# Chapter 1: Emerald Ash Borer Biology and Invasion History

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## INTRODUCTION

The emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is native to eastern Asia and is primarily a pest of ash (*Fraxinus*) trees (Fig. 1). Established populations of EAB were first detected in the United States and Canada in 2002 (Haack et al., 2002), and based on a dendrochronology study by Siegert et al. (2009), the original EAB introduction likely occurred in the early to mid-1990s in Michigan. In European Russia, EAB was first found near Moscow in 2003, but not officially identified until 2005 (Izhevskii and Mozolevskaya, 2010). EAB has become a serious pest of ash in North America and European Russia, is causing widespread tree mortality, and is spreading rapidly on both continents (Cappaert et al., 2005; Poland and McCullough, 2006; Kovacs et al., 2010; Baranchikov, 2013; EAB Info, 2013; Orlova-Bienkowskaja, 2013; Straw et al., 2013; Herms and McCullough, 2014). In this chapter, we discuss the biology of EAB, its native and introduced range through 2013, and the likely pathways by which it was introduced and spread.

### General Biology

The life cycle of EAB is typically completed in one year, but two years is often required, especially in vigorous hosts, in cooler climates, or when eggs are laid late in the season (Cappaert et al., 2005; Wei et al., 2007; Wang et al., 2010). In addition, Petrice and Haack (2007) reported that EAB may require two years to complete development in cut logs or firewood, especially when the wood has dried. EAB can successfully infest both healthy and stressed ash trees in North America and European Russia, where the native ash species did not coevolve with EAB (Liu et al., 2003; Wei et al., 2004; Poland and McCullough, 2006; Baranchikov et al., 2008; Rebek et al., 2008). However, within EAB's native range in China and the Russian Far East, species of Asian ash are usually resistant to the borer, except during periods of environmental stress such as prolonged drought (Yu, 1992; Zhao et al., 2005; Baranchikov et al., 2008). In addition, EAB has been reported to kill species of North American ash that were planted in China and Russia (Liu et al., 2003; Zhao et al., 2005; Baranchikov et al., 2008). EAB infests nearly all sizes of ash trees, from saplings that measure 2-3 cm in diameter to mature trees (Haack et al., 2002; Wei et al., 2007), and infests both open-grown and interior-forest trees (Poland and McCullough, 2006; McCullough et al., 2009; Wang et al., 2010) (Figs. 2-3).


**Figure 1.** Adult emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). (Photo credit: David Cappaert, Michigan State University, Bugwood.org)

In China and the Russian Far East, the principal native hosts of EAB include *Fraxinus mandshurica* Ruprecht and *Fraxinus chinensis* Roxburgh (Yu, 1992; Zhao et al., 2005; Wei et al., 2007; Baranchikov et al., 2008; Izhevskii and Mozolevskaya, 2010), whereas in North America, EAB has been able to infest and kill all species of native *Fraxinus* so far encountered, including *F. americana* L., *F. nigra* Marshall, *F. pennsylvanica* Marshall, *F. profunda* (Bush) Bush, and *F. quadrangulata* Michx. (Anulewicz et al., 2008; EPPO, 2013). In European Russia, EAB has infested and killed primarily the introduced North American species *F. pennsylvanica* and the native European species *Fraxinus excelsior* L. (Baranchikov et al., 2008; Izhevskii and Mozolevskaya, 2010; Duan et al., 2012). It is important to note that Jendek (1994) synonymized two other Asian *Agrilus* species and one subspecies with *A. planipennis*, type China (EAB), including *Agrilus feretrius* Obenberger (type Taiwan), *Agrilus marcopoli* Obenberger (type Mongolia), and *Agrilus marcopoli* ulmi Kurosawa (type Japan) (Jendek and Grebennikov, 2011). Besides ash, which is the only larval host reported for *A. planipennis* in China (Yu, 1992; Liu et al., 2003; Zhao et al., 2005), other tree genera (*Juglans*, *Pterocarya*, and *Ulmus*) were reported as larval hosts in Korea and Japan for A. *marcopoli* and A. *marcopoli ulmi* (Ko, 1969; Akiyama and Ohmomo, 1997). However, in a recent EAB pest risk assessment prepared by the European and Mediterranean Plant Protection Organization (EPPO, 2013), it was reported that Japanese buprestid specialists now consider the non-*Fraxinus* host records for Japan to be in error.

The adult flight season of EAB usually begins in May or June in the Great Lakes region of North America and at similar latitudes in Asia, with peak flight occurring in June to July, and usually ending by September (Cappaert et al., 2005; Wei et al., 2007; Wang et al., 2010). Adults are most active on sunny days when air temperatures exceed 25° C (Wang et al., 2010), but during rainy or cool weather the adults often rest in bark crevices and on leaves (Rodriguez-Saona et al., 2007). EAB adults consume host foliage throughout their life and can live for several weeks under favorable laboratory conditions (Fig. 4; Wang et al., 2010; EPPO, 2013).

EAB adults use visual and olfactory cues to locate host trees and mates. Shades of purple and green are highly attractive to EAB adults (Francese et al., 2005, 2008, 2010; Crook et al., 2009). Moreover, EAB


**Figure 2.** Recently planted ash trees showing thinning crowns and epicormic shoots typical of EAB infestation. (Photo credit: Leah Bauer, USDA Forest Service, Bugwood.org)


**Figure 3.** Mature ash tree showing dieback typical of EAB infestation and bark removal by woodpeckers as they search for EAB life stages. (Photo credit: Steven Katovich, USDA Forest Service, Bugwood.org)

adults are attracted to dead EAB adults when placed on foliage or traps as decoys (Lelito et al., 2007, 2008; Petrice et al., 2013). This is not surprising given that EAB adult males are known to hover near host trees when searching for mates, and then landing on or near prospective mates when they are located (Lelito et al., 2007; Rodriguez-Saona et al., 2007). Various volatiles from ash bark and foliage elicit positive responses in EAB adults under laboratory conditions, and some of these compounds increase EAB attraction to purple or green traps (Rodriguez-Saona et al., 2006; Crook et al., 2008; Crook and Mastro, 2010; Grant et al., 2011; Poland et al., 2011; Poland and McCullough, 2014). Also, close range sex pheromones have been identified for EAB, and field testing has found them to increase attraction of EAB to traps (Lelito et al., 2009; Silk et al., 2011; Ryall et al., 2012).

EAB adults mate on the trunk, branches, and foliage of their host plants. Oviposition usually begins about 5-10 days after adult emergence. Eggs are laid individually or in small clusters between layers of bark and in bark crevices along the trunk, major branches, and exposed roots (Wei et al., 2007; Anulewicz et al., 2008; Wang et al., 2010; Jennings et al., 2014) (Fig. 5). Under laboratory conditions, average adult female longevity is about 7-9 weeks, with total fecundity usually averaging between 40 to 74 eggs per female and with a maximum of 307 eggs (Rutledge and Keena, 2012; Jennings et al., 2014). Average EAB adult male longevity is about 43 days (EPPO, 2013).

Egg hatch usually occurs after 7-18 days, depending on local temperatures. Neonate larvae chew through the surface of the egg that is in contact with the tree, and tunnel directly through the outer bark to the cambial region where they feed on the inner bark (phloem) and outer sapwood, creating frass-filled galleries (Wei et al., 2007; Wang et al., 2010). Larval galleries tend to be more serpentine-shaped in vigorous host trees (Fig. 6), while more meandering in less vigorous hosts or when larval densities are high (Wei et al., 2007; Wang et al., 2010) (Fig. 7).

Chamorro et al. (2012) described the morphology of EAB eggs, larvae, and pupae in great detail. Briefly, EAB has four larval instars, and as is typical of larvae in the genus *Agrilus*, there are two heavily sclerotized processes, often called urogomphi, at the terminal


**Figure 4.** Typical leaf feeding damage by EAB adults. (Photo credit: Deborah Miller, USDA Forest Service, Bugwood.org)

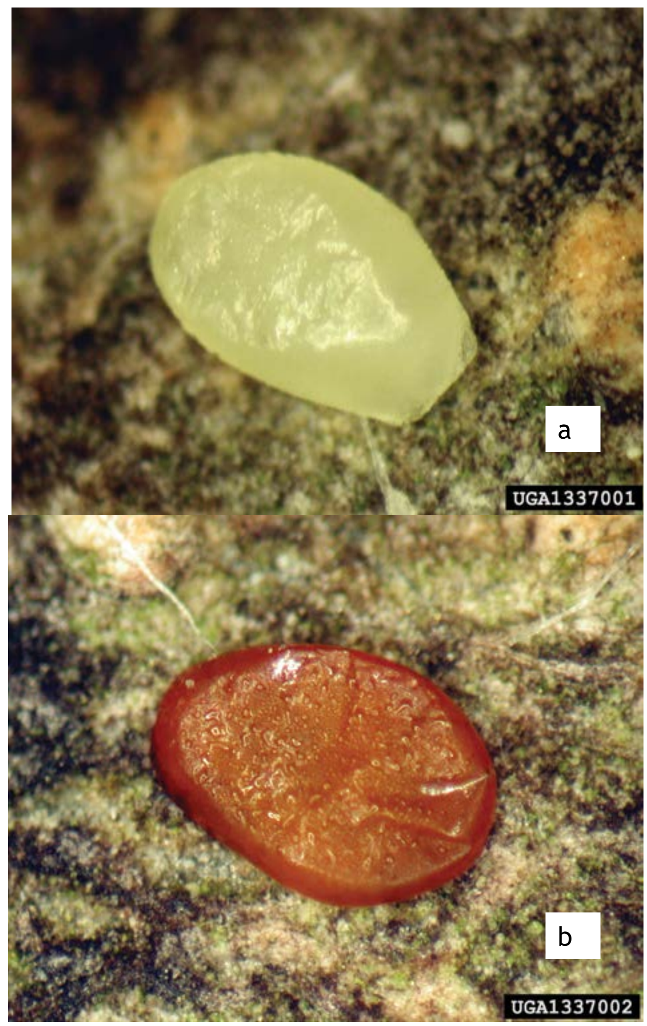


**Figure 5.** EAB eggs are white in color when first deposited (a) and then turn yellowish-brown within a few days (b). (Photo credit: Houping Liu, Michigan State University, Bugwood.org)

end of the abdomen (Fig. 8). Measurements of the urogomphi can be used to distinguish the larval instars (Liu et al., 2007; Petrice et al., 2009; Wang et al., 2010). For individuals that complete their life cycle in one year, larvae overwinter as mature fourth instars (Cappaert et al., 2005; Wang et al., 2005, 2010). For individuals that develop over two years, the first winter is usually spent as early instar larvae. Once a larva completes its feeding as a fourth instar (Fig. 9) it constructs a pupal cell, usually in the outer sapwood of thin-barked branches or trees or in the outer bark of thick-barked trees (Abell et al., 2012). Before creating the pupal cell, 4th-instar larvae construct a tunnel that extends nearly to the surface of the outer bark that will later be used by the new adult when it exits the tree (Wang et al., 2010). In the newly completed pupal cell, the 4th-instar larva folds itself into a J-shape or U-shape before overwintering (Fig. 10).

In spring, the larvae that overwintered in pupal cells develop into prepupae by gradually unfolding their body as they become shorter and more cylindrical. Prepupae then molt into naked or exarate pupae (Wang et al., 2010). Pupation occurs in late spring and early summer and usually lasts 3-4 weeks (Fig. 11). After eclosion, the newly formed or pharate adult will remain in its pupal cell for about one week before it chews its way out of the tree by enlarging the exit tunnel that it created earlier when it was a mature larva (Wei et al., 2007; Wang et al., 2010). The exit hole constructed by the adults is typically D-shaped, with the flat side of the "D" corresponding


**Figure 6.** EAB larval gallery in a vigorous host as evidenced by the tight zig-zag pattern of the gallery and the attempt by the tree to compartmentalize the gallery. (Photo credit: Edward Czerwinski, Ontario Ministry of Natural Resources, Bugwood)

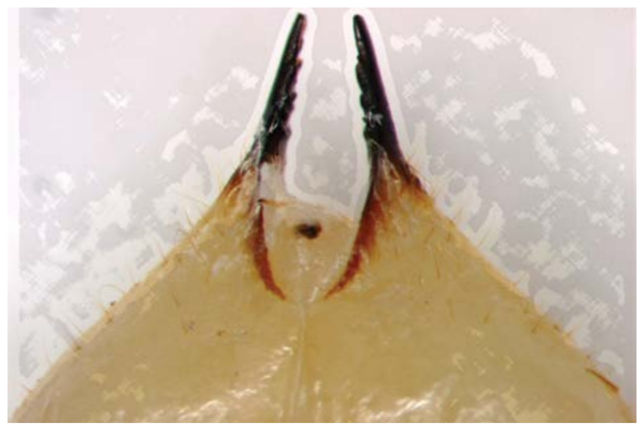

**Figure 8.** Close-up of the paired terminal processes found at the tip of the last abdominal segment of EAB larvae. (Photo credit: Pennsylvania Department of Conservation and Natural Resources, Bugwood.org)


**Figure 7.** EAB larval galleries on a less-vigorous host tree as evidenced by the meandering pattern of the galleries. (Photo credit: Edward Czerwinski, Ontario Ministry of Natural Resources, Bugwood.org)


**Figure 9.** Fourth instar EAB in its gallery, which is constructed in the cambial region of the tree. (Photo credit: Pennsylvania Department of Conservation and Natural Resources, Bugwood.org)

to the upper side of the adult's body (Fig. 12). Upon emergence, adults readily walk or fly to host foliage and feed (Wang et al., 2010).

As is typical for many *Agrilus* species, trees often die after 1-3 years of successive borer infestation, with death usually beginning in the crown branches and moving downward in subsequent years to the main trunk (Haack and Benjamin, 1982; Cappaert et al., 2005; Ryall et al., 2011; Foelker et al., 2013). However, in small diameter ash trees, initial EAB infestations often begin on the main trunk (Timms et al., 2006; Wei et al., 2007; Tluczek et al., 2011). In many EAB-infested ash trees, epicormic branches develop along the lower trunk before the tree dies (Cappaert et al., 2005; Wang et al., 2010) (Figs. 2, 13).

### Native Range of Emerald Ash Borer

EAB is native to China, Japan, Korea, Mongolia, the Russian Far-East, and Taiwan (Yu, 1992; Jendek, 1994; Jendek and Grebennikov, 2011; Chamorro et al., 2014). The recent report of EAB from Laos (Jendek and Grebennikov, 2011) is no longer considered valid given that the specimens examined from Laos were later described as a new species: *Agrilus tomentipennis* (Jendek and Chamorro, 2012). Although EPPO (2013) raised doubts on the occurrence of EAB in Mongolia, Jendek and Grebennikov (2011) state that the type specimen for A. *marcopoli* is from Mongolia. In addition, as stated above, the occurrence of EAB in Japan and Taiwan is based on specimens that were formerly considered A. *marcopoli ulmi* and A. *feretrius*, respectively (Jendek, 1994; Jendek and Grebennikov, 2011).

## INITIAL DISCOVERY AND SPREAD OF EAB IN NORTH AMERICA

EAB was first discovered in North America in 2002 (Haack et al., 2002; Cappaert et al., 2005; Poland and McCullough, 2006; Herms and McCullough, 2014). The first adults were reared from declining ash trees near Detroit, Michigan, in May 2002, and were sent to several taxonomists for identification. Later, in July 2002, they were positively identified as *A. planipennis* by Eduard Jendek in Slovakia, who is the world authority on Asian *Agrilus*. Moreover, beetles that looked similar to EAB were collected in July 2002 in Windsor, Ontario, and identified as EAB in August 2002.

Michigan and Canada enacted quarantines on all known EAB-infested counties starting in July and September 2002, respectively (Haack et al., 2002). A federal EAB quarantine was first enacted

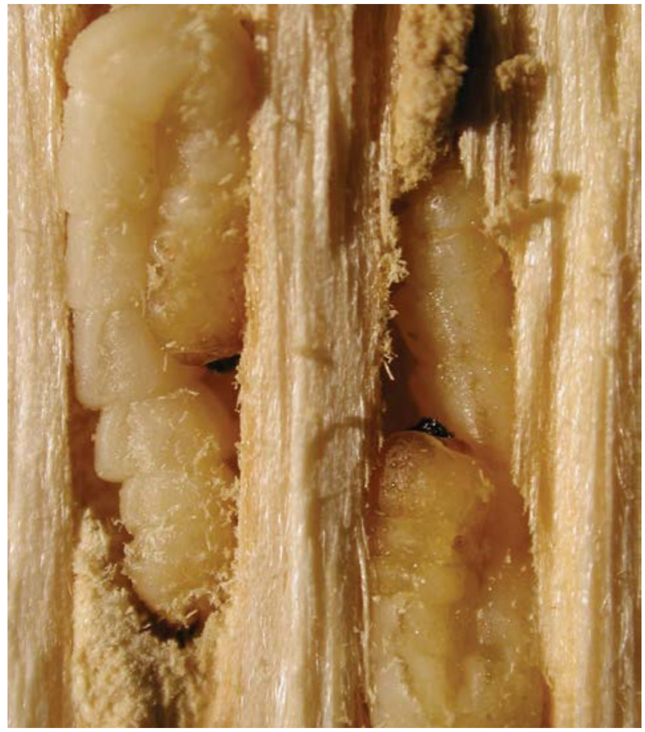

**Figure 10.** Fourth instar EAB larvae in their typical overwintering position (J-larvae) inside pupal cells that were constructed in the outer sapwood. (Photo credit: Houping Liu, Michigan State University, Bugwood.org)

**Figure 11.** EAB pupae are naked and gradually mature into adults within their individual pupal cells during spring and summer. (Photo credit: Deborah Miller, USDA Forest Service)

in the United States in October 2003 (USDA APHIS, 2003). The EAB quarantine zone has expanded each year since 2002 in both the United States and Canada as a result of regional surveys in several states and provinces. When new EAB populations were discovered, quarantines were usually enacted at the county level. As a result of intense survey efforts, the steady range expansion of EAB has been well documented in North America (Fig. 14). However, it is important to realize that it usually takes several years before EAB populations are large enough to be detected during surveys. Range expansion of EAB is a result of both natural spread and artificial movement of infested ash material.

By the end of 2002, EAB had been found in six southeastern Michigan counties in the Detroit area. This number increased to 13 counties by the end of 2003, and 20 by 2004, all still within Michigan's Lower Peninsula. In 2005, EAB was found for the first time in Michigan's Upper Peninsula. EAB was first found in Ohio in 2003; Indiana in 2004; Illinois and Maryland in 2006; Pennsylvania and West Virginia in 2007; Wisconsin, Missouri and Virginia in 2008; Minnesota, New York, and Kentucky in 2009; Iowa and Tennessee in 2010; Connecticut, Kansas, and Massachusetts in 2012; and Colorado, Georgia, New Hampshire, and North Carolina in 2013 (EAB Info, 2013) (Fig. 14). In Canada, EAB has been detected in just two provinces as of 2013, first in Ontario in 2002, and then in Quebec in 2008 (Fig. 14). Overall, as of December 2013, EAB was known to occur in 22 U.S. states and two Canadian provinces.

**Figure 12.** EAB adults construct D-shaped exit holes as they chew through the bark and emerge from their host tree. (Photo credit: Deborah Miller, USDA Forest Service)


**Figure 13.** EAB infested ash tree with epicormic shoots that often develop during the latter years of infestation prior to tree death. (Photo credit: Edward Czerwinski, Ontario Ministry of Natural Resources, Bugwood.org)

## INTRODUCED RANGE AND SPREAD OF EAB IN RUSSIA

There are few early records of EAB from Russia. During the 1900s, all EAB records were from southern Primorskiy Kray in the Russian Far East and consisted of small numbers of specimens collected during 1935-1999 (Alekseyev, 1979; Jendek, 1994; Volkovich, 2007; Yurchenko et al., 2007; Fig. 15). In 2004, EAB populations were also found in southern Khabarovsk Kray in the Russian Far East in the area between Khabarovsk and Dzonki, a distance of about 100 km as measured along the Amur River

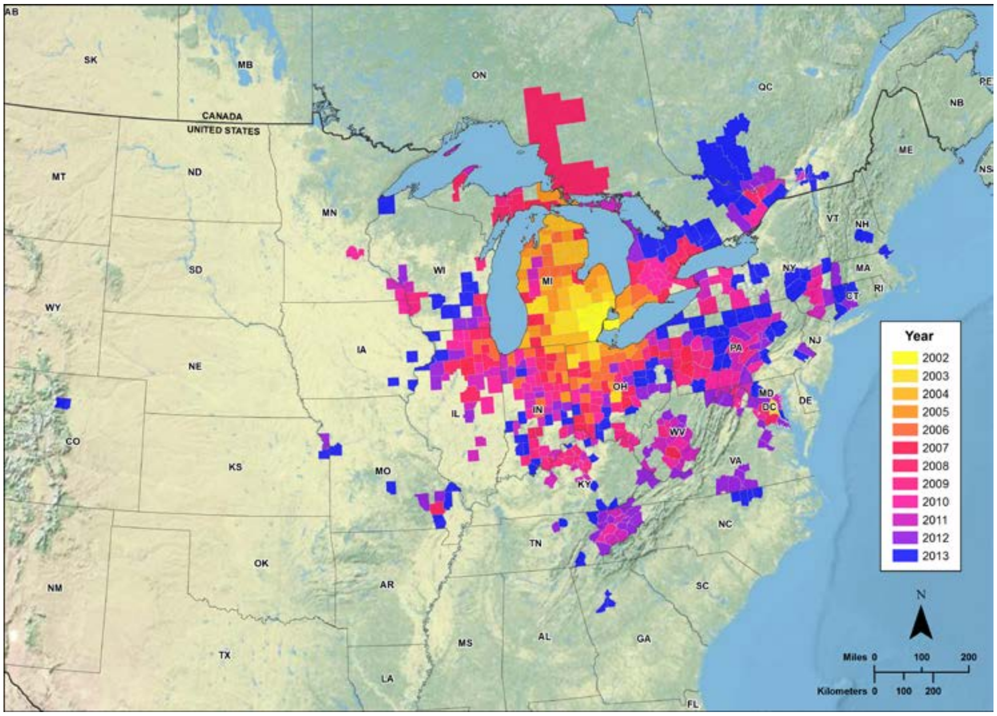


**Figure 14.** (top) Annual spread of EAB in North America from 2002 through 2013 as determined by year of first detection. Service layer credits: US National Park Service. Data sources: USDA Animal & Plant Health Inspection Service (APHIS), Canadian Food Inspection Agency (CFIA). Map developed by USDA Forest Service, Northeastern Area State and Private Forestry, Office of Knowledge Management (T. Luther 04/15/2014).

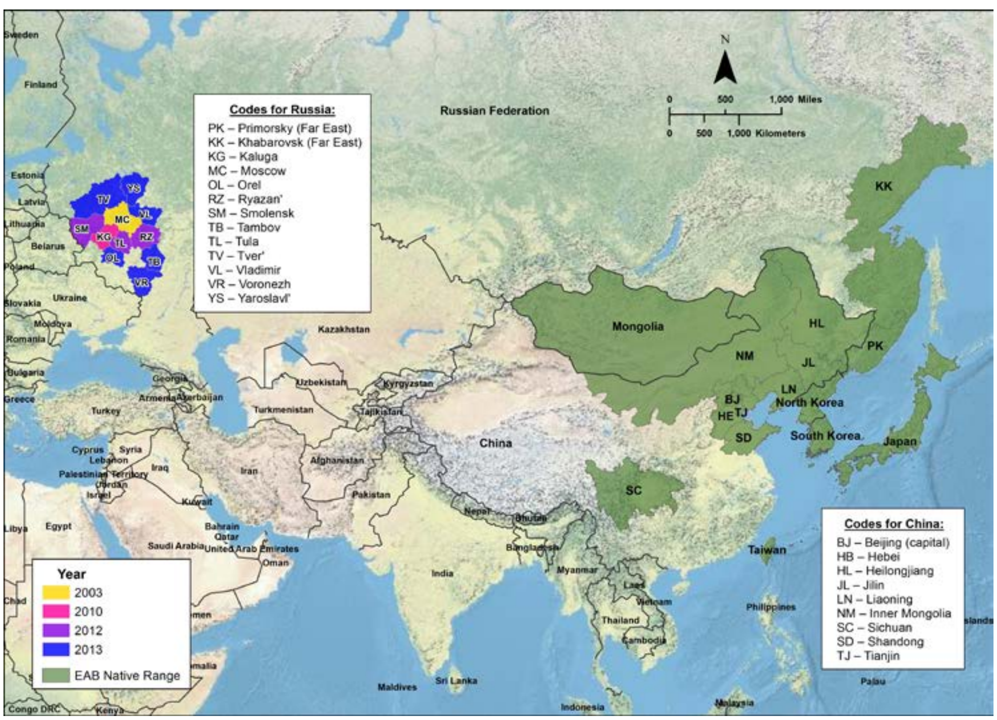


**Figure 15.** (bottom) Known range of EAB in Asia and introduced area of EAB in European Russia as of 2013. Service layer credits: US National Park Service. Data sources: https://sites.google.com/site/eduardjendek/world-distribution-of-agrilus-plannipennis_ and Baranchikov (2013). Map developed by USDA Forest Service, Northeastern Area State and Private Foresty, Office of Knowledge Management (T. Luther 04/15/2014).

(Yurchenko, 2010; Fig. 15).

Historically, EAB was a rare species in the Russian Far East, where it was associated exclusively with weakened and dying local native ash trees such as *F. mandshurica* and *F. chinensis*. Widespread tree mortality associated with EAB was first noticed in the Russian Far East in 2004, affecting introduced North American ash trees (*F. pennsylvanica*) that were growing along streets in Vladivostok (Yurchenko, 2010), many of which were rather mature trees with trunks measuring 20-40 cm in diameter. Subsequent detailed investigations of dead North American ash trees (*F. americana* and *F. pennsylvanica* ) in parks and arboreta in Khabarovsk demonstrated that these trees had been killed by EAB during the previous 5-10 years when the trees were 28-35 years old (Yurchenko, 2010).

In European Russia, beetles that were later to be identified as EAB were first collected on the streets of Moscow in June 2003 (Fig. 15; Volkovich, 2007). These beetles were positively identified as *A. planipennis* in 2005 by A. B. Alekseyev – the leading Russian expert on Buprestidae (Izhevskii and Mozolevskaya, 2010). It was soon recognized that EAB was responsible for the widespread ash dieback in Moscow (Baranchikov et al., 2008; Mozolevskaya et al., 2008). From 2006-2013, EAB spread outward from Moscow (Fig. 15). In 2006, 10 EAB adults were collected 30 km west of the Moscow Ring Highway (Volkovich, 2007), and by 2009, EAB-killed ash trees were found in many settlements of the Moscow Oblast region, with the most westward known infestation in Mozhaisk, about 100 km from Moscow (Baranchikov et al., 2010a). EAB was found in the Kaluga Region in 2010, and in the Smolensk and Ryazan Regions in 2012 (Baranchikov and Kurteyev, 2012; Baranchikov, 2013). Similarly, in 2013, EAB was first reported in the Orel, Tambov, Tula, Tver, Vladimir, Voronezh, and Yaroslavl Regions (Baranchikov, 2013, Orlova-Bienkovskaya, 2013). The current known range of EAB in European Russia is close to the borders of Belarus and Ukraine (Fig. 15).

Special EAB surveys were conducted during 2008-2009 on *F. pennsylvanica* in several cities throughout southern Siberia (Abakan, Krasnoyarsk, Novosibirsk, Tomsk, and Ulan-Ude) and the central Urals (Yekaterinburg). However, no additional EAB populations were found during these surveys (Baranchikov et al., 2010b).

## PATHWAYS OF EMERALD ASH BORER DISPERSAL

It is not known for certain how EAB reached North America or European Russia. In North America, wood packaging material such as pallets and crating from Asia is considered the most likely source (Haack et al., 2002, Cappaert et al., 2005, Haack, 2006). Recent genetic analyses by Bray et al. (2011) and Keever et al. (2013) found that North American EAB populations were most similar to Chinese populations, less so with Korean populations, and least similar to Japanese populations. As for European Russia, Izhevskii and Mozolevskaya (2010) suggested that EAB could have been introduced on ash nursery stock imported from North America or on wood packaging material from Asia. Genetic analyses may not help determine the source of the Moscow EAB population because molecular testing has shown high similarity among North American, Chinese, Far-East Russian, and Moscow EAB populations (EPPO 2013).

In North America and Europe, EAB can spread naturally through adult flight, which can expand the infested area by several kilometers each year (Taylor et al., 2010; EPPO, 2013). However, EAB dispersal over distances of 10s or 100s of kilometers most likely results from human movement of infested host material such as ash nursery stock, logs, and firewood (Cappaert et al., 2005; Haack, 2006; Poland and McCullough, 2006; Haack et al., 2010; Herms and McCullough, 2014). For example, a nursery in Michigan sold EAB-infested nursery stock to a Maryland nursery in 2003, which then sold some of the trees to individuals living in Maryland and Virginia before realizing the trees were infested (Muirhead et al., 2006). Similarly, a sawmill near Shipshewana, Indiana, which regularly purchased ash sawlogs from southern Michigan was apparently responsible for introducing EAB to the local area (Robertson and Andow, 2009). Firewood is believed to be a major pathway by which EAB has been introduced to many residential areas, vacation properties, and campgrounds (McCullough et al., 2003; Robertson and Andow, 2009; Haack et al., 2010). In addition, EAB adults have been documented to hitchhike on or inside vehicles, as well as on passengers, which may explain their high frequency of establishment along major highways, especially at rest areas and truck stops (Buck and Marshall, 2008). The means of long-distance EAB dispersal in European Russia is not clear given that movement of ash nursery stock, firewood, and logs is rare in Russia, and therefore hitchhiking by EAB adults on vehicles is considered the most likely explanation (Straw et al., 2013).

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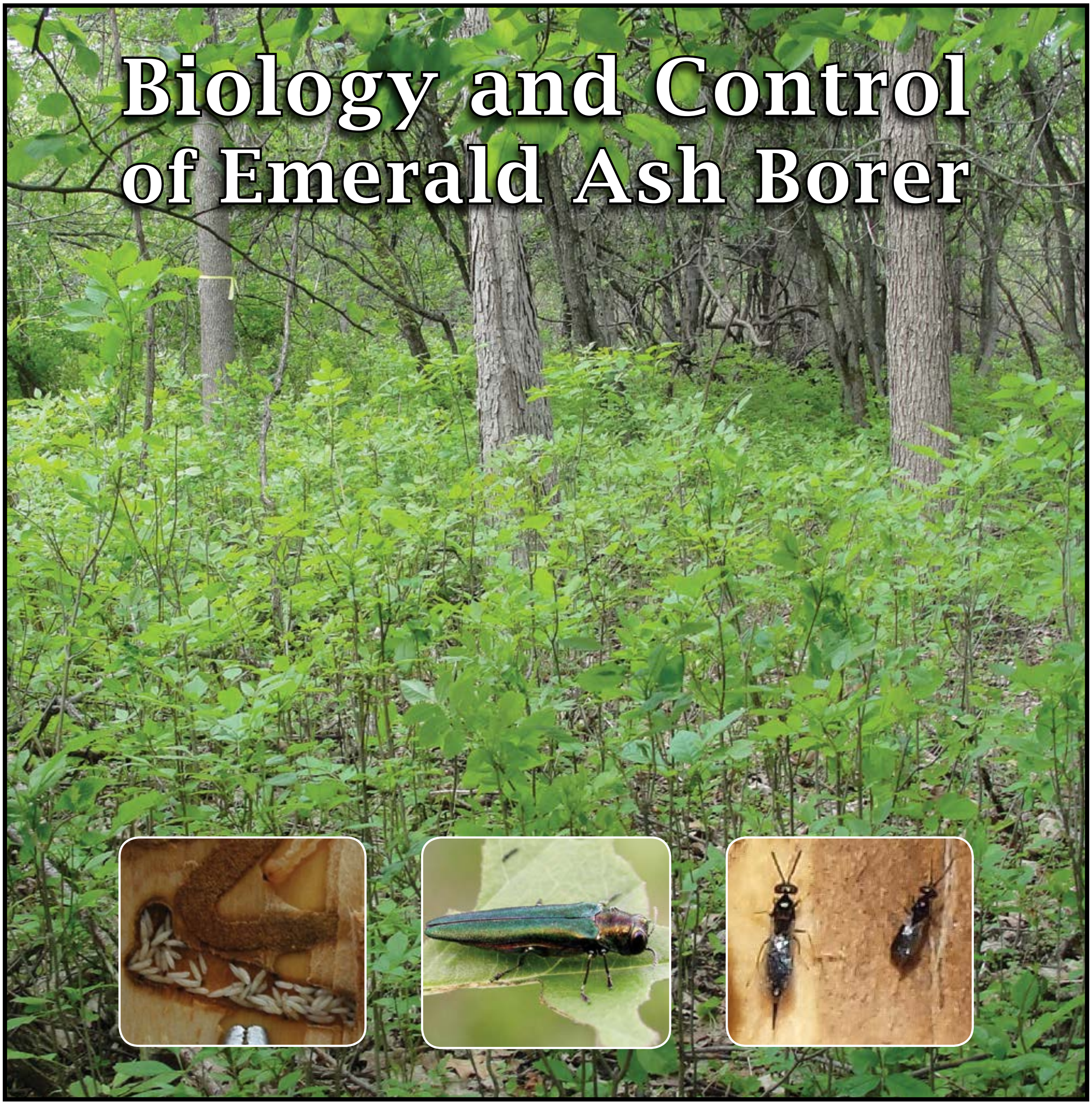
Technology Transfer

*Non-native Pest*

# Biology and Control of Emerald Ash Borer



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On the cover: Cover design by Sheryl Romero and Denise Binion, Forest Health Technology Enterprise Team. Background image: Understory green ash seedlings (*Fraxinus pennsylvanica*, Oleaceae) released after large ash trees were killed by emerald ash borer in Okemos, Michigan in 2014, photo by Leah S. Bauer; (bottom row, left to right) Fully mature *Tetrastrichus planipennisi* larvae break free of emerald ash borer larval skin and pupate in the larval gallery under the tree bark. (Photo credit: Clifford Sadof); EAB adult and typical leaf feeding damage. (Photo credit: Deborah Miller, USDA Forest Service, Bugwood.org); Emerging *Tetrastrichus plannipennisi* adults. (Photo credit Leah S. Bauer).

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