* species, tolerate a wide range of site conditions (MacFarlane and Meyer, 2005), and like other ash species, often occur in mixed-species stands (Griffith, 1991; Gucker, 2005). Other native ash species in the EAB-invaded range include black ash (*F. nigra*), commonly found in mesic or swampy sites in northern states (Erdmann *et al.*, 1987; Wright and Rauscher, 1990), blue ash (*F. quadrangulata*), usually encountered in mixed hardwood stands in upland sites (MacFarlane and Meyer, 2005), and pumpkin ash (*F. profunda*), a lowland species which is rarely abundant and is considered a threatened species in parts of its range (Liu and Miller, 2014; Missouri Botanical Garden, 2019).

Ash trees ranging in size from 2.5 cm to more than 90 cm diameter at breast height (DBH) have been killed by EAB and local ash mortality rates can be catastrophic. Early reports from plots established in forested areas of southeast Michigan and Ohio indicated nearly all green, white or black ash trees were killed by EAB by the mid-2000s (Burr and McCullough, 2014; Klooster *et al.*, 2014; Knight *et al.*, 2013; Smith *et al.*, 2015). Smith *et al.* (2015) evaluated an array of tree and stand-level variables in the southeast Michigan plots, but found the rate of ash mortality from 2004 to 2007 was related only to the distance between sites and the original EAB epicentre. Mortality of green ash trees, recorded in 2011 in forests spanning an east–west gradient across southern Michigan, averaged 79 per cent in southeastern sites invaded by EAB in the early 2000s, 45 per cent in central sites invaded in the mid 2000s, and 20 per cent in newly invaded southwestern sites (Burr and McCullough, 2014). A regional assessment using US Forest Service Forest Inventory and Analysis data indicated annual ash mortality and volume loss increases for several years following initial EAB detections until most live ash were dead (Morin *et al.*, 2017).

Interspecific differences in EAB host preference

Interspecific differences in EAB host preference among North American ash species continue to be observed and can affect EAB impacts, as well as management opportunities. Although black ash and green ash mortality rates are consistently high following EAB invasion, white ash survival varies considerably and blue ash appears to be relatively resistant to EAB (Herms and McCullough, 2014). For example, in three urban landscapes, green ash trees were consistently colonized earlier and at higher densities than the similar-sized white ash trees (Anulewicz *et al.*, 2007). In two southeast Michigan woodlots where white ash and blue ash co-occurred, nearly all-white ash trees were killed by EAB by 2010, while 60–70 per cent of the original blue ash trees remain healthy (Tanis and McCullough, 2012).

A plantation study consisting of 21 randomized blocks, each comprised of five ash species, exemplifies interspecific variation in EAB host preference. When trees were debarked in autumn following exposure to the local EAB population, larval densities on black ash and green ash trees averaged (\pm SE) 236 ± 36 and 220 ± 40 larvae per m^2 of surface area, respectively (Tanis and McCullough, 2015). To put these densities into perspective, each EAB larva requires ~10 cm^2 of phloem to develop and on average, ~89 EAB adults can potentially be produced per m^2 of phloem area (McCullough and Siegert, 2007; Mercader *et al.*, 2011a). Not surprisingly, all black and green ash trees in the plantation died by late summer and intraspecific competition for phloem resulted in mortality of most larvae on those trees. In contrast, only six blue ash and seven *F. mandshurica*, an Asian species that co-evolved with EAB, were colonized, with larval densities on both species averaging ≤ 2 per m^2 . Three white ash were heavily infested and died, but seven white ash had less than 10 larvae per m^2 and overall larval densities averaged 41 ± 12 larvae per m^2 (Tanis and McCullough, 2015).

More recently, an extensive survey assessed condition of white ash trees in 28 forested sites spanning 11 counties in southeast and central Michigan, all of which were invaded by EAB by the early or mid-2000s (Robinett and McCullough, 2019). In contrast

to reports of individual 'lingering' ash trees surrounded by dead conspecifics (Knight *et al.*, 2013, Koch *et al.* 2015), more than 50 per cent of the white ash trees (DBH > 10 cm) and basal area in 14 of the sites were alive and nearly all live trees had healthy canopies.

Substantial research has been directed at physiological, chemical and proteomic response of ash species to larval feeding (e.g. Eyles *et al.*, 2007; Villari *et al.*, 2015; Whitehill *et al.*, 2011, 2012), but host preference of female EAB beetles, who select trees for oviposition, is arguably the most critical factor in determining which trees become infested and at what densities. Host preference is likely driven by multiple factors, including tree condition, species and physical traits such as bark texture and hyperspectral signatures (Anulewicz *et al.*, 2007, 2008; Bartels *et al.*, 2008; De Groot *et al.*, 2008; Rebek *et al.*, 2008; Rodriguez-Saona *et al.*, 2006). Bioassays with EAB adults caged with ash seedlings or saplings, excised ash leaves, or on intact leaves on mature trees, have indicated longevity of beetles tends to be lower on blue ash trees (Tanis and McCullough, 2015), but leaf consumption rates and beetle survival are not consistently related to interspecific differences in nutritional or chemical composition of foliage (e.g. Chen and Poland, 2010, Limback, 2010, Pureswaran and Poland, 2009, Tanis and McCullough, 2015).

Whether EAB host preference or host resistance will vary among European species, including *F. excelsior*, *F. ornus* and *F. angustifolia*, is not yet known. Bioassays with *F. excelsior*, four North American and one Asian ash species, showed EAB adults would feed on *F. excelsior* leaves (Pureswaran and Poland, 2009). Comparisons of EAB leaf consumption among ash species, however, were inconsistent, likely reflecting the short duration of the bioassays (48 h), the use of detached leaves that could affect inducible responses of ash to feeding and the quality of foliage from greenhouse-grown seedlings, which is consistently less suitable than foliage from ash grown outdoors. In a Michigan plantation that included three to six trees of various European, Western US and Southern US ash species, all three European species were suitable EAB hosts and were killed in 1–2 years after trees were exposed to the local EAB population (McCullough, unpubl. data). Although European ash species seem almost certain to be vulnerable to EAB, differential EAB attraction or variability in survival rates among the species may become apparent in their native range.

Sociocultural and economic effects of EAB

Indirect impacts of extensive ash mortality following the EAB invasion can include the loss of ecological services and sociocultural consequences. Cascading effects of ash mortality in forested settings may affect other invertebrates (Gandhi and Herms, 2010; Gandhi *et al.*, 2014; Perry and Herms, 2017; Ulyshen *et al.*, 2011; Wagner and Todd, 2016), along with forest hydrology (Robertson *et al.*, 2018; Van Grinsven *et al.*, 2017; Youngquist *et al.*, 2017) and carbon cycling (Flower *et al.*, 2013). Mortality and potential extirpation of black ash are a particular issue for many Native American and First Nation tribes in eastern North America who have valued this species as an economic, cultural and spiritual resource for generations (Benedict and David, 2004; Diamond and Emery, 2011; Garibaldi and Turner, 2004; McCullough, 2013; Willow, 2011). Strips of black ash wood

are woven into utilitarian baskets, as well as highly valued, artistic baskets (Benedict and David, 2004; McCullough, 2013; Siegert *et al.*, 2014a). Many tribal members are deeply concerned about the ongoing loss of harvestable black ash trees and mature trees to provide seed (Ranco *et al.*, 2012; Siegert *et al.*, 2014a; Costanza *et al.*, 2017). Sociological effects of EAB may also extend to human health and safety. Recent studies have linked human health, including mortality attributable to cardiovascular disease, and urban crime rates to EAB-caused ash mortality (Donovan *et al.*, 2013, 2015; Jones and McDermott, 2015).

Economic costs associated with EAB largely reflect the abundance of valuable ash trees in landscapes, parks and along roads in residential and urban areas. Cultivars of green ash (*F. pennsylvanica*) and white ash (*F. americana*) are common landscape and roadside trees in many US municipalities, often comprising more than 25 per cent of the urban forest canopy (MacFarlane and Meyer, 2005; McCullough and Mercader, 2012; Poland and McCullough, 2006; Sadof *et al.*, 2017). Landscape ash trees are typically highly vulnerable to EAB, given the limited genetic variability of popular cultivars and often stressful growing conditions (Poland and McCullough, 2006). A comprehensive evaluation of invasive forest insects in the US projected that by 2019, economic costs of EAB would exceed \$1 billion USD annually, most of which will be borne by municipalities and private property owners who must either remove or protect ash trees with insecticide (Aukema *et al.*, 2011). Economic costs of removing or treating less than 50 per cent of landscape ash trees in the US cities expected to be invaded by 2019 will likely exceed \$10.6 billion USD and including trees in adjacent suburbs doubles the number of vulnerable trees and associated costs (Kovacs *et al.*, 2010).

Systemic insecticides to protect ash from EAB

Although ash trees in North America continue to succumb to EAB, our ability to protect individual trees and moreover, to slow EAB population growth across larger spatial scales, has advanced substantially over the past decade. This improvement reflects the development of more effective systemic insecticides, in terms of chemistry and application methods, along with increasing knowledge of EAB life history and interactions between EAB and North American ash species in the invaded range.

Advances in treatment effectiveness

In the early 2000s, many arborists and municipal foresters in southeast Michigan attempted to protect the valuable landscape and roadside ash trees from EAB using the insecticide products available at the time. Cover sprays of broad-spectrum pyrethroid, organophosphate or acephate insecticides could be effective, but were unpopular because of concerns about spray drift, environmental contamination, effects on non-target organisms and applicator exposure, especially when large trees had to be sprayed (McCullough *et al.*, 2004, 2007). Arborists were already beginning to replace cover sprays of broad-spectrum insecticides with systemic insecticides to avoid drift and harm to beneficial insects and to control insect pests feeding in the upper canopy of large trees. Systemic insecticides are typically applied by injecting the product into active sapwood every 8 to

10 cm around the base of the trunk, or by pouring or injecting the product into the soil for uptake by roots (Herms *et al.*, 2014). Systemic insecticides are transported within xylem tissue up the trunk to canopy branches and foliage (Mota-Sanchez *et al.*, 2009; Tanis *et al.*, 2012), minimizing many problems associated with cover sprays.

Unfortunately, early efforts to protect ash trees yielded inconsistent and sometimes disappointing results (Cappaert *et al.*, 2006, 2007; McCullough *et al.*, 2006; Smitley *et al.*, 2006). Relatively few systemic insecticides were available to arborists in the early 2000s. Efficacy of annual applications of imidacloprid and dinotefuran varied depending on tree size, growing conditions, the extent of EAB injury already sustained and the local EAB population level. Field studies showed spring applications were generally more effective than fall applications of the same product and that initiating treatment while trees were still healthy was more likely to be effective than waiting until trees were symptomatic (Bick *et al.*, 2018; Herms *et al.*, 2014; McCullough *et al.*, 2011a, 2019; Smitley *et al.*, 2010, 2015). Often, however, municipalities and private landowners paid for annual insecticide treatments, only to see their trees continue to decline and ultimately succumb or require removal a few years after most untreated trees had died.

Perhaps driven in part by potential markets for effective ash treatments, new systemic insecticide chemistries were developed and application technology improved markedly in the US. Field studies to identify optimal timing, rates and persistence of systemic insecticides were conducted. Advances included new imidacloprid formulations, approval of dinotefuran applied via basal trunk spray and systemic insecticides with either azadirachtin or emamectin benzoate as the active ingredients. Research in the US and Canada found trunk injections of products with azadirachtin, a compound derived from kernels of neem (*Azadirachta indica*) trees, provided effective EAB protection for one year and perhaps two years, depending on local EAB population levels (McKenzie *et al.*, 2010; Herms *et al.*, 2014).

Emamectin benzoate—efficacy and economics

Arguably the most notable advance came about when an emamectin benzoate insecticide sold as TREE-age™ was registered in the US in 2010. Large-scale field trials beginning in 2007 and 2008 demonstrated trunk injections applied in spring, even at the lowest label rates, provided nearly complete EAB control for at least 2 years (Bick *et al.*, 2018; McCullough *et al.*, 2011a; Herms *et al.*, 2014; Lewis and Turcotte, 2015; Smitley *et al.*, 2010). Multi-year protection substantially reduced costs and logistical issues associated with annual treatments. Several economic evaluations and simulations compared costs of removing and replacing landscape ash trees with annualized costs of treating the same ash trees in alternate years with the TREE-age® product. Results consistently demonstrated that treating trees was substantially less expensive than removing and replacing trees, either proactively or as they succumbed to EAB (Hauer and Peterson, 2017; Kovacs *et al.*, 2014; McCullough and Mercader, 2012; McKenney *et al.*, 2012; Sadof *et al.*, 2017; Vannatta *et al.*, 2012). More recent studies have shown that emamectin benzoate applied at low or moderate rates provided 3 years of

highly effective EAB control (Bick *et al.*, 2018; McCullough *et al.*, 2019), further reducing costs.

Additional benefits of protecting ash with emamectin benzoate or other highly effective insecticides have become apparent, particularly in municipalities where ash trees comprise a substantial portion of the urban canopy. As EAB densities build, ash trees typically decline and die over a relatively compressed 4–6 year period (Knight *et al.*, 2013; Klooster *et al.*, 2014; McCullough *et al.*, 2019; Sadof *et al.*, 2017). Declining, dying and dead trees reduce property values, become increasingly dangerous for tree-climbing arborists and utility lines, and property owners are legally liable for ‘hazard trees’ if they break and fall. Treating municipal ash trees with systemic insecticides is less disruptive and generates less anxiety for residents than removing large trees, particularly when apparently healthy trees are proactively removed (Sadof *et al.*, 2017; Vanatta *et al.* 2012). Protecting mature landscape ash trees from EAB retains the often substantial ecological services provided by those trees (Hauer and Peterson, 2017, McPherson *et al.*, 2005, Nowak *et al.*, 2016, Sadof *et al.*, 2017). Economic benefits associated with stormwater uptake by municipal ash trees, for example, more than offset costs of treating the trees at two-year intervals with emamectin benzoate in Milwaukee, Wisconsin USA (Sivyer, 2011). Predictable treatment costs facilitate labour stability and enable municipalities to incorporate ash management, including gradual replacement of ash trees, into long-term planning. An intensive economic analysis demonstrated the benefits resulting from cooperation and budget aggregation among affected municipalities and suggested treating ash trees on private land as well as municipal property was advantageous both in terms of costs and EAB control (Kovacs *et al.*, 2014). Given the extent of ecological, economic and social impacts of EAB invasion, scientists, municipal foresters and major conservation organizations in the US endorsed systemic insecticides for urban ash protection (Coalition for Urban Tree Conservation, 2011).

In addition to urban trees, emamectin benzoate is also used to protect ash trees in forested settings in the US. For example, in Pennsylvania, emamectin benzoate is used to protect valuable trees in white ash seed orchards and to conserve genetic diversity on state forest lands (Liu and Miller, 2014). Some Native American tribes are treating selected black ash trees as a means to retain seed sources and to conserve genetic diversity (McCullough, 2013).

Potential negative ‘side effects’ of emamectin benzoate and other systemic insecticides used for ash protection were summarized by Hahn *et al.* (2011). North American ash species are wind-pollinated and the short duration of pollen production in early spring occurs before systemic products are typically applied, limiting pollinator exposure. Emamectin benzoate residues in foliage decline rapidly within a year of application (Lewis and Turcotte, 2015; McCullough *et al.*, 2011a) and recent analyses indicate residues are absent in ash pollen (Johnson, 2017).

Challenges of managing EAB

Life-history traits of EAB that contribute to difficulties of detecting, delineating and monitoring infestations are summarized below. Foresters, arborists and pest managers will need to be

aware of these challenges and able to communicate the challenges, as well as potential EAB impacts, to local property owners and residents.

Visual detection surveys for EAB are problematic

Early detection of newly established, low-density populations of EAB is ideal because it provides time to institute regulatory, communication and management activities before substantial damage occurs. Visual surveys may be undertaken for EAB detection, delimitation or monitoring, often when infested trees are known to be in nearby areas but have not yet been found locally. Trees with low densities of EAB larvae, however, exhibit few, if any, external signs of infestation. Ash xylem is highly sectored and healthy trees readily compartmentalize minor injuries, including a low density of EAB larval galleries (McCullough *et al.*, 2009b; Tanis and McCullough, 2016; Tanis *et al.*, 2012; Zwieniecki *et al.*, 2011). Beetles usually colonize the upper portion of the main leader or large branches in the upper canopy before lower branches or the trunk become infested, plus most larvae in healthy, recently colonized ash trees commonly require two years to complete development (Cappaert *et al.*, 2005b; Siegert *et al.*, 2010; Tluczek *et al.*, 2011). A few small D-shaped exit holes left by emerged EAB adults, therefore, are seldom present until at least two years after a tree becomes infested and will be difficult to see in the upper canopy of most trees. Larger holes left by woodpeckers preying on late instar and prepupal EAB larvae in the upper canopy of infested trees may be the first external evidence of EAB in a newly invaded area.

Over time, as larval densities increase, canopies thin and girdled branches may die. Epicormic sprouts, EAB adult exit holes and vertical bark cracks above larval galleries become apparent on large branches and the trunk. Data collected from felled and debarked green ash and white ash trees showed that ~80–120 EAB adults can potentially develop per m² of phloem area before trees succumb (McCullough and Siegert, 2007). Declining canopy condition, however, is not likely to be apparent until densities build up to at least 25–35 EAB per m² (Anulewicz *et al.*, 2007). Few EAB infestations in North America have been detected until at least 4–6 years after establishment (Knight *et al.*, 2013; Poland and McCullough, 2006).

Attracting and capturing EAB with artificial traps remains challenging

Difficulties of detecting and delimiting low-density EAB infestations also reflect the challenges of attracting and capturing EAB adults with artificial traps. Like other North American *Agilus* species, EAB adults are not known to produce long-range pheromones, although some studies reported a close range or contact pheromone may facilitate mating (Crook and Mastro, 2010; Lelito *et al.*, 2009; Ryall, 2015). Beetles appear to rely largely on visual cues and volatiles emitted by ash trees to initially locate suitable hosts, where they encounter conspecifics for mating (Cappaert *et al.*, 2005b; Crook *et al.*, 2009; Rodriguez-Saona *et al.*, 2007). In operational EAB survey programs in the US, traps are baited with ash volatiles, primarily the green leaf compound (Z)-3-hexanol (Rodriguez-Saona *et al.*, 2006; De Groot *et al.*, 2008; Grant *et al.*, 2010). In past years,

traps also included lures with Manuka oil, derived from the New Zealand tea tree (*Leptospermum scoparium* Forst and Forst) or Phoebe oil, an extract of Brazilian walnut (*Phoebe porosa* Mez.), which contain sesquiterpenes similar to those in ash wood or bark (Crook *et al.*, 2012; De Groot *et al.*, 2008). Procuring consistent supplies of those compounds proved difficult, however, and in recent years, most traps were baited with only (Z)-3-hexanol lures (USDA APHIS, 2018).

Years of research on adult EAB response to light and colour are reflected in the purple or green prisms and funnel traps used in operational EAB detection programs in the US and Canada (Crook and Mastro, 2010; Crook *et al.*, 2009, 2012; Francese *et al.*, 2010). Adult EAB beetles are positively phototactic, and beetle activity is greater on open-grown trees that are fully exposed to the sun compared with partially shaded trees, while fully shaded trees may be largely ignored, especially in recently infested areas (McCullough *et al.*, 2009a, 2009b; Wang *et al.*, 2010). In the US, regulatory trapping guidelines recommend hanging prisms or funnels from branches of ash trees growing along roads or on the edge of wooded areas (USDA APHIS, 2018).

When baited traps are hung in ash trees, however, lures must compete with the array of volatile compounds produced by surrounding ash trees and visual cues associated with the trap colour may be partially obscured. A modified trap, the self-supported and multicomponent double-decker trap, was designed to overcome such issues. Two sticky prisms are attached to a 3 m tall PVC pipe that slides over a t-post embedded in the ground, enabling traps to be placed near ash trees but fully exposed to the sun (McCullough *et al.*, 2011b; McCullough and Poland, 2017; Poland *et al.*, 2011). Double-decker traps resemble the silhouette of a small tree, provide a distinct volatile plume and attractive colour, exploit EAB adult preference for full sun (McCullough *et al.*, 2009a, 2009b, Wang *et al.*, 2010) and minimize problems such as leaves adhering to and obscuring prism panels or traps blowing out of trees (McCullough and Poland, 2017; McCullough *et al.*, 2011b; Poland *et al.*, 2011; Poland and McCullough, 2014). Highly replicated studies in sites with low or very low EAB densities indicated double-decker traps have higher detection rates and beetle captures (standardized per unit of trapping surface) than prism or funnel traps hung on ash trees (Burr *et al.*, 2018, Marshall *et al.*, 2010, McCullough *et al.*, 2011b, Poland *et al.*, 2011, 2014). Double-decker traps may be particularly appropriate for sites deemed to be at high risk for EAB introduction, while less expensive single prism or funnel traps may be preferred for extensive surveys.

Adult EAB dispersal behaviour complicates detection

Detection is further complicated by EAB adult dispersal behaviour, along with the resilience of ash trees to tolerate low densities of EAB larvae. In large-scale field studies, ash trees within 800 m of the known origin of newly established satellite populations were systematically selected, felled and debarked to assess the distribution of the larval cohort produced by the emerged EAB adults (Mercader *et al.*, 2009; Siegert *et al.*, 2010, 2015). Results consistently showed that ~90 per cent of larvae were on trees within 100 m of the point where adults emerged and the vast majority of the larval cohort were within 200 m. Galleries were also identified on trees more than 400 m from the origin,

however, indicating that a few females dispersed further, despite an abundance of suitable host trees nearby (Mercader *et al.*, 2009, 2012; Siegert *et al.*, 2010). Flight mill studies in a laboratory indicated a small proportion of mature EAB females appear to be physiologically capable of flying more than 5 km over their life span (Taylor *et al.* 2007), but straight-line, directional dispersal is unlikely to occur under natural conditions. Whether long-range EAB dispersal is triggered by environmental cues such as wind, disturbance or interactions with other EAB beetles, or if a small proportion of females are simply inclined to fly further than others, is also unknown. Using data from several field studies, Mercader *et al.* (2012) varied the percentage of EAB females dispersing either 1 or 2 km and modelled probabilities of detecting newly infested trees at varying distances and post-establishment time intervals. Results illustrated the difficulty of detecting infestations that are less than 6 years old, even if only 1 per cent of females colonize trees 1000 m away. Pruning and debarking branches on the roadside or landscape ash trees may provide a means to assess EAB distribution in municipal settings (Ryall, 2015, Ryall *et al.*, 2011), but is rarely used as a detection tool.

Girdled trees for EAB detection and management

Stressed ash, including girdled trees, are highly attractive to EAB

Adult EAB beetles preferentially colonize stressed trees over healthy ash trees, a trait with potential applications for detection and management efforts. This behaviour is not surprising given that in its native range in Asia, EAB is a secondary pest, colonizing only very stressed or dying ash trees (Herms and McCullough, 2014; Liu *et al.*, 2003). Stress alters volatile profiles and perhaps visual cues used by EAB to locate suitable hosts (Bartels *et al.*, 2008; Rodriguez-Saona *et al.*, 2006; De Groot *et al.*, 2008; Grant *et al.*, 2010). Factors such as compacted soil, ephemeral flooding, severe drought, or chronic problems that affect water or nutrient transport can increase the likelihood of early infestation compared with healthier trees (Burr *et al.*, 2018; Siegert *et al.*, 2010, 2015). In contrast, efforts to increase ash tree vigour with fertilization or application of a plant growth regulator to improve root to shoot ratios appear to have little effect on EAB host preference or host resistance (Limback, 2010; Tanis and McCullough, 2015).

Girdling ash trees in spring or early summer by removing a 15–20 cm wide band of outer bark and phloem results in host trees that are remarkably attractive to EAB adults, including ovipositing adult females. Larval densities on girdled trees may be five to ten times higher than on nearby ungirdled but otherwise similar trees (McCullough *et al.*, 2009a, 2009b, 2011b; Mercader *et al.*, 2011a; Tluczek *et al.*, 2011). Debarking girdled trees in fall or winter to locate larval galleries remains the single most effective method of detecting low or very low-density EAB infestations, well before any external signs of infestation become apparent. For example, using data from an extensive, multi-year project, Mercader *et al.* (2013) determined that the probability of EAB detection at very low population densities (<10 larvae per tree) was at least four to

five times higher with small (10–15 cm DBH) girdled ash ‘detection trees’ than with baited purple prism traps hung in ash trees. Grids of small girdled ash trees used in operational EAB detection programs in Michigan and Ohio between 2004 and 2008 led to the identification of several previously unknown infestations (Hunt, 2007; Rauscher, 2006; McCullough *et al.*, 2015). Debarking girdled ash trees also yields larval density and development rates, providing information on the status and distribution of local EAB populations (McCullough *et al.*, 2015). Of course, as local EAB densities build and many ash trees in an area become stressed by larval galleries, preferential attraction to girdled trees wanes (Mercader *et al.*, 2013, 2016; Siegert *et al.*, 2017).

Girdled ash trees can also function as trap trees or act as ‘sinks’ to reduce EAB density in recently established populations. Concentrating oviposition on girdled trees then removing or destroying those trees before larvae emerge as adults can significantly slow the growth of low-density EAB populations (Mercader *et al.*, 2011a, 2015) and even modify the spatial distribution of an EAB population. In replicated 4 ha areas within a recently infested forest with abundant green ash, most EAB females laid eggs either on one of three girdled ash trees clustered in the centre of a 4 ha area or on trees near the girdled tree cluster, while most ash trees in adjacent 4 ha areas remained uninfested or had low larval densities (Siegert *et al.*, 2017). A spillover effect, whereby ungirdled trees growing near girdled trees have higher larval densities than would otherwise be expected, has been observed in other low-density infestations (Mercader *et al.*, 2011a, 2015) as well in this study. This spillover effect may be problematic if not anticipated, but could also provide a means to retain EAB and perhaps reduce dispersal of mature female beetles (Mercader *et al.*, 2015, 2016). To ensure larvae cannot complete development, girdled trees that are not debarked are usually chipped or burned. In the field study mentioned above, however, girdled trees colonized by EAB during the summer were felled and sectioned into 1 m lengths in winter. Close examination of the bolts after adult EAB activity ceased the following summer showed only a few EAB were able to successfully develop and emerge as adults from the dry logs (Siegert *et al.*, 2017). Although any adult EAB emergence would be unacceptable in an eradication effort, a negligible number of emerged beetles would have little effect on the dynamics of an established population. Felling and sectioning potentially infested ash trees to enhance desiccation could be a low-cost management option suitable for some forested areas, rights of way or locations that are difficult to access.

Natural enemies and biological control

Woodpecker predation of EAB larvae

Despite the relatively recent establishment of EAB in North America, several native natural enemies can attack EAB life stages. Woodpecker predation of EAB larvae is relatively common and consistently accounts for more EAB mortality in North America than other factors (Cappaert *et al.*, 2005a; Duan *et al.*, 2010, 2014, 2015; Herms and McCullough, 2014; Jennings *et al.*, 2013, 2016; Lindell *et al.*, 2008). Woodpeckers prey on late instars and prepupae in fall, winter and early spring, but rarely attack early instars (Duan *et al.*, 2014; Jennings *et al.*, 2013, 2016; Siegert *et al.*, 2017). Consequently, trees have already sustained

the injury caused by larval galleries even when the larvae are subsequently consumed by woodpeckers. In some areas, EAB mortality attributable to woodpecker predation appeared to increase as larval densities built and ash tree canopies declined (Flower *et al.*, 2014; Jennings *et al.*, 2015). However, high rates of larval mortality from woodpecker predation have also been documented in recently infested trees where EAB densities remain low. For example, woodpecker predation was a major source of larval mortality in newly invaded forests in central Michigan where infested trees were scattered and EAB larval densities were very low (McCullough *et al.*, 2019; Siegert *et al.*, 2017). Moreover, the distinct holes in the outer bark left by woodpeckers preying on EAB are often the first evidence of EAB infestation in local areas (Cappaert *et al.*, 2005b).

Although native woodpecker species will preferentially forage on infested ash trees in mixed-species stands (Lindell *et al.*, 2008), woodpeckers have not slowed rates of ash mortality and predation can be highly variable among sites and even between adjoining trees (Cappaert *et al.*, 2005a; Lindell *et al.*, 2008; Lyons, 2015). An analysis of reports from citizen science volunteers who recorded the species they observed at their backyard bird feeders during a specific week in winter led Koenig *et al.* (2013) to speculate that woodpecker densities had increased in areas 'highly impacted' by EAB (i.e. within 50 km of the EAB epicentre in southeast Michigan). However, woodpeckers raise their offspring in summer when late-stage EAB larvae are not available. Frequent sightings of woodpeckers by the volunteers may largely reflect the abundance of infested ash trees in residential and urban landscapes in the affected areas (MacFarlane and Meyer, 2005), rather than actual increases in woodpecker populations. Retaining large snags for nesting habitat and supplemental feeding (e.g. with suet) in summer when woodpeckers are rearing offspring could perhaps enhance local woodpecker populations and EAB predation (Lindell *et al.*, 2008; Poland and McCullough, 2010), but such tactics have not been evaluated.

Invertebrate predators

Several North America invertebrate predators will occasionally capture and feed on EAB life stages but predation rates are minimal and there is no evidence of appreciable effects on EAB populations (Bauer *et al.*, 2004; Liu *et al.*, 2003; Lyons, 2015). The native smoky winged beetle bandit wasp, (*Cerceris fumipennis* Say), provisions its nest almost exclusively with adult buprestid beetles. Nests of these wasps have been monitored as a means to detect local EAB infestations (Careless *et al.*, 2014; Swink *et al.*, 2013), but this sporadic predation is much too low to affect EAB densities.

Pathogens

Pathogens have had minimal effects on EAB life stages in North America, which is perhaps not surprising given that EAB spends most of its life span protected beneath the bark. Larvae killed by pathogenic organisms are rarely observed in debarked trees, although cadavers colonized by secondary fungi are sometimes present (Bauer *et al.*, 2015; Macquarrie and Scharbach, 2015). In-field studies, EAB mortality attributed to *Beauveria* spp. or other naturally occurring pathogenic organisms has been consistently

very low (Castrillo *et al.*, 2010; Duan *et al.*, 2014; Johnny *et al.*, 2012). Researchers have explored cover sprays and autodissemination methods to facilitate infection of EAB adults by *Beauveria bassiana* (e.g. Liu and Bauer, 2007; Lyons *et al.*, 2012; Srei *et al.*, 2019), although potential effects of this generalist pathogen on non-target insects, including native parasitoids of EAB, is a concern (Lyons, 2015). To date, pathogens have not been used in operational EAB management programs and there is no evidence that naturally occurring entomopathogens will exert detectable effects on EAB populations in North America.

Parasitoids and classical biological control

Hymenopterous parasitoid wasps, including North American species and introduced species native to Asia, also cause EAB mortality. Early surveys in the US reported that native parasitoids occasionally attacked EAB larvae but parasitism rates were consistently very low (Bauer *et al.*, 2004; Liu *et al.*, 2003; Duan *et al.*, 2009). Over time, however, several species of native parasitoids that attack native phloem- and woodboring larvae in North America appear to 'learn' that suitable hosts are available in ash trees. Larval parasitism by *Atanycolus* spp., particularly *Atanycolus cappaerti* Marsh and Stazanac 2009 (Braconidae), is most common and has been recorded in newly invaded sites, high density areas and aftermath forests where nearly all overstory ash have been killed (Cappaert and McCullough, 2009; Cappaert *et al.*, 2005a; Duan and Schmude, 2016; Duan *et al.*, 2009, 2014, 2015; Lyons, 2015; McCullough *et al.*, 2019). An array of other native parasitoids, including *Phasgonophora sulcata* Westwood (Chalcidae) and *Balcha indica* Mani and Kaul (Hymenoptera: Eupelmidae), are occasionally recorded when infested ash trees are debarked (Bauer *et al.*, 2004; Duan *et al.*, 2011; Lyons, 2015). Native larval parasitoids may affect local EAB population growth to some extent, but as with woodpecker predation, parasitism rates vary considerably over time, among trees within sites and among sites (Cappaert and McCullough, 2009; Duan *et al.*, 2011, 2012, 2015, 2017).

Federal agencies, primarily in the US, have invested considerable resources in classical biological control for EAB and recent reviews describe the development and current status of the EAB biological control programme (Bauer *et al.*, 2015; Duan *et al.*, 2015, 2018; Lyons, 2015). Efforts to evaluate rear and release EAB parasitoids, native to China and more recently eastern Russia, have been underway in the US for more than a decade (Bauer *et al.*, 2015; Duan *et al.*, 2018; US Federal Register, 2007). Releases of an egg parasitoid *Oobius agrili* Zhang (Encyrtidae), and two larval parasitoids, *Spathius agrili* Yang (Braconidae), a gregarious ectoparasitoid, and *Tetrastichus planipennis* Yang (Eulophidae), a gregarious endoparasitoid, began in 2007 in Michigan (Bauer *et al.*, 2015). Post-release evaluations indicate that *S. agrili* is not cold hardy and has failed to establish in northern states, although this species continues to be released in southern states (Duan *et al.*, 2018). The tiny egg parasitoid *O. agrili*, which is notably difficult to monitor, has been recovered from EAB eggs in several release sites, although dispersal and spread appear slow (Abell *et al.*, 2014). To date, the larval parasitoid *T. planipennis* appears to be the most successful of the introduced species. It has become established in numerous release sites, spreads quickly and relatively high parasitism rates

have been observed in heavily infested ash saplings (Bauer *et al.*, 2015; Duan *et al.*, 2014, 2015). Parasitism of EAB larvae in larger trees, however, is likely to be limited by the small size of *T. planipennisi* adults (Duan *et al.*, 2014, 2018), who cannot access EAB larvae under thick bark. Release of another larval parasitoid, *Spathius galineae* Belokobylskij, native to eastern Russia, began in the US in 2015. This species appears to be cold hardy and has a longer ovipositor, suggesting it may be able to attack EAB larvae in larger branches or trees (Duan *et al.*, 2018; Murphy *et al.*, 2017).

To date, however, cumulative effects of native and introduced natural enemies of EAB have not slowed the rate or progression of ash mortality in North America and evidence of density-dependent effects of natural enemies on EAB population growth is limited (Hermes and McCullough, 2014). Additionally, when North American ash trees were planted in China as part of reforestation efforts, nearly all were killed by EAB, despite the complexity of native parasitoids (Liu *et al.*, 2003; Wei *et al.*, 2004). Expectations that classical biological control alone will eventually regulate EAB populations in North America should perhaps be tempered. Scientists have proposed that biological control may be most important in aftermath forests where overstory ash have been killed but ash saplings and recruits persist (Duan *et al.*, 2017; Hermes and McCullough, 2014; Klooster *et al.*, 2018). Whether the complex of introduced parasitoids and native natural enemies can regulate EAB populations at low enough densities to facilitate long-term survival of ash regeneration in aftermath forests remains to be seen. Higher densities of white ash saplings in some southeast Michigan aftermath forests were attributed to parasitoid introductions (Margulies *et al.*, 2018), but pre-EAB sapling abundance was unknown and neither EAB densities nor parasitism rates were quantified in the release and control sites. White ash survival varies considerably across southeast Michigan (Robinett and McCullough, 2019), making it difficult to confirm the influence of introduced parasitoids. Continued research to evaluate introduced and native biological control agents in sites at varying stages of EAB invasion and dominated by different ash species would be useful.

Area-wide EAB management

Tactics such as mating disruption, sterile male release or aerial application of microbial insecticides that are successfully used for management of various Lepidopteran or Dipteran pests (Suckling *et al.*, 2012) seem unlikely to be viable options for EAB management without significant and unforeseen technological advances. Removing infested ash trees in isolated populations can reduce local EAB density by destroying developing larvae and limiting the availability of phloem for subsequent generations (Fahrner *et al.*, 2017; Mercader *et al.*, 2011a). Rigorously parameterized models, however, indicated reducing the availability of ash phloem has substantially less effect on EAB population growth and spread than either employing girdled trap trees or treating trees with emamectin benzoate (Mercader *et al.*, 2011a, 2011b). Dispersal capabilities of EAB adults, the low probability of detecting newly or recently

colonized trees, and the probable increase in density-dependent larval development rates indicate that without employing additional tactics, more trees will become infested and require removal.

Effectively managing EAB to protect the ash population, as well as individual ash trees in a given area, is likely to require the use of systemic insecticides, particularly emamectin benzoate. Simulations parameterized with data from multiple field sites have shown that treating even a relatively small portion of the ash trees in an area with emamectin benzoate slowed EAB population growth, consequently delaying the onset and progression of ash decline across the area. Effectiveness of area-wide management can vary depending on how quickly treatment begins following EAB establishment as well as the proportion and distribution of treated trees (McCullough and Mercader, 2012; Mercader *et al.*, 2011b, 2016).

The SLOW Ash Mortality Pilot Project

The SLOW Ash Mortality (SLAM) Pilot Project was an extensive and collaborative effort to develop, implement and evaluate an EAB management strategy involving personnel from state and federal forestry and regulatory agencies and universities. The SLAM project was initiated when a girdled trap tree in the Upper Peninsula of Michigan led to the detection of an isolated 4- to 5-year-old EAB infestation (McCullough *et al.*, 2015). Grids of small (15–20 cm DBH) girdled ash detection trees supplemented with baited purple prism traps were used to monitor the distribution of EAB across an area that eventually encompassed nearly 400 km² of National Forest, state and private forest lands, rural areas and small communities. Annually, 444 to 855 ash trees were girdled and debarked between 2008 and 2011 to assess EAB distribution and larval density. A very small proportion of the ash trees within the project area, 229 trees and 358 trees in 2009 and 2010, respectively, were treated with emamectin benzoate. Distribution of the insecticide-treated trees was less than optimal; most treated trees were on a few parcels of private land or on right-of-ways along roads. Ash trees across the project area were inventoried by diameter class using a grid overlaid on the project area, enabling ash phloem area (m²) and the potential EAB production in the absence of any management to be calculated for each grid cell (McCullough and Siegert, 2007). Condition of more than 1000 untreated ash trees across the project area was visually assessed by surveyors in 2011 and 2012, who recorded variables such as canopy condition and external signs of EAB infestation. Effects of the insecticide and the girdled ash trees were evaluated by comparing the observed EAB density and distribution with that expected in the absence of any management (Mercader *et al.*, 2015, 2016).

Results showed that treating a very small proportion (<1 per cent) of the ash trees with emamectin benzoate significantly slowed expected EAB population growth and rates of ash decline across the project area (Mercader *et al.*, 2015, 2016). The number of treated trees had a significant effect on the EAB population but the area of phloem within treated trees did not have an effect (Mercader *et al.*, 2015). This validated earlier simulations that indicated treating more ash trees with a given amount of insecticide would be more effective than applying the same amount of insecticide to fewer but larger trees (Mercader *et al.*, 2011a).

Systematically distributing the treated trees across the project area increases the probability that EAB adults will encounter a toxic tree. In an operational programme, treating a portion of ash trees with emamectin benzoate on a three-year rotation (McCullough *et al.*, 2019) would presumably enhance area-wide effects on the EAB population. Although the insecticide treatment slowed EAB population growth, it had little effect on the expected rate of EAB spread in the SLAM project area (Mercader *et al.*, 2016).

Grids of girdled ash trees functioned as both detection tools and trap trees in the SLAM Pilot Project (Mercader *et al.*, 2013, 2015, 2016). Larval densities in ungirdled trees near girdled trees had higher larval densities than would be otherwise expected, indicative of a spillover effect. This had a small but significant effect on slowing EAB population growth but perhaps more importantly, also retained EAB in the local area, slowing overall spread rates (Mercader *et al.*, 2016). Other research in forested areas with low EAB densities has similarly demonstrated that girdling a small proportion of ash trees can concentrate EAB on trees near the girdled trees, slowing spread into areas without girdled trees (Siebert *et al.*, 2017). A few private landowners in the SLAM project area were able to negotiate timber sales that included harvesting large merchantable ash trees (e.g. >30 cm DBH) along with more desirable species (e.g. *Acer saccharum*). Results from simulations, however, have consistently demonstrated that ash removal, has much less effect on EAB population growth than either insecticide treatments or girdling, and will eventually increase spread (Mercader *et al.*, 2011a, 2011b, 2016).

Integrating EAB tactics

Ideally, replicated studies would be undertaken in multiple regions of North America invaded by EAB to evaluate the efficacy of individual management tactics and combinations of tactics. Such research, however, is exceedingly difficult to conduct across appropriately large spatial and temporal scales. Nevertheless, several field studies, in addition to the SLAM pilot project, have shown that practical options exist for integrating two or more EAB control tactics to slow EAB population growth and ash decline.

Emamectin benzoate and girdled trees

Injecting emamectin benzoate then girdling the injected trees 5–14 days later produces lethal trap trees that are both highly attractive to ovipositing EAB adult females but also highly toxic to leaf-feeding beetles and neonate larvae (McCullough *et al.*, 2016). In contrast to girdled but untreated trees that must be debarked, felled and sectioned, or chipped before larvae can develop, lethal trap trees can remain in place until they can conveniently be removed. This bait-and-kill approach can be readily employed in forested areas where declining or dead trees are unlikely to affect property values or become hazard trees. The strategy can also be employed in residential or urban areas, however, where low-value ash trees on public property are destined for removal. Although simply removing a girdled trap tree in fall or winter destroys the larvae feeding in that tree, lethal trap trees will exert a greater effect on EAB population growth by con-

trolling foliage-feeding beetles. Attracting and controlling adult females, each of which is likely to lay 50–60 eggs during her life span, amplifies the impact of both the girdling and the systemic insecticide. Similarly, surrounding or intermixing girdled trees and trees treated with emamectin benzoate should enhance effects of both treatments. The spillover effect observed in field studies, including the SLAM Pilot Project, suggests surrounding clusters of girdled trees with treated trees or intermixing treated and girdled trees should yield additive or even synergistic effects of the two tactics. Coupling girdled and treated trees could perhaps also decrease the number of trees that require treatment, further reducing costs (Mercader *et al.*, 2011a).

Systemic insecticides and biological control

Combining two or more pest management tactics can be an effective strategy if the tactics are not redundant and do not interfere with each other. Ideally, integrating two tactics should yield at least additive effects and perhaps even synergistic effects (Barclay, 1992; Barclay and Chao, 1991; Suckling *et al.*, 2012). Current and recent research indicates systemic insecticides, particularly highly effective emamectin benzoate products, can be successfully integrated with biological control in areas invaded by EAB. In contrast to insecticide cover sprays, systemic insecticides are unlikely to interfere with EAB parasitoids nor with woodpeckers preying on EAB larvae. Neither parasitoids nor woodpeckers will attack dead EAB larvae nor will they come into contact with the insecticides, which are transported in xylem tissue (Mota-Sanchez *et al.*, 2009). Davidson and Rieske (2016) applied imidacloprid as a soil drench at either the full label rate or at a reduced rate in areas of Kentucky where Asian parasitoids were also released. They found neither full nor reduced rates of imidacloprid had negative effects on either the introduced parasitoids or native pollinators. Not surprisingly, however, applying reduced rates of imidacloprid, which would still incur some costs, failed to protect the treated trees, negating the practical value of this strategy. In an ongoing field study, emamectin benzoate treatment of ash trees representing ~35 per cent of the live ash phloem slowed local EAB population growth across a 10 ha area, while larval EAB mortality attributable to woodpecker predation, native larval parasitoids (*Atanycolus* spp.), or introduced *T. planipennis* parasitoids was similar on trees sampled in areas with and without insecticide application (D.G. McCullough, unpublished data). The absence of live EAB larvae on trees treated with emamectin benzoate could potentially enhance the success of natural enemies by focusing the activity of woodpeckers and parasitoid wasps on untreated trees where prey or hosts will be encountered. Additional research to monitor EAB population densities, parasitism rates and ash condition in the forest and urban areas with and without emamectin benzoate applications would be valuable for areas at all stages of the EAB invasion.

Conclusions

Given the millions of ash trees that have been killed by EAB to date, there can be an attitude of resigned acceptance when EAB is found in a new area. Responses of property owners, municipal foresters and land managers to new detections of EAB in the

US have ranged from a passive 'do nothing' approach to simply removing ash trees, either proactively or as they decline and die. Harvesting merchantable ash may provide some value to forest landowners and replacing ash with other genera can improve diversity in forests or urban forests. Simply removing ash trees, however, has less effect on EAB population growth than other tactics, will likely increase spread rates and can generate strong negative reactions in urban and residential areas. Numerous analyses have demonstrated the economic benefits of protecting urban ash with emamectin benzoate or other highly effective systemic insecticides compared with tree removal. The benefit-to-cost ratios increase further if the value of ecological services provided by mature trees is considered and if collaborative management efforts across property lines and political boundaries are undertaken. Area-wide management programs, ideally tailored to local conditions, can integrate emamectin benzoate treatments, strategic deployment of girdled ash trap trees, removal of heavily infested trees and biological control. These efforts can slow EAB population growth and while established EAB infestations are unlikely to be eradicated, the period between detection and the relatively rapid progression of ash decline and mortality can be extended for years. This buys time, both for the gradual replacement of ash in landscapes or forests, and for further scientific advances. Research, for example, may eventually yield resistant ash cultivars, repellents or acoustic signals for push-pull strategies, and methods to enhance native or introduced biological controls. Active and adaptive management to reduce both direct and cascading, indirect impacts of EAB-related ash mortality can be practical, economically viable and effective and warrant strong consideration in invaded areas of North America and potentially Europe.

Acknowledgements

This paper was given at the conference *Preparing Europe for invasion by the beetles EAB and bronze birch borer, two major tree-killing pests* in Vienna, Austria on 1-4 October 2018, and which was sponsored by the Organisation for Economic Co-operation and Development (OECD) Co-operative Research Programme: Biological Resource Management for Sustainable Agricultural Systems, whose financial support made it possible for the author to participate in the workshop. The opinions expressed and arguments employed in this paper are the sole responsibility of the authors and do not necessarily reflect those of the OECD or of the governments of its Member countries.

Conflict of interest statement

None declared.

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