



The Ecology, Economics, and Management of *Agrilus* Beetles

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Abstract

Purpose of Review The invasion of North America by the Asian beetle *Agrilus planipennis* has caused severe economic and ecological damage to ash (*Fraxinus*) tree populations. *Agrilus planipennis* has recently entered eastern Europe and is spreading there. Many other *Agrilus* species can potentially become invasive pests due to the cryptic nature of their immature stages that can be inconspicuously transported within infested plant material. We review the ecology, economic impacts, and management strategies of *Agrilus* worldwide and highlight research gaps.

Recent Findings Much has been learned in recent decades about the basic biology and control tactics for a few *Agrilus* species, especially *A. planipennis*.

Summary The genus *Agrilus* has over 3,341 described species, making it the largest genus in the Animal Kingdom. Most *Agrilus* are univoltine and have a narrow host range. Chemical, tactile, and visual cues of host plants are used by adult *Agrilus* to select suitable hosts for consumption by adults and larvae. Most *Agrilus* larvae develop within the cambial region, constructing galleries that effectively girdle the host plant. Mechanisms of host plant resistance are being explored. Diverse groups of natural enemies attack all life stages of *Agrilus* species, with some coevolved specialist parasitoids being introduced successfully to suppress *A. planipennis* in North America. Climate change, leading to warmer and drier conditions, will influence the distribution and population dynamics of many *Agrilus* species. Many research gaps still exist in the areas of biocontrol, host plant resistance, and sustainable management strategies for this important group of plant pests.

Keywords Buprestidae · Invasive species · Woodborers · Natural enemies · Biological control · Integrated pest management

Introduction

Worldwide, the genus *Agrilus* (Coleoptera: Buprestidae) has over 3,341 described species, making it the largest genus in the Animal Kingdom [1]. Among these species, ~39% (1,292 species) occur in the Americas, 36% (1,189) in Asia, 23% in Africa (753), 4% in Oceania (135), and 2% in Europe (79) [1]. *Agrilus* are found in boreal, temperate, subtropical,

and tropical zones [1, 2]. New *Agrilus* species are being described annually, indicating their real diversity is even greater than currently realized [1, 3].

Almost all *Agrilus* develop in eudicot angiosperms [3, 4], with the one known exception being a species (*A. schwerdtfegeri*) reared from *Pinus* in Guatemala [5]. Most *Agrilus* larvae develop in a single plant genus or a few genera of the same plant family [3]. Although several *Agrilus* are pests that damage agricultural crops and forest trees, some are beneficial, such as *A. hyperici* (Fig. 1J), a biocontrol agent against the weed St. John's wort (*Hypericum perforatum*) [6].

The Asian species *A. planipennis* (emerald ash borer, EAB, Figs. 1A, 2A, E) has caused the most damage of any *Agrilus*, especially in North America, where it was first discovered in 2002 [7]. Since its discovery, EAB has spread to 36 USA states and five Canadian provinces, killing millions of North American ash (*Fraxinus*) trees in both managed and unmanaged forests [8]. EAB was likely introduced inadvertently from China to North America via infested wood

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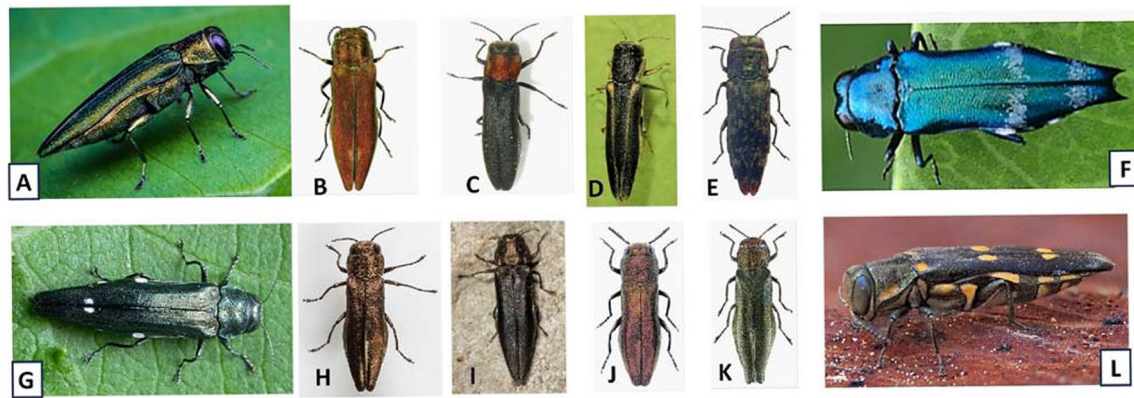


Fig. 1 Adults of several of the *Agrilus* species discussed in this paper. **A** *Agrilus planipennis* (Photo William Ravlin). **B** *A. sinuatus* (Gilles San Martin). **C** *A. ruficollis* (Chris Rorabaugh). **D** *A. bilineatus* (Robert Haack). **E** *A. occipitalis* (Eduard Jendek). **F** *A. acutus*

(Subash Jeyan). **G** *A. biguttatus* (Trevor and Dilys Pendleton). **H** *A. mali* (A. V. Kovalev). **I** *A. anxius* (Tom Murray). **J** *A. hyperici* (U. R. Schmidt). **K** *A. viridis* (U. R. Schmidt). **L** *A. auroguttatus* (Mike Lewis)

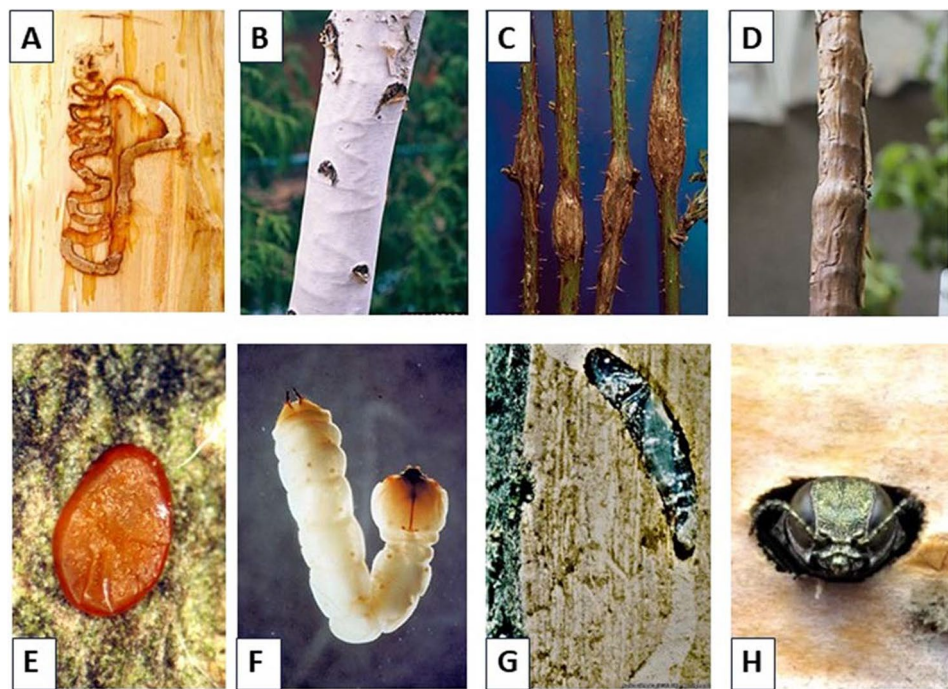


Fig. 2 **A** Typical meandering larval gallery of *A. planipennis* on sapwood surface of *Fraxinus* tree (JJD). **B** Trunk of *Betula* tree indicating callus formation of the sapwood surface along the larval galleries of *A. anxius* (Steven Katovich). **C** Gall formation on stems of *Rubus* plants at the site of infestation by *A. ruficollis* larvae (James Solomon). **D** Spiral larval gallery pattern of *A. cuprescens* along stem of a *Rubus* plant (Justin O'Dea). **E** Egg of *A. planipennis* on

bark of a *Fraxinus* tree. Eggs turn golden-brown with age (Houping Liu). **F** Typical shape of an *Agrilus* larva when removed from its fully completed pupal cell (Robert Haack). **G** Pupa of *A. bilineatus* that has nearly transformed to an adult within its pupal cell that was constructed in the thick outer bark (Robert Haack). **H** Typical D-shaped exit hole constructed by *Agrilus* adults as they emerge from their host plant (Deborah Miller)

packaging materials in the 1990s [9, 10]. Due to the severe damage caused by EAB, it has become the most studied *Agrilus* species in the world [11].

Many other *Agrilus* have caused notable economic and ecological damage, such as the bronze birch borer (*A. anxius*, Figs. 1I, 2B, H) on *Betula*, goldspotted oak borer (*A.*

auroguttatus, Fig. 1L) on *Quercus*, oak splendor beetle (*A. biguttatus*, Fig. 1G) on many tree species, twolined chestnut borer (*A. bilineatus*, Figs. 1D, 2F, G) on *Quercus*, rose stem girdler (*A. cuprescens*, Fig. 2D) on *Rosa* and *Rubus*, and apple jewel beetle (*A. mali*, Fig. 1H) on *Malus* (Table 1). The rising pest status of several *Agrilus* species worldwide has

Table 1 Global summary of prominent *Agrilus* pest species, including scientific and common names, as used in this paper, major native plant hosts, native and known invaded ranges of each *Agrilus* species, respective pest status and host plant genera most impacted, and references associated with the table information

Scientific name (common name, acronym used herein)	Major host plant genera	Native range of <i>Agrilus</i> species; pest status	Expanded range of <i>Agrilus</i> species; introduced pest status	References
<i>Agrilus acutus</i> (Spiral stem borer)	<i>Carica</i> , <i>Hibiscus</i>	Bangladesh, South India, Indonesia, Papua New Guinea, Sri Lanka; primarily pest of cultivated <i>Hibiscus</i> crops, but also <i>Abelmoschus</i> , <i>Corchorus</i> , <i>Malachra</i> and <i>Urena</i>	Andhra Pradesh (India); pest of cultivated <i>Hibiscus</i> crops	[1, 11–15]
<i>Agrilus anxius</i> (Bronze birch borer)	<i>Betula</i>	Eastern North America (USA and Canada); intermittently impactful outbreaks in forests on <i>Betula</i> , pest of introduced Eurasian <i>Betula</i>	Western USA; pest of introduced Eurasian <i>Betula</i>	[2, 16, 17]
<i>Agrilus auriventris</i> (Citrus flatheaded borer)	<i>Citrus</i>	China, Southeast Asia, Japan; pest of cultivated <i>Citrus</i> crops	Polynesia ^a ; pest of <i>Citrus</i> crops	[1, 18, 19]
<i>Agrilus auroguttatus</i> (Goldspotted oak borer)	<i>Quercus</i>	Arizona (USA), Northern Mexico; not known as a pest	California (USA), serious pest of multiple native <i>Quercus</i> tree species	[20–22]
<i>Agrilus biguttatus</i> (Oak splendor beetle)	<i>Fagus</i> , <i>Castanea</i> , <i>Quercus</i> , <i>Tilia</i> , <i>Populus</i> , <i>Ulmus</i>	Europe; intermittently impactful outbreaks in forests on <i>Quercus</i>	No range expansion reported	[23–25]
<i>Agrilus bilineatus</i> (Twolined chestnut borer)	<i>Castanea</i> , <i>Quercus</i>	Eastern North America (USA and Canada); intermittently impactful outbreaks in forests on <i>Quercus</i> , historical pest of <i>Castanea</i>	Established in Turkey, pest status is not known	[26–28]
<i>Agrilus cuprescens</i> (Rose stem girdler)	<i>Rubus</i> , <i>Rosa</i>	Eurasia; intermittently serious pest of cultivated <i>Rubus</i> and <i>Rosa</i> crops	North America (USA and Canada), intermittently serious pest of cultivated <i>Rubus</i> and <i>Rosa</i> crops	[1, 29–31]
<i>Agrilus fleischeri</i> (Spotted poplar borer)	<i>Populus</i> , <i>Salix</i>	East Asia; intermittent pest of native <i>Populus</i> trees, localized outbreaks on introduced <i>Populus</i> in China	No range expansion reported	[32–34]
<i>Agrilus mali</i> (Apple jewel beetle)	<i>Cydonia</i> , <i>Malus</i> , <i>Pyrus</i> , <i>Prunus</i> , <i>Emmenopterys</i>	Eastern Asia; intermittent pest of <i>Malus</i> and <i>Pyrus</i> in orchards	Northwest China, serious pest of native wild <i>Malus sieversii</i> trees	[2, 33, 35, 36]
<i>Agrilus occipitalis</i> (Citrus bark borer)	<i>Citrus</i>	Southeast Asia, Indonesia; pest of cultivated <i>Citrus</i> crops	Micronesia ^a , pest of cultivated <i>Citrus</i> crops	[1, 65]
<i>Agrilus planipennis</i> (Emerald ash borer, EAB)	<i>Fraxinus</i> , <i>Chionanthus</i>	Northeast Asia; intermittent pest of native <i>Fraxinus</i> trees, pest of introduced <i>Fraxinus</i>	North America (USA and Canada), significant pest of all <i>Fraxinus</i> trees	[37–40]
<i>Agrilus prionurus</i> (Soapberry borer)	<i>Chionanthus</i> , <i>Sapindus</i>	Northern Mexico; pest status unknown	Texas (USA), serious pest of western soapberry trees (<i>Sapindus saponaria</i> var. <i>drummondii</i>)	[2, 41]
<i>Agrilus pseudocoryli</i> (Hazel stem borer)	<i>Corylus</i>	North America (USA and Canada); emerging pest of cultivated hybrid <i>Corylus americana</i> x <i>Corylus avellana</i>	No range expansion reported	[42]

Table 1 (continued)

Scientific name (common name, acronym used herein)	Major host plant genera	Native range of <i>Agrilus</i> species; pest status	Expanded range of <i>Agrilus</i> species; introduced pest status	References
<i>Agrilus ribesi</i> (Currant borer)	<i>Ribes</i>	Europe; West-central Asia; pest of cultivated <i>Ribes</i> crops	North America (USA and Canada); pest of cultivated <i>Ribes</i> crops, damage attributed to <i>A. cuprescens</i> until 2015	[43]
<i>Agrilus ruficollis</i> (Red-necked cane borer)	<i>Rubus</i>	Eastern North America; intermittently serious pest of cultivated <i>Rubus</i> crops	Introduced to New Zealand as biocontrol for feral <i>Rubus</i> , but did not establish	[44–47]
<i>Agrilus sexsignatus</i> (Varicose borer)	<i>Eucalyptus</i>	Indonesia, Philippines, Melanesia; pest of cultivated <i>Eucalyptus</i> crops	No range expansion reported	[48, 49]
<i>Agrilus sinuatus</i> (Sinuate pear borer)	<i>Crataegus</i> , <i>Pyrus</i> , <i>Malus</i> , <i>Mespilus</i> , <i>Prunus</i> , <i>Sorbus</i>	Southern and Central Europe; primarily intermittent pest of <i>Pyrus</i>	Northern Europe, UK, North America, Japan; regional intermittent pest of <i>Pyrus</i>	[50, 51]
<i>Agrilus viridis</i> (Beech splendour beetle)	15 genera, see Jendek and Polakova 2014	Eurasia; intermittent pest of cultivated <i>Corylus</i>	No range expansion reported	[3, 52]
<i>Agrilus zanthoxylumi</i>	<i>Zanthoxylum</i>	Southern-Central China; pest of cultivated <i>Zanthoxylum</i> crops	Shandong province (China) pest of cultivated <i>Zanthoxylum</i> crops	[53]

^aSuspected introduction via infested *Citrus* nursery crop plant material

raised concerns about their potential damage to both forests and agricultural crops worldwide, particularly if introduced outside their native ranges.

Previous reviews on *Agrilus* beetles have examined their morphology and general biology [54], larval host plants [3], and native geographic distribution [1]. Specific reviews of individual pest species addressed *A. anxius* [16], *A. cuprescens* [29], and EAB [55, 56]. The aim of the current review is to examine both historical and recent literature on the ecology, economic significance, and management strategies for all *Agrilus* and highlight research needs to help develop sustainable management strategies. In many cases, we will focus on recent EAB research, given that it has been the focus of many studies in Asia, Europe, and North America [11, 56].

Ecology

Agrilus Biology and Life History

Volitinism In temperate latitudes, most *Agrilus* are univoltine [57–59]. At times, two years is required to complete one generation, especially in cooler climates, when developing in vigorous hosts, or when developing from eggs laid in late summer [20, 23, 60, 61]. However, some *Agrilus* in temperate areas are typically semivoltine, such as *A. guerini*, *A. horni*, *A. pensus*, and *A. torquatus* [57–59, 62]. Multivoltinism may occur in some subtropical and tropical species (e.g., *A. acutus* Fig. 1F, *A. occipitalis* Fig. 1E, and *A. viridissimus*), given that generation times of only 2–4 months have been reported [63–65].

Adult Emergence, Seasonality, Diurnal Activity, and Food As *Agrilus* adults emerge from their host, they chew a characteristic D-shaped exit hole [58, 66] Fig. 2H]. Adults can fly several kilometers [67], but likely disperse short distances when suitable host plants are nearby [10]. In temperate latitudes, *Agrilus* adults are active throughout the summer months, starting in late spring, peaking in early to mid-summer, and ending in late summer. For species with a broad geographic range, emergence can begin 1–2 months earlier in warmer regions compared to cooler regions [58, 59]. The sex ratio of most *Agrilus* is 1:1 [18, 32, 68–70]; however, more female-biased sex ratios have been reported [48, 71].

Agrilus adults are most active from late morning through the afternoon and prefer sun-exposed hosts [31, 72]. Adults typically feed for 1–2 weeks before mating and laying eggs [20, 31, 32, 44, 57, 66, 73–75], although some may require 3–4 weeks to become sexually mature [58]. Adults usually consume foliage of the larval host plant but can feed on other plants [73, 76]. *Agrilus* adults usually live 2–5 weeks [31,

32, 44, 60, 66, 68, 69, 73, 74, 77, 78], but some can survive as long as 10–11 weeks [20, 79].

Mating, Oviposition, Fecundity, Eggs Adults typically mate on the trunk, branches, or foliage of the larval host plant. Mating is common during late morning and afternoon, with oviposition peaking in early afternoon [57, 80]. On woody hosts, females can lay eggs on smooth bark but often deposit eggs within bark cracks or under bark flakes [20, 28, 32, 57, 58, 77, 81, 82]. Some *Agrilus* lay eggs singly [Fig. 2E], especially on small diameter hosts [29, 31, 58, 63, 82, 83], or in small clusters [58, 62, 80]. Clusters with up to 28 eggs have been documented in *A. macer* [84] and 30 eggs in *A. biguttatus* [23]. Females often deposit a semi-transparent substance over the eggs, which cements the eggs to the bark and slows desiccation [74, 77, 84].

Eggs usually hatch in 1–2 weeks, but 3–4 weeks has been reported [31, 32, 44, 58]. Total fecundity is difficult to determine in nature. However, under favorable laboratory conditions mean lifetime fecundity was 23–110 eggs per female for various *Agrilus* [85–89], with as many as 614 eggs laid by a single *A. fleischeri* [32].

Larval Development *Agrilus* larvae enter the host through the side of the egg in contact with the host tissue. In woody plants, larvae tunnel through the outer bark to the cambial region and construct galleries that score both the inner bark (phloem) and outer sapwood (xylem) (Fig. 2A). *Agrilus* larvae use their terminal processes (urogomphi) to pack their frass behind them as they feed [54, 57 Fig. 2A, F]. Most larvae construct individual galleries [58], however, *A. macer* larvae feed gregariously [84]. *Agrilus* larvae have four [54, 68, 82, 90, 91] or five instars [23, 57, 63, 74, 92–94].

In woody plants, *Agrilus* larvae often depart the cambial region and enter the sapwood to molt or in response to high host resistance such as rapid callus formation [57, 7895 Fig. 2B–D]. With *Agrilus* of shrub hosts such as *A. cuprescens*, the larva will leave the cambium and tunnel into stem's pith by autumn [31]. In some root (*A. horni* and *A. vittaticollis*) and branch-infesting (*A. mali*) species, larvae initially tunnel in the cambial region and then in the xylem [57, 77, 79, 94].

The linear length of *Agrilus* larval galleries is often under 1 m, but some galleries have measured 1.5–2 m in length [23, 48, 77, 79]. Host conditions can influence the shape of a larval gallery, being longer and more sinuate in high-vigor hosts versus shorter and straighter in low-vigor hosts [57, 60, 74, 95].

Overwintering Most temperate *Agrilus* species overwinter as last-instar larvae in pupal cells constructed in the sapwood, outer bark, pith, or roots [20, 31588283 Fig. 2G]. If larvae of some species fail to reach their final instars

(mostly J-shaped larvae, Fig. 2F) before winter, they typically overwinter in the cambial region and resume feeding the following spring, and then pass a second winter before pupating and transforming to adults. However, in China, *A. mali* overwinters as early larval instars and then completes development and emerges as adults the following summer [94]. Some *Agrilus*, such as *A. subcinctus*, which develops in recently dead ash twigs, overwinter as pupae [82].

As larvae construct their pupal cells, they often extend their gallery to near the outer bark surface, and then use this same path later when they emerge as adults [77, 7928 Fig. 2G]. If bark is sufficiently thick, pupal cells are usually constructed in the outer bark, or in the sapwood if the bark is too thin [20, 23, 71]. On small diameter branches and stems, pupal cells are usually in the xylem or pith [29, 82].

Pupation Pupation usually occurs in late spring and early summer in temperate areas. Pupation typically takes 1–4 weeks [23, 28, 31, 32, 44, 58, 66, 77]. Newly formed adults remain in the pupal cell for a few days to a week before they chew out of the host [68].

Insect-Plant Interactions

Host Plant Selection by Adults Upon emergence, *Agrilus* adults must feed, find mates, and select host plants suitable for oviposition. These tasks are facilitated by chemical, physical or tactile, and visual stimuli associated with host plants and conspecifics [96–103]. Understanding how these environmental stimuli influence *Agrilus* behavior can lead to novel management strategies.

At longer distances, when adults are in flight, host plant selection is likely driven by plant-produced volatile compounds that are often particular to a plant species or host condition [104, 105]. For *Agrilus* considered to be secondary pests, volatiles associated with stressed plants, such as alcohols and green-leaf volatiles from foliage or sesquiterpenes from bark, often elicit strong antennal responses [106, 107] and are attractive to *Agrilus* adults [68, 102, 108–110]. Evidence from EAB suggests that newly emerged females only respond to foliage volatiles until they complete maturation-feeding, after which they shift to volatiles associated with oviposition locations [102, 111]. This behavioral sequence may reflect a general pattern within the *Agrilus*, where their response to host cues is regulated by internal physiological changes [111].

At short distances, when the adults are near or have landed on a potential host plant, visual cues associated with the color and shape of the host plant influence adult behavior. For example, studies using traps of various colors found that more adults of EAB, *A. egeniformis*, *A. egenus* and *A. subcinctus* were captured on green or yellow traps

compared with purple or white traps [112–114]. Green or yellow color has the spectrum of reflective light (540–560 nm) corresponding to the reflectance of host foliage as well as the spectral sensitivity of many *Agrilus* [112, 113]. The strong response to green is found in many *Agrilus* adults that feed on foliage or use foliage as a cue to locate oviposition locations [115]. For *Agrilus* adults that feed on flowers or pollen, traps colored with floral colors such as blue, yellow, and white often are attractive [116–118]. Altogether, these findings should be considered carefully because relatively few of the world's 3,341 *Agrilus* species have been evaluated, and some studies have indicated differences in response by males and females of the same species [112–114].

The shape of a plant, as well as the light spectra reflected from different plant tissues, may also play a role in host location. For example, EAB adults can distinguish between a live and an artificial host plant when in view, but not when hidden from view and required to use only host-associated volatiles [119]. Further, EAB can differentiate between leaves of different sizes, preferring larger leaves for consumption [119].

After landing on a potential host, adult *Agrilus* must assess host plant suitability for their own consumption as well as for oviposition or larval development. It is presumed that volatiles from the entire host plant, or the portion they consume, are correlated with a plant's suitability as a food source. In laboratory studies, EAB adults showed differences in consumption of foliage between coevolved and non-coevolved hosts [120], as well as between different species of non-coevolved hosts [121]. These findings may be related to variation in nutrients and defensive compounds in plant tissues [102, 122, 123], and thereby can influence consumption and adult fitness [123]. Within a host plant, these same factors, as well as moisture content can influence *Agrilus* larval feeding [123, 124].

Female *Agrilus* likely use multiple cues to find suitable oviposition sites. Specific cues that stimulate or discourage *Agrilus* oviposition are poorly known. Studies with other wood- and stem-boring insects indicate that short-range, chemical cues can reflect host tissue condition, presence and quantity of conspecifics and competitors, and frass from current or previous occupants [125]. In addition, vibrational cues may correspond to differences in density or structure of plant tissues, as well as chewing by both feeding conspecifics or competitors [126, 127]. Lastly, tactile cues such as the amount of resistance detected by female's ovipositor could predict the degree of protection their offspring would have from natural enemies, or whether a neonate larva is likely to bore into its preferred plant tissue [128]. A deeper understanding of these cues may allow for improved methods to monitor and manage *Agrilus* pests [103].

Larva-Plant Interactions *Agrilus* larvae have an intimate relationship with their host plants given that larvae develop over 1–2 years in the meristematic cambial region of their host (Fig. 2A–D). Therefore, the physiological condition of the host often has a strong influence on survival and fitness of *Agrilus* larvae (see Host Plant Resistance).

Agrilus utilize many plants as larval hosts, including herbaceous perennials, vines, shrubs, and trees. In a review of all known larval hosts for the world's *Agrilus* [3], host records were only found for 686 *Agrilus* species (22%), with the most complete records being for the Nearctic and Palearctic *Agrilus*. The top 10 genera of host plants worldwide are *Acacia* (used by 133 *Agrilus* species), *Quercus* (98), *Celtis* (46), *Salix* (35), *Prosopis* (24), *Populus* (22), *Albizia* (21), *Ulmus* (21), *Carpinus* (17), and *Juglans* (17). About 50% of *Agrilus* use a single plant species as a larval host, 64% use a single plant genus, and 75% use a single plant family. However, some *Agrilus* have a large host range, including *A. viridis* (Fig. 1K) reared from 49 plant species, *A. roscidus* from 23 plant genera, and *A. roscidus* from 10 plant families [3].

Multiple *Agrilus* species can infest the same host plant concurrently in some woody plants [24, 129, 130]. In these situations, smaller species tend to colonize the crown branches, while larger species favor the trunk. For *Agrilus* species that infest both the branches and trunk of a tree, infestation usually begins in the branches and upper trunk and then proceeds downward along the trunk in subsequent years, with tree death occurring in 2–4 years [24, 61, 68, 74, 78]. In contrast, root-feeding *Agrilus* oviposit along the lower trunk or stem, near groundline [58, 77]. Shrub-infesting *Agrilus* such as *A. cuprescens* and *A. ruficollis* (rednecked cane borer, Figs. 1C, 2C) commonly oviposit near the base of a stem on younger stems, but further up on older stems which may have multiple infestation points; *A. ruficollis* has also been observed to uniquely prefer ovipositing near leaf axils [29].

Factors Affecting *Agrilus* Population Dynamics and Outbreaks

Both biotic and abiotic factors can affect *Agrilus* population dynamics. Outbreaks of many *Agrilus* pests in both their native and invaded ranges are often associated with variation (or lack thereof) in host plant conditions (i.e., susceptibility or resistance), natural enemies, and climatic factors.

Host Plant Resistance Most *Agrilus* that attack live plants prefer plants that are weakened or stressed. Vigorous hosts can kill young larvae by flooding larval galleries with plant exudates or overgrowing the larvae with callus tissue [57, 95]. However, in situations where an *Agrilus* species

encounters a naïve host plant, i.e., where the plant and insect did not coevolve, the naïve host may lack resistance mechanisms, which can favor successful infestation of apparently healthy plants.

An encounter with a naïve host can occur when a host plant is moved to a new continent such as when Asian and European *Betula* are planted in North America and then infested by native *A. anxius* [16, 131] or when North American *Fraxinus* were planted in China and infested by native EAB [37, 132]. A similar situation can occur when an *Agrilus* species is moved to a new continent such as when EAB was introduced to North America [133]. At times, both the plant and insect can be moved, such as when North American *Fraxinus* that were planted in European Russia and Ukraine were infested by EAB after its introduction there from Asia [134], or *A. cuprescens* introduction to North America in infested *Rosa* nursery stock (14). These novel encounters can also occur in the same country, such as when the *Quercus*-infesting *A. auroguttatus* was moved from Arizona to California, USA [20], or when the *Malus*-infesting *A. mali* was moved from eastern to western China [35].

Outbreaks of several *Agrilus* species often follow successive years of drought or defoliation [16, 19, 23, 60, 80, 116, 135–139]. By contrast, some root-infesting *Agrilus* prefer vigorous host plants [6, 57]. Some *Agrilus* pests such as *A. auriventris* (citrus flatheaded borer) have been noted to prefer older plants [19], while others such as *A. sinuatus* (sinuate pear borer, Fig. 1B) or *A. cuprescens* will readily attack young plants or young stems [29, 138]. It is not known if or to what degree stress events are associated with recent outbreaks of several *Agrilus* species that have been introduced to other regions, such as *A. cuprescens* [29] and *A. auroguttatus* in North America [21, 140], and *A. mali* and *A. fleischeri* in China [32, 33, 35, 141].

With the arrival of EAB in North America, several field studies have explored host plant resistance in Asian and North American *Fraxinus* species. Asian species such as *F. chinensis*, *F. mandschurica* and *F. rhynchophylla* are the coevolved hosts and thus more resistant than North American *Fraxinus* to EAB [37, 133, 142, 143]. However, among the non-coevolved North American *Fraxinus* species, some species such as *F. americana*, *F. nigra*, and *F. pennsylvanica* are more often killed by EAB than others such as *F. quadrangulata* [144]. More recently, certain surviving *F. pennsylvanica* trees (often termed as “lingering ash”) have shown the genetic capacity to tailor their response to EAB infestation by killing enough EAB larvae to prevent lethal damage to their vascular tissues [145]. Tree resistance to EAB likely involves multiple mechanisms, including higher constitutive and inductive concentrations of bark lignans, coumarins, proline, tyramine, defensive proteins, secoiridoids, and other phenolic compounds that reduce adult feeding and oviposition, as well as larval feeding and survivorship [146–149].

Although host resistance has been well studied in EAB, similar advances are lacking for nearly all other *Agrilus* species.

Natural Enemies There are diverse groups of natural enemies that attack all life stages of *Agrilus* species, primarily parasitoids, but also avian predators, and pathogens. As of this review, approximately 15 species of hymenopteran parasitoids are known to attack *Agrilus* eggs, and at least 51 hymenopteran (36 genera) and 3 coleopteran (3 genera) species attack *Agrilus* larvae in Asia, Europe, and North America (Table 2). Most egg parasitoids are Encyrtidae, while the larval parasitoids are members of seven hymenopteran families: Braconidae, Ichneumonidae, Eulophidae, Eupelmidae, Eurytomidae, Bethyridae and Chalcididae. The rate of parasitism varies with the species of *Agrilus* and parasitoid, as well as the geographic area where parasitism occurs (Table 2). The highest rates of *Agrilus* egg parasitism (ca. 50%) were by encyrtid wasps (4 species) in North America, Asia, and Europe. In contrast, the highest rates of *Agrilus* larval parasitism (> 50%) were caused by species of two braconid genera (*Atanycolus* in North America; [150, 151] and *Spathius* in Asia [152, 153], North America [154], and Europe [155], and two eulophid genera: *Tetrastichus* and *Baryscapus* in Eurasia [142, 156–158] and in North America [159, 160]. *Agrilus* larval parasitism by ichneumonids was frequently reported in North America and Asia, but generally at low rates (< 10%).

The primary predators of tree-infesting *Agrilus* are woodpeckers (Picidae), which often feed on the overwintering larval stages, causing up to 60% larval mortality [151, 154]. More recently, pathogenic fungi and microsporidian species were also isolated from several pest *Agrilus* adults, including *A. anxius*, *A. cuprescens*, and EAB [188–190].

Climate Change *Agrilus* populations dynamics will be directly and indirectly affected by climate change and these effects can be positive or negative depending on the climate event, host plant species impacted, and world region affected. Warming climates will speed *Agrilus* development times, especially at the cooler extremes of their range, allowing a higher proportion of the population to be univoltine rather than semivoltine [191–193]. For northern temperate *Agrilus* species, populations may expand northward with a warming climate if suitable hosts are present [192, 193]. By contrast, near the southern edge of an *Agrilus* species’ range, populations may recede northward if winter temperatures do not provide sufficient cold periods needed to complete obligatory diapause [29, 191, 194]. Increased occurrences of severe polar vortices could increase winter mortality of some *Agrilus* [191, 195], while extreme heat events could negatively impact development rates [196].

Table 2 Parasitoids associated with *Agrilus* species (adapted from and updated since Taylor et al. 2012). x = level of parasitism undetermined/ not found in the literature

Parasitoid guild	Order: Family	Species	<i>Agrilus</i> host/Host's food plants (genus)	Regions where parasitism was reported	Levels of parasitism reported	References
Egg parasitoids	Hym: Aphelinidae	<i>Ablerus</i> sp.	<i>A. anxius</i> / <i>Betula</i>	USA, Canada	< 0.2%	[90]
	Hym: Encyrtidae	<i>Oobius</i> (= <i>Avetianella</i>) sp.	<i>A. anxius</i> / <i>Betula</i>	USA, Canada	< 3.5%	[90]
		<i>Coccidencyrtus</i> sp.	<i>A. liragus</i> / <i>Populus</i>	USA, Canada	~ 55%	[80]
		<i>Ooencyrtus erionotae</i>	<i>A. sexsignatus</i> / <i>Eucalyptus</i>	Philippines	32–57%	[161]
		<i>Ooencyrtus</i> sp.	<i>A. anxius</i> / <i>Betula</i>	USA, Canada	< 2.4%	[90]
		<i>Oobius agrili</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	China	> 50%	[162, 163]
		<i>Oobius zhaikevitshi</i>	<i>A. viridis</i> / <i>Corylus</i>	Italy	8–58%	[164]
		<i>Oobius minusculus</i>	<i>A. subcinctus</i> / <i>Fraxinus</i>	USA	8.6–9.4%	[82, 164]
			<i>A. egenus</i> / <i>Robinia</i>			
		<i>Oobius whiteorum</i>	<i>A. anxius</i> / <i>Betula</i>	USA	x	[164]
		<i>Oobius primorskyensis</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	Russian Far East	23–44%	[165, 166]
		<i>Oobius saimaensis</i>	<i>A. fleischeri</i> / <i>Populus</i>	China	6–48%	[32, 167]
		<i>Oobius fleischeri</i>	<i>A. fleischeri</i> / <i>Populus</i>	China	6–48%	[32, 167]
		<i>Orianos brazai</i>	<i>A. sexsignatus</i> / <i>Eucalyptus</i>	Philippines	x	[168]
		Signichorini tribe	<i>A. anxius</i> / <i>Betula</i>	USA, Canada	< 1%	[90]
	Hym: Signiphoridae	<i>Thysanus</i> sp.	<i>A. liragus</i> / <i>Populus</i>	USA, Canada	~ 12%	[74]
Larval parasitoids	Hym: Braconidae	<i>Atanycolus charus</i>	<i>A. anxius</i> / <i>Betula</i> <i>A. liragus</i> / <i>Populus</i>	USA, Canada	0.3–52%	[74, 80]
		<i>Atanycolus cappaerti</i>	<i>A. planipennis</i> / <i>Fraxinus</i> <i>A. liragus</i> / <i>Populus</i> <i>A. bilineatus</i> / <i>Castanea</i> , <i>Quercus</i> <i>A. sulcicollis</i> / <i>Quercus</i>	USA, Canada	9–71%	[71, 150]
		<i>Atanycolus simplex</i>	<i>A. liragus</i> / <i>Populus</i> <i>A. bilineatus</i> / <i>Castanea</i> , <i>Quercus</i>	USA, Canada	< 1%	[74, 169]
		<i>Atanycolus hicorie</i>	<i>A. planipennis</i> / <i>Fraxinus</i> ; other native <i>Agrilus</i> wood borers	USA, Canada	< 2%	[170, 171]
		<i>Atanycolus tranquebariae</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	USA	< 1%	[172]
		<i>Atanycolus disputabilis</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	USA	< 1%	[172]
		<i>Atanycolus nigropopyga</i> (= <i>A. disputabilis</i>)	<i>A. planipennis</i> / <i>Fraxinus</i> ; other native <i>Agrilus</i> wood borers	USA	< 3%	[173]
		<i>Atanycolus nigriventris</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	Russian Far East	< 50%	[167]
		<i>Atanycolus ivanowi</i>	<i>A. mali</i> / <i>Malus</i>	China	~ 27%	[174]
		<i>Bracon</i> sp.	<i>A. ruficollis</i> / <i>Rubus</i>	USA	5%	[58, 175]
		<i>Microbracon xanthostigmus</i>	<i>A. ruficollis</i> / <i>Rubus</i>	USA	x	[47, 58]
		<i>Doryctes farthus</i>	<i>A. anxius</i> / <i>Betula</i> <i>A. liragus</i> / <i>Populus</i>	USA, Canada	< 0.1%	[169]
		<i>Doryctes rufipes</i>	<i>A. anxius</i> / <i>Betula</i> <i>A. liragus</i> / <i>Populus</i>	Northeastern US/Canada	< 0.1%	[169]
		<i>Doryctes atripes</i>	<i>A. anxius</i> / <i>Betula</i>	Northeastern US/Canada	< 0.1%	[169]
		<i>Doryctes undulatus</i>	<i>A. mali</i> / <i>Malus</i>	China, Xinjiang province	x	[174]

Table 2 (continued)

Parasitoid guild	Order: Family	Species	<i>Agrilus</i> host/Host's food plants (genus)	Regions where parasitism was reported	Levels of parasitism reported	References
		<i>Ecphyllus</i> sp.	<i>A. subcinctus</i> / <i>Fraxinus</i>	USA	x	[82]
		<i>Heterospilus</i> sp.	<i>A. subcinctus</i> / <i>Fraxinus</i>	USA	x	[49]
		<i>Iphiaulaz impostor</i>	<i>A. biguttatus</i> / <i>Populus</i>	Europe	~ 13%	[176]
		<i>Leluthia astigma</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	USA	~ 2.1%	[71, 177–179]
			<i>A. difficilis</i> / <i>Gleditsia</i> ; <i>A. bilineatus</i> / <i>Quercus</i> <i>A. sulcicollis</i> / <i>Quercus</i> <i>A. cuprescens</i> / <i>Rosa</i> & <i>Rubus</i> Other <i>Agrilus</i> sp.			
		<i>Spathius</i> sp.	<i>A. auriventris</i> / <i>Citrus</i>	Japan, China	7%	[20, 180]
		<i>Spathius agrili</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	Northern China	60—90%	[181]
		<i>Spathius galinae</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	Vladivostok, Russia	~ 64%	[172, 182]
		<i>Spathius curvicaudis</i>	<i>A. biguttatus</i> / <i>Quercus</i>	Europe	~ 25%	[176, 183]
		<i>Spathius floridanus</i>	<i>A. planipennis</i> / <i>Fraxinus</i> ; other North American native wood-borers	USA	< 0.5%	[173]
		<i>Spathius laflammei</i>	<i>A. planipennis</i> / <i>Fraxinus</i> ; other North American native wood-borers	USA	< 1%	[173]
		<i>Spathius similimus</i>	<i>A. anxius</i> / <i>Betula</i> <i>A. liragus</i> / <i>Populus</i> <i>A. planipennis</i> / <i>Fraxinus</i> <i>A. bilineatus</i> / <i>Quercus</i> <i>A. sulcicollis</i> / <i>Quercus</i>	USA, Canada	< 0.5%	[71, 171]
		<i>Spathius polonicus</i>	<i>A. planipennis</i> / <i>Fraxinus</i> ; other European native wood borers	Russia/Europe	~ 50%	[155]
		<i>Spathius sinicus</i>	<i>A. mali</i> / <i>Malus</i>	China	x	[174]
		<i>Spathius brevicaudis</i>	<i>A. mali</i> / <i>Malus</i>	China	x	[174]
		<i>Polystenus rugosus</i>	<i>A. mali</i> / <i>Malus</i> <i>A. flecheri</i> / <i>Populus</i>	China/Europe	< 1%	[32, 174]
		<i>Paramblynotus</i> sp	<i>A. flecheri</i> / <i>Populus</i>	Northeast China	~ 52%	[32]
		<i>Pareucorystes varinervis</i>	<i>A. mali</i> / <i>Malus</i>	China/Europe	x	[174]
		<i>Wroughtonia</i> (<i>Helconidea</i>) <i>ligator</i>	<i>A. planipennis</i> / <i>Fraxinus</i> <i>A. liragus</i> / <i>Populus</i> <i>A. bilineatus</i> / <i>Castanea</i> , <i>Quercus</i>	Northeastern US/Canada	< 1%	[74, 169]
	Hym: Bethyridae	<i>Sclerodermus pupariae</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	Northern China	~ 13%	[153]
	Hym: Chalcididae	<i>Phasgonophora sulcata</i>	<i>A. anxius</i> / <i>Betula</i> <i>A. liragus</i> / <i>Populus</i> <i>A. bilineatus</i> / <i>Quercus</i> <i>A. planipennis</i> / <i>Fraxinus</i>	US/Canada	< 20%	[67, 80, 90, 184]
	Hym: Cleonimidae	<i>Cleonimus magnificus</i>	<i>A. cuprescens</i> / <i>Rosa</i> & <i>Rubus</i> <i>A. ruficollis</i> / <i>Rubus</i>	North America (US)	14%	[58, 175, 179]

Table 2 (continued)

Parasitoid guild	Order: Family	Species	<i>Agrilus</i> host/Host's food plants (genus)	Regions where parasitism was reported	Levels of parasitism reported	References
		<i>Tetrastichus</i> nr. <i>rugglesi</i>	<i>A. anxius</i> /Betula; <i>A. planipennis</i> /Fraxinus	US/Canada	< 0.1%	[74, 80]
	Hym: Eulophidae	<i>Baryscapus</i> nr. <i>endemus</i>	<i>A. cuprescens</i> /Rubus & Rosa	Europe	58% ^b	[157]
		<i>Tetrastichus agrili</i>	<i>A. sinuatus</i> /Pyrus	North America (US)	< 49% ^b	[179]
			<i>A. cuprescens</i> /Rosa			
		<i>Tetrastichus heeringi</i>	<i>A. sinuatus</i> /Pyrus	Europe	43—93%	[51, 157, 158]
			<i>A. cuprescens</i> /Rosa & Rubus			
			<i>A. ribesi</i> /Ribes			
		<i>Tetrastichus</i> sp.	<i>A. sexignatus</i> /Eucalyptus	Philippines	2—50%	[161]
		<i>Tetrastichus planipennisi</i>	<i>A. planipennis</i> /Fraxinus	China, Russian Far East	22—40%	[142]
		<i>Baryscapus</i> (<i>Tetrastichus</i>) <i>rugglesi</i>	<i>A. arcuatus</i> /Quercus	USA, Canada	≥ 9%	[44, 80, 160]
			<i>A. champlaini</i> /Ostrya			
			<i>A. cuprescens</i> /Rubus & Rosa			
			<i>A. ruficollis</i> ^a			
			<i>A. liragus</i> /Populus ^a			
		nr. <i>Hadrotrichodes</i>	<i>A. subcinctus</i>	USA	x	[82]
	Hym: Eupelmidae	<i>Balcha indica</i>	<i>A. planipennis</i> /Fraxinus	USA, Asia	< 4%	[71, 185]
			<i>A. sulcicollis</i> /Quercus; other Asian and North American woodborers			
		<i>Eupelmus pini</i>	<i>A. planipennis</i> /Fraxinus	USA	< 0.2%	[186]
	Hym: Metapelmatidae	<i>Metapelma</i> sp.	<i>A. planipennis</i> /Fraxinus	China	< 4%	[185]
	Hym:	<i>Metapelma</i> sp.	<i>A. subcinctus</i> /Fraxinus	USA	x	[82]
		<i>Metapelma schwarzi</i>	<i>A. cuprescens</i> /Rosa & Rubus	USA	x	[179]
		<i>Metapelma spectable</i>	<i>A. bilineatus</i> /Quercus	USA	x	[71]
			<i>A. sulcicollis</i> /Quercus			
	Hym: Eurytomidae	<i>Bephratoides agrili</i>	<i>A. anxius</i> /Betula	USA, Canada	< 1%	[74, 169]
		<i>Eurytoma rosae</i>	<i>A. cuprescens</i> /Rosa & Rubus	USA, Europe	x	[157, 179]
			<i>A. bilineatus</i> /Castanea			
		<i>Eurytoma</i> sp.	<i>A. anxius</i> /Betula	USA, Canada	< 1%	[74, 169]
	Hym: Ichneomoniidae	<i>Cubocephalus</i> sp.	<i>A. planipennis</i> /Fraxinus	USA	< 0.2%	[186]
		<i>Dolichomitius messorperlongus</i>	<i>A. anxius</i> /Betula	USA, Canada	< 0.4%	[74, 169]
			<i>A. liragus</i> /Populus			
		<i>Dolichomitius vitticrus</i>	<i>A. planipennis</i> /Fraxinus	USA	< 0.2%	[186]
		<i>Ephialtes</i> sp.	<i>A. anxius</i> /Betula	USA, Canada	< 0.4%	[80]
			<i>A. liragus</i> /Populus			
		<i>Glypta</i> sp.	<i>A. anxius</i> /Betula	USA, Canada	< 1%	[169]
		<i>Ichneumon</i> sp.	<i>A. anxius</i> /Betula	USA, Canada	< 1%	[169]
		<i>Olesicampe</i> sp.	<i>A. anxius</i> /Betula	USA, Canada	< 1%	[169]
		<i>Orthizema</i> sp.	<i>A. anxius</i> /Betula	USA, Canada	< 1%	[169]
		<i>Pimploterus</i> sp.	<i>A. anxius</i> /Betula	USA, Canada	< 1%	[169]
		<i>Baruchnemon</i> sp.	<i>A. ruficollis</i> /Rosa	USA	x	[187]

Table 2 (continued)

Parasitoid guild	Order: Family	Species	<i>Agrilus</i> host/Host's food plants (genus)	Regions where parasitism was reported	Levels of parasitism reported	References
		<i>Xorides</i> sp.	<i>A. planipennis</i> / <i>Fraxinus</i>	Northeast China	< 10.6%	[185]
	Hym: Stephanidae	<i>Foenatopus</i> sp.	<i>A. sexsignatus</i> / <i>Eucalyptus</i>	Southeast Asia (Philippines)	< 50%	[161]
	Hym: Pteromalidae	<i>Oodera</i> sp.	<i>A. subcinctus</i> / <i>Fraxinus</i>	USA	x	[82]
	Col: Cleridae	<i>Tenerus</i> sp.	<i>A. planipennis</i> / <i>Fraxinus</i>	Northeast China	< 21%	[185]
	Col: Trogossitidae	<i>Xenoglena quadrisignata</i>	<i>A. planipennis</i> / <i>Fraxinus</i>	Northeast China	< 1.2%	[185]

x = estimated of level of parasitism undetermined/not found in literature

^aIll-defined identity or association with associated parasitoid, unconfirmed

^bStated level of parasitism unconfirmed or lacking specificity to species

Because *Agrilus* populations are strongly driven by bottom-up forces, the effects of climate change on host plants will likely have significant indirect effects on *Agrilus* population dynamics. Warmer climates and higher CO₂ levels will increase primary growth and secondary production of defensive compounds for many plant species, which could make some hosts less vulnerable to *Agrilus* attack [197–199]. However, warmer climates may reduce growth and vigor for plant species that are more adapted to cooler climates, such as *Betula papyrifera*, making them more susceptible to *Agrilus* attack [16, 136, 200]. This effect is expected to be most pronounced near the southern geographic distribution of heat sensitive plant species in the northern hemisphere. More frequent and pronounced droughts, and other extreme weather events, including fluctuating winter temperatures, late season frosts, extreme heat, and high winds, can also reduce plant vigor and increase their vulnerability to *Agrilus* attack [201, 202].

Effects of climate change on natural enemies will also affect top-down pressures on many *Agrilus*. For example, several *Agrilus* larval parasitoids are multivoltine and require a proportion of the *Agrilus* population to be semivoltine, so suitable larval hosts are available when adult parasitoids emerge in the spring of every year [203]. As the proportion of semivoltine *Agrilus* declines in warming climates, host-parasitoid synchrony will likely decrease [193]. Also, some parasitoids may be more adapted to cooler climates compared to their host, such as the EAB egg parasitoid *Oobius agrili* [204]. Like many insect species, extreme weather events may negatively affect parasitoid survival and development, but parasitoids may be more sensitive than their *Agrilus* hosts. For example, overwintering *Tetrastichus planipennisi* and *Spathius galinae* suffered higher mortality from an extreme cold weather event compared to EAB larvae [191].

Economic and Ecological Impacts

Economic and ecological damage has been reported from multiple *Agrilus* species (Table 1). Much of this damage is caused by *Agrilus* that have been accidentally introduced to areas where a naïve (non-coevolved host) occurs or vice versa. Generally, many *Agrilus* pests characteristically cause damage in an intermittently severe pattern when populations flare up and reach outbreak levels and then decline again. For several of these *Agrilus* (e.g., *A. anxius*, *A. biguttatus*, and *A. bilineatus*), intermittent widespread mortality to their coevolved hosts appears to be partially driven by preceding periods of environmental stress [25, 136, 202]. Given these threats, many world regions have heightened their awareness or enacted stricter quarantines on certain plant species or plant products that could harbor high-risk *Agrilus* pests [33, 34, 141].

Of all the *Agrilus* species worldwide, EAB is by far the most damaging species, especially in its invaded range of North America. An early cost projection for EAB remediation in just 25 northeastern USA communities for one decade (2009–2019), which covered treatment, removal, and replacement of landscape ash trees, was US\$25 billion [205], making it the costliest wood-boring insect to have invaded the USA [206]. In addition to economic damage, EAB has negatively impacted many ash-dependent biodiversity and degraded North American forest ecosystem functions and services [162, 207–212]. In the invaded range of European Russia and Ukraine, EAB may negatively impact European ash, *F. excelsior* [213]. Throughout its native range in East Asia, however, EAB rarely reaches outbreak levels, but has killed Asian ash that are stressed [37]. However, EAB outbreaks are common in areas where North American ash species have been planted in China [37, 66, 69, 142, 214] and the Russian Far East [152]. Currently, North American ash

is only planted in China as monoculture plantations or as landscape and street trees [132].

Of the many *Agrilus* pests, *A. cuprescens* is the most globally widespread [1]. It is a pest of cultivated *Rubus* and *Rosa* crops, both in its native range of Eurasia and in North America where it was introduced [29]. *A. cuprescens* remains an economically important pest in Eurasia [158, 215, 216] and North America, where it has caused losses up to ~90% of *Rubus* crops and nursery closures for *Rosa* production [29]. *A. cuprescens* spread from northeastern North American in the 1910s–1920s, to the Great Lakes region in the 1920s–1940s, then to Utah in the 1950s–1980s, and then to the Pacific Northwest in the 1990s, where it has become a serious pest of concern in *Rubus* production [29]. *Agrilus cuprescens* was also observed to ecologically impact native Canadian prairie *Rosa* stands [217, 218].

The Nearctic *A. ruficollis* has been a pest of cultivated *Rubus* throughout eastern North America since the mid-1800s [219] and remains a pest today [45]. Crop losses of up to 72% have been reported for *A. ruficollis* [220]. Damage from both *A. cuprescens* and *A. ruficollis* vary widely (Fig. 2C, D), and it is not understood whether outbreaks of these pests are preceded by environmental stress or heavily influenced by population fluctuations of their larval parasitoids [158, 160, 220].

In citrus crop production in Asia and Oceania, *A. auriventris* is a serious orchard pest [38, 221]. During an 8-year outbreak of *A. auriventris* in Japan, estimated ~70 K *Citrus* trees were killed [19]. Many of the infested trees were older, and drought was considered a precursor to the outbreak. Moreover, recent outbreaks of *A. auriventris* in China [222], and its current classification as quarantine pest in Western Australia illustrate its ongoing economic relevance. In addition, the six species of the Asian *A. angulatus* species group are also known citrus pests and could cause economic damage if introduced to other citrus growing regions of the world [223].

Agrilus sinuatus is a European species that primarily impacts *Pyrus* production and remains economically relevant today in multiple European countries [50]. This species was introduced to North America in the late 1800s, where it became a devastating pest of *Pyrus* production in the Northeast [73, 138] and intermittently remains a regional pest.

Agrilus mali is another economically damaging *Agrilus* that intermittently impacts cultivated *Malus* in eastern China and Korea [224]. More recently, *A. mali* became established in western China where it is now a serious pest of wild *Malus* [33, 35]. The rate of spread and severity of damage caused by *A. mali* in western China is like EAB, with near complete infestation of wild *Malus* forests and 40–50% tree mortality [35, 94, 225].

Like *A. mali*, *A. auroguttatus* and *A. prionorus*, are pests recently introduced to regions proximal to their native range, where outbreaks have caused damage to native *Quercus* in

California and *Sapindus* in Texas USA, respectively. Forest products of some major tree pests such as *A. anxius*, *A. biguttatus*, and *A. bilineatus* have been quarantined by multiple countries to reduce the risk of introduction and thereby safeguard local forest and horticultural industries and environments.

Other more recently emerging *Agrilus* pests of concern to crops include *A. viridis* as a native pest of cultivated *Corylus avellana* nut trees in Europe [226], *A. pseudocoryli* as a native pest of cultivated hybrid *Corylus americana* × *Corylus avellana* in North America [42], and introduction of *A. acutus* into a major Hibiscus-producing region in India [13].

Alternatively, some *Agrilus* have been employed as biocontrol agents of invasive plants. *Agrilus hyperici* was intentionally introduced to Australia and the USA to control *H. perforatum*. It successfully established in North America and contributed significantly to *H. perforatum* control [83, 227] but did not significantly suppress *H. perforatum* in Australia [6]. *Agrilus ruficollis* was also introduced to New Zealand as a biocontrol agent for feral, invasive *Rubus* [228], although it did not become established. *A. cuprescens* was assessed for *Rosa multiflora* control in North America but was not found to be highly impactful [186]. In the future, it is possible that other *Agrilus* species will be used for weed biocontrol.

Management

Management of many native *Agrilus* within their historical geographic range is infrequent. This is largely because most damage caused by native *Agrilus* occurs to stressed forest trees, where active management is not practical, and outbreaks subside when tree vigor returns. By contrast, active control methods, including eradication efforts, are often undertaken for invasive tree-killing *Agrilus* species, like EAB. Alternatively, *Agrilus* pests of cultivated small trees or shrubs (crops) may be more readily managed. For example, cultural practices were developed against *Agrilus* pests of *Rosa* and *Rubus* prior to use of pesticides [219, 229]. These practices include pruning out infested stems before adult *Agrilus* emergence, followed by destruction (usually burning) and remain relevant today [30, 225, 230]. Other methods, such as those developed for *A. sinuatus* centered on using physical barriers or repellents to prevent or deter oviposition [73].

Several advances in management strategies for *Agrilus* pests of healthy plants have been developed in recent decades following the discovery of EAB in North America. These have focused on setting quarantine boundaries, survey methods, eradication, spread prevention, biological control, host plant resistance, silvicultural practices, insecticide treatments, and area-wide integrated pest managements [37, 142, 144, 154, 203, 231–234]. Unlike EAB, many *Agrilus* species are native and considered secondary pests that primarily colonize stressed host plants [202]. Therefore, a key strategy

to manage these secondary *Agrilus* species is through prevention, i.e., by maintaining good plant health. Avoiding soil compaction, watering during dry periods, and harvesting overmature trees are often effective in preventing attack by secondary *Agrilus* pests. However, for *Agrilus* crop pests, regular scouting, cultural practices, and chemical control may be necessary to prevent significant economic damage. For some *Agrilus* crop pests, insecticide controls have been transformative, such as the account of insecticides effectively ending a major outbreak of *A. auriventris* in Japan [19]. In the following sections, we will discuss several management strategies that were developed primarily for EAB but are likely applicable to many other *Agrilus* species.

Early Detection and Eradication or Prevention An eradication strategy was initially implemented in the USA and Canada following the EAB discovery in Michigan and Ontario in 2002 [235]. However, the eradication effort was later abandoned because of difficulties detecting EAB at low population densities, primarily due to the lack of effective monitoring tools. In subsequent years, many advances were made in trap designs [113, 236], host-plant based lures [96, 110], and sex pheromones [100, 101]. The improved traps were used to detect and delineate the leading edge of the EAB invasion [237]. Although the detection efficacy of current traps and lures is still limited at low EAB population levels, these traps have been useful for monitoring EAB spread and have been used to capture other *Agrilus* species in other countries [238, 239].

Considering the severe negative impacts of the EAB invasion in North America, it is still prudent to adopt pest prevention strategies in regions where EAB and other potentially invasive *Agrilus* have not yet established. For example, proactive research efforts have been recently initiated in Europe to develop a preparedness toolbox to deal with the potential arrival of EAB, *A. anxius* and other buprestids [31, 240, 241]. Similar proactive efforts have been developed in Europe for other potentially invasive species such as *A. anxius*, *A. bilineatus*, *A. fleischeri*, and *A. mali* [26, 34]. Likewise, in agricultural pest control, trapping is a key component of determining management action thresholds for IPM (Integrated Pest Management) programs, and have been explored for *A. cuprescens*, *A. ruficollis*, and *A. sinuatus* [29, 45, 223]. Colored sticky traps or funnel traps have not yet proven to be effective for *A. cuprescens* [29]. However, Kim et al. [45] found that 542 nm, 49% reflectance green funnel traps that are used for EAB were also effective for trapping *A. ruficollis*. Similarly, light green and transparent sticky traps were effective for trapping *A. sinuatus* [223].

Biological Control Although many natural enemies are considered important biological control agents of *Agrilus* pests, few studies have quantified their role within IPM programs except for EAB [151, 154, 159, 242], *A. cuprescens* [158,

160] and *A. ruficollis* [175]. In the case of EAB, a classical biological control program was initiated in 2007 after US federal and state regulatory agencies approved release of three parasitoids from China: *Oobius agrili* (Encyrtidae), *Spathius agrili* (Braconidae), and *Tetrastichus planipennisi* (Eulophidae). A fourth EAB parasitoid, *Spathius galinae* (Braconidae) from Russia, was approved for release in the USA in 2015. By fall of 2023, one or more of these four biocontrol agents had been released in over 32 USA states and three Canadian provinces [154, 243]. Field studies have documented successful establishment at numerous release sites of the egg parasitoid *O. agrili* and the larval parasitoids *S. galinae* and *T. planipennisi*. Long-term life table studies have demonstrated that *S. galinae* and *T. planipennisi* have significantly suppressed EAB populations within 3–5 years after release [151, 154, 159, 191]. Moreover, suppression of EAB is likely to expand in North America geographically as these parasitoids spread to new areas. Development of such large-scale biological control programs for other invasive *Agrilus* pests will require foreign exploration for specialized natural enemies, assessment of native natural enemies for conservation, and long-term support for large-scale rearing and release programs.

Host Plant Resistance Host plant resistance has been recognized as an ideal management tool for many insect pests of trees [244, 245] and crops [29]. Planting pest-resistant plants would reduce insecticide usage, which often has inadvertent off-target effects and may be limited to high value trees in forests or ornamental contexts. This has been suggested as a strategy for reducing *A. anxius* infestations of *Betula* trees in urban forests and ornamental landscapes [16, 246]. Research is currently underway to develop EAB-resistant *Fraxinus* cultivars, including hybridizing coevolved (e.g., *F. mandshurica*) and naïve North American ash species, as well as crossing with naïve hosts that show high levels of natural EAB resistance [144, 145]. Due to the intermittent nature of many *Agrilus* crop pests, investment in developing new resistant cultivars may not always be justifiable, but selection of existing cultivars may be useful. Multiple past reports and studies have attempted to discern patterns of cultivar resistance in *Rubus* crops for *A. cuprescens* or *A. ruficollis* [31, 44, 158, 220, 247] but considerable variability has been observed [29].

Cultural Control Cultural practices such as planting selective host plant species, as well as thinning, pruning, watering, and fertilizing trees have all been promoted in North America and Europe against several *Agrilus* pests, including *A. anxius*, *A. bilineatus*, *A. cuprescens*, *A. mali* and *A. ruficollis*. For *A. cuprescens* and *A. ruficollis*, destruction of infested canes before adult emergence is effective [30, 230] and can often be integrated with routine cane pruning and trellising activities [29]. Other practices that maintain tree

health, such as matching the tree's hardiness and sun requirements to the planting location, irrigating during drought, proper mulching, and preventing severe defoliation, are all important components of plant health care programs for landscape trees [246, 248–250]. However, although fertilization is commonly recommended, there is no evidence it increases tree resistance to BBB [251].

In forest situations, increasing stand age diversity is recommended for reducing susceptibility of *B. papyrifera* to *A. anxius* [252]. In the case of EAB, some have recommended preemptive logging of ash during the initial EAB invasion, combined with planting non-host trees of EAB [253–255]. Other cultural practices should be explored to lessen the impact of both native and invasive *Agrilus* [256].

Chemical and Gene-Based Control Historically, many insecticides have been used to protect plants against *Agrilus* attack. Many of these products were aimed at the adult beetles. These applications must be timed to be active after adult emergence and before oviposition to be effective. Models predicting adult emergence of EAB [257, 258], and *A. cuprescens* [29, 259] have been used to time insecticide applications. Many insecticides have shown good control, but multiple applications are often required for species that emerge over several weeks. Many insecticides have been tested against *Agrilus* adults and larvae [16, 18, 29, 51, 55, 260–264]. Many have proven effective, but a number of older products such as lead arsenate and dichlorodiphenyltrichloroethane (DDT) have since been phased out and may not be approved in many countries. Some more current effective, non-systemic products that are more widely approved include multiple pyrethroids, carbaryl, malathion, and neem oil [233, 263, 265]. More recently, several systemic insecticides (e.g., azadirachtin, dicotophos, dimethoate, dinotefuran, emamectin benzoate, and imidacloprid) when applied via soil drench, bark basal spray, or trunk micro-injection have shown multi-year control against both *Agrilus* larvae and adults [261, 266–269].

Among the systemic insecticides, emamectin benzoate appears very effective against EAB, providing control for 2–3 years [233, 268]. Recent economic analyses have revealed that treating landscape ash trees with systemic insecticides is less costly than the cost of tree removal [233]. Moreover, simulation studies suggest that treating large-diameter *Fraxinus* trees with systemic insecticides can slow the spread of EAB in individual forest stands [232, 234, 270]. More importantly, the trunk micro-injection technique directly places the insecticide within the tree and thus reduces contamination to the surrounding environment [271]. Although nontarget organisms such as insects that directly feed on treated trees can be adversely affected by systemic insecticides, direct exposure to predators and parasitoids of target *Agrilus* pests is largely eliminated [272–274]. That said, off-target effects of systemic insecticides may be impractical for *Agrilus* pests of some food

crops. For instance, effective timing of systemic insecticides for *A. cuprescens* control in *Rubus* crops simultaneously poses unacceptable risks to humans via high levels of pesticide residues on harvested fruit and unacceptable insecticide exposure to pollinators [30, 194].

Since many insecticides often have inadvertent off-target effects on the environment, this warrants exploration of alternative control strategies [273, 274]. For instance, research has recently begun developing RNA interference (RNAi) technology for EAB control [275–279]. The mode of action of RNAi products involves “silencing” specific target genes that can lead to species-specific pest control. However, this technology is still in the early stages of development, and its efficacy and safety remain untested; currently no commercial products of RNAi technology have yet been developed for EAB or any other *Agrilus* species.

Areawide Integrated Pest Management (IPM) An areawide IPM strategy has been recently explored for managing EAB in North America [231, 280–282]. This strategy integrates EAB monitoring, selective treatments of trees with trunk injection of systemic insecticides to minimize adverse effects on natural enemies, and use of girdled *Fraxinus* trap trees, along with biological control and has been shown to slow and reduce EAB impacts at both small (local) and large (regional) scales [114, 234, 282]. However, success of this areawide IPM strategy is strongly influenced by the initial condition of the ash trees and EAB densities, tree species composition and proximity to insecticide-treated ash trees [234, 282]. Usage of such areawide IPM programs for other *Agrilus* pests remains to be studied.

Conclusions

The genus *Agrilus* is the most speciose genus in the Animal Kingdom [1]. By far, EAB has been the most destructive and costly *Agrilus* species, especially in its invaded range of North America and Europe. Several other *Agrilus* species occasionally reach outbreak levels, especially during periods of drought, or when they encounter naïve hosts, causing widespread plant mortality. Several *Agrilus* species have become established in areas outside their native range, likely the result of inadvertent movement of infested solid wood packaging, nursery plants, and firewood [283]. More *Agrilus* species could be moved in future years, both within and between countries, and thereby threaten local economies and ecosystems. Climate change will likely exacerbate the pest status of many *Agrilus* species by altering their geographic range and voltinism, as well as by altering host susceptibility to *Agrilus* infestation [284]. Moreover, the dynamic interplay of how *Agrilus* species' natural enemies and climate change will alter *Agrilus* population dynamics

is poorly understood. Much more basic biology needs to be learned for the vast majority of *Agrilus* species worldwide, as exemplified by the fact that the larval host plants are unknown for about 78% of the world's *Agrilus* [3]. Similarly, although many advances have been made in chemical control of *Agrilus* pest species, much more remains to be learned about host plant resistance, the chemical ecology of *Agrilus* and their natural enemies, and how such findings can be incorporated into future management strategies.

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