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Historical Population Increases and Related Inciting Factors of Agrilus anxius, Agrilus bilineatus, and Agrilus granulatus liragus (Coleoptera: Buprestidae) in the Lake States (Michigan, Minnesota, and Wisconsin)

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Cover Page Footnote

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Historical Population Increases and Related Inciting Factors of *Agrilus anxius, Agrilus bilineatus,* and *Agrilus granulatus liragus* (Coleoptera: Buprestidae) in the Lake States (Michigan, Minnesota, and Wisconsin)

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Abstract

Three native species of tree-infesting *Agrilus* (Coleoptera: Buprestidae) have regularly reached outbreak levels in the Lake States (Michigan, Minnesota, and Wisconsin), including *A. anxius* Gory (bronze birch borer), *A. bilineatus* (Weber) (twolined chestnut borer), and *A. granulatus liragus* Barter & Brown (bronze poplar borer). The main host trees for these *Agrilus* are species of *Betula* for *A. anxius*, *Castanea* and *Quercus* for *A. bilineatus*, and *Populus* for *A. granulatus liragus*. Based on 197 annual forest health reports for Michigan (1950–2017, 66 years), Minnesota (1950–2017, 64 years), and Wisconsin (1951–2017, 67 years), *A. bilineatus* was the most often reported *Agrilus* species in all three states (mentioned in 90 annual reports), with *A. anxius* second (71 reports) and *A. granulatus liragus* third (21 reports). Drought was the most commonly reported inciting factor for outbreaks of all three *Agrilus* species, with defoliation events ranking second. The top two defoliators reported as inciting outbreaks of each species were, in decreasing order, *Fenusa pumila* Leach (Hymenoptera: Tenthredinidae; birch leafminer) tied with *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae; forest tent caterpillar) for *A. anxius*; *M. disstria* and *Alsophila pometaria* (Harris) (Lepidoptera: Geometridae; fall cankerworm) for *A. bilineatus*; and *M. disstria* and *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae; large aspen tortrix) for *A. granulatus liragus*. Other environmental factors occasionally listed as inciting *Agrilus* outbreaks included late spring frosts, ice storms, and strong wind events.

Keywords: Jewel beetles, flatheaded borers, aspen, birch, oak, environmental stress, outbreak

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The genus *Agrilus* (Coleoptera: Buprestidae) is considered the most speciose in the Animal Kingdom with over 3200 recognized species worldwide as of April 2019 (Jendek and Poláková 2014; E. Jendek, pers. comm.). The continental United States is known to have at least 194 recognized *Agrilus* species and subspecies, of which 13 species are exotic to the USA (Chamorro et al. 2015; Hoebeke et al. 2017, DiGirolomo et al. 2019). In the Lake States [a collective term for Michigan (MI), Minnesota (MN), and Wisconsin (WI)] there are at least 60 known *Agrilus* species, of which 4 are exotic (Wellso et al. 1976, Jendek 2013a, 2014).

Among the native tree-infesting *Agrilus*, there are three species that regularly reach outbreak levels in the Lake States: *Agrilus anxius* Gory (bronze birch borer), *A. bilineatus* (Weber) (twolined chestnut borer), and *A. granulatus liragus* Barter & Brown (bronze poplar borer) (Millers et al. 1989). They are similar in size (adults are about 7–11 mm long) and have similar life histories with the most significant difference being their larval host plants: *A. anxius* on *Betula* (birch), *A. bilineatus* on *Castanea* (chestnut) and *Quercus* (oak), and *A. granulatus liragus* on *Populus* (aspen, cottonwood and poplar) (Solomon 1995). Each species is known to infest overmature trees as well as trees stressed by drought, defoliation, and other factors (Dunbar and Stephens 1976, Dunn et al. 1986, Millers et al. 1989, Haack and Acciavatti 1992, Solomon 1995, Muilenburg and Herms 2012, Haack and Petrice 2020).

Several life-history studies have been conducted on *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* in eastern North America (Balch and Prebble 1940, Barter and Brown 1949, Barter 1957, 1965, Carlson and Knight 1969, Cote and Allen 1980, Haack and Benjamin 1982, Loerch and Cameron 1984, Muilenburg and Herms 2012). Their life cycle is generally completed in one year, but at times two years are needed, especially when summers are cool or when eggs are laid on vigorous host trees or laid during late summer. In the Lake States, or other areas of similar latitude, adult emergence of these three species usually starts in late May or early June, peaks in late June, and then diminishes through July and August. Adults feed on host foliage for several days to become sexually mature and then mate and oviposit in bark cracks and crevices along the major branches and trunks of host trees. Eggs are laid singly or in small clusters. Upon eclosion, larvae tunnel through the bark and feed in the cambial region, constructing zig-zag galleries that score both the inner bark (phloem) and outermost sapwood (xylem). There are four larval instars and larvae often enter the outer sapwood to molt. In late summer and autumn, mature last-instar larvae construct individual pupal cells in the outer sapwood on thin-barked trees, which is common in *Betula* and *Populus*, or in the outer bark on trees with thick bark, which is common in *Castanea* and *Quercus*. Pupation occurs in late spring and early summer. Newly formed adults exit through the bark by creating D-shaped exit holes that are characteristic for the genus. The sex ratio of emerging adults is about 1:1.

Over the past several decades many changes have occurred in the taxonomic status of these three *Agrilus* species. *Agrilus anxius* was initially described by Gory (1841), and included what we now refer to as *A. granulatus liragus*. Over a century later, Barter and Brown (1949) named *Agrilus liragus* as a new species, separating it from *A. anxius* based on color, male genitalia, and larval host plants. Carlson and Knight (1969) reevaluated the *Agrilus anxius* complex and reclassified *A. liragus* as a subspecies of *A. granulatus*. Later, Bright (1987) recognized *A. liragus* as a distinct species, then Nelson et al. (2008) once again recognized the subspecies *A. granulatus liragus*. Although both combinations have appeared in recent scientific literature, we use *A. granulatus liragus* in the present paper. *Agrilus bilineatus* was first described in 1801 under the name *Buprestis bilineata* Weber (Fisher 1928). For many years, two subspecies of *A. bilineatus* were recognized based on their larval hosts and subtle morphological differences, with *A. bilineatus bilineatus* larvae feeding in *Castanea* and *Quercus*, and larvae of *A. bilineatus carpini* Knull, feeding in *Carpinus* (hornbeam), *Fagus* (beech), and *Ostrya* (hophornbeam) (Knull 1923). This latter subspecies was later elevated to species status under the name *Agrilus carpini* Knull (Nelson and Hespenheide 1998). Given the above history, it is understandable that there has been some confusion in the literature on the actual larval hosts of these three *Agrilus* species.

Since the discovery of the Asian species *Agrilus planipennis* Fairmaire (emerald ash borer) in North America in 2002 and in European Russia in 2005 (Haack et al. 2002, 2015), there has been growing concern in Europe, as well as in other countries, that various exotic species of *Agrilus* could enter and greatly impact European urban and forest trees (Flø et al. 2015). For example, as of April 2019, EPPO (European and Mediterranean Plant Protection Organization) has conducted formal pest risk analyses (PRAs) for four *Agrilus* species, including *A. anxius* in 2010 (EPPO 2011), *A. planipennis* in 2013 (EPPO 2013), *A. bilineatus* in 2018 (EPPO 2019a), and *Agrilus fleischeri* Obenberger in 2018 (EPPO 2019b). We were team members of the Expert Working Groups that conducted the above four *Agrilus* PRAs: RAH for *A. anxius* and *A. planipennis* and TRP for *A. bilineatus* and *A. fleischeri*. During the PRAs for *A. anxius* and *A. bilineatus*, we provided the team members of the Expert Working Groups with details on the outbreak history of these two species in the Lake States, and in turn the team members encouraged us to summarize these data into a formal publication. In addition, the recent discovery of *A. bilineatus* in Turkey (Hızal and Arslangündoğdu 2018), has further increased interest in *A. bilineatus* and its potential threat to European *Castanea* and *Quercus* trees (EPPO 2019a, Haack and Petrice 2020). Given the above, we reviewed several decades of annual forest pest reports from the Lake States and recorded the number of times each native *Agrilus* species was mentioned as reaching pest status, as well as any biotic and abiotic factors that could have incited the outbreaks.

Materials and Methods

We reviewed all annual forest pest reports that we could locate from Michigan (1950–2017, 66 reports, missing 1951 and 1973), Minnesota (1950–2017, 64 reports, missing 1956, 1963, 1967, and 1973), and Wisconsin (1951–2017, 67 reports). Formal forest pest surveys, often involving aerial surveys, ground surveys, and on-site visits in response to calls from foresters and the public, have been conducted in Wisconsin since 1949, and in Michigan and Minnesota since 1950 (WI CD 1953). Therefore, our dataset represents nearly all published forest pest reports for these three US states. Moreover, in 1951, forest health staff from the Lake States met in Madison, WI, to coordinate their reporting and survey methods for forest pests of mutual concern (WI CD 1953), therefore we feel comfortable comparing infestation records across the Lake States. We located most reports in our USDA Forest

Table 1. Number of reports (and percent of the total reports) by state where *Agrilus anxius*, *A. bilineatus* or *A. granulatus liragus* were mentioned as being pests in the annual forest health reports published by the Departments of Natural Resources in Michigan (MI; 1950–2017), Minnesota (MN; 1950–2017), and Wisconsin (WI; 1951–2017).

	State		
Insect	**MI (66 reports)**	**MN (64 reports)**	**WI (67 reports)**
Agrilus anxius	11 (17 %)	33 (52 %)	27 (40 %)
Agrilus bilineatus	16 (24 %)	34 (53 %)	40 (60 %)
Agrilus granulatus liragus	7 (11 %)	11 (17 %)	3 (4 %)

Service library on the Michigan State University campus, where our Insect Research Unit has been located since 1956 (Haack 2006). For any missing years, we contacted the individual states, and in most cases they had copies available. Many of the reports since the 1990s are now online for the Lake States as well as all other US states (FHP 2018). Although the structure of state government has changed over time in the Lake States, these reports were typically prepared by the Forest Health staff within each state's Department of Natural Resources (DNR). The titles of these DNR reports changed over the decades, usually starting as *Forest Pest Reports* in the 1950s and 1960s, changing to *Forest Insect and Disease Report*s in the 1970s and 1980s, and then to *Forest Health Reports* in the 1990s to the present.

When reviewing each report, we looked for any mention of *Agrilus* beetles, either by scientific name or common name. We concentrated on native *Agrilus* species, but after discovery of the exotic species *A. planipennis* in each state (2002 in MI, 2008 in WI, 2009 in MN), *A. planipennis* was mentioned in every subsequent annual report. For each mention of a native *Agrilus* species, we recorded the year of the report, where in the state the species reached pest status, and information on the severity of the infestation.

As a simple means to visualize the infestation levels for each species over time, we assigned a value of 1 to infestations ranked low and a value of 2 to infestations ranked moderate to severe by year and state. The ranking of "low" was given when the description of the infestation was described in terms of being local, scarce, light, spotty, scattered, etc. By contrast, a ranking of "moderate to severe" was given to infestations that were described as abundant, widespread or statewide, and usually causing severe tree dieback or mortality. On a few occasions, however, a ranking of low was given to situations where infestations occurred statewide but were restricted to urban situations, such as when *A. anxius* infested primarily ornamental birch trees.

Given that populations of many native *Agrilus* species increase when host trees are weakened by various inciting factors such as drought and defoliation (Millers et al. 1989, Solomon 1995), we also recorded any mention in the reports of the possible inciting factors that could have triggered the *Agrilus* outbreaks. We recognize that changes in staffing, funding, and priorities have taken place in each DNR Forest Health Unit in the Lake States, but feel confident that the major forest pests were recorded each year and therefore the annual forest health reports represent a good approximation of changes in *Agrilus* populations over time.

Results

Agrilus anxius, *A. bilineatus*, and *A. granulatus liragus* were the only three native *Agrilus* species that were reported multiple times as forest pests in the Lake States. *Agrilus bilineatus* was reported most often in all three states, being mentioned in 90 of the 197 annual reports (16 MI, 34 MN, and 40 WI reports; Table 1). *Agrilus anxius* was the next most frequently reported species, being mentioned in 71 reports (11 MI, 33 MN, and 27 WI reports). *Agrilus granulatus liragus* was mentioned in 21 annual reports (7 MI, 11 MN, and 3 WI reports). Based on all 197 reports, *A. anxius* was first reported in 1951 in Minnesota, and *A. bilineatus* and *A. granulatus liragus* were both first reported in Wisconsin in 1966 and 1977, respectively.

Various weather-related phenomena and several defoliators were listed as suspected inciting factors that could have weakened trees and thereby led to population increases of *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* in the Lake States (Table 2). Inciting factors were presented for 72% of the 182 listings of when these three *Agrilus* species reached reportable levels (62% of the 71 *A. anxius* listings, 74% of 90 *A. bilineatus* listings, and 95% of 21 *A. granulatus liragus* listings). Drought was the most commonly reported inciting factor for all three *Agrilus* species combined (listed 119 times), as well as individually for *A. anxius* (44 times), *A.*

Table 2. Frequency (number of annual reports by state) of various inciting factors that were associated with population increases of *Agrilus anxius*, *A. bilineatus* and *A. granulatus liragus* in Michigan (MI; 66 reports during 1950–2017), Minnesota (MN; 64 reports during 1950–2017), and Wisconsin (WI; 67 reports during 1951–2017) based on each state's published annual forest health reports.

	State		
Inciting factor by *Agrilus* species (including defoliator species, family, and common name)	**MI (66 yr)**	**MN (64 Yr)**	**WI (67 yr)**
***Agrilus anxius*, bronze birch borer**			
Drought	10	18	16
Late spring frost	1	–	–
Hymenoptera			
Fenusa pumila Leach, Tenthredinidae, birch leafminer	–	4	1
Lepidoptera			
Bucculatrix canadensisella Chambers, Bucculatricidae, birch skeletonizer	–	1	–
Malacosoma disstria Hübner, Lasiocampidae, forest tent caterpillar	–	5	–
***Agrilus bilineatus*, twolined chestnut borer**			
Drought	16	19	23
Hail or ice storm	–	–	2
Late spring frost	–	–	2
Strong wind event	–	1	1
Orthoptera			
Dendrotettix quercus Packard, Acrididae, post–oak locust	–	–	4
Lepidoptera			
Acleris semipurpurana (Kearfott), Tortricidae, oak leaftier	–	–	2
Alsophila pometaria (Harris), Geometridae, fall cankerworm	–	3	9
Archips argyrospila (Walker), Tortricidae, fruittree leafroller	–	–	1
Archips semiferanus (Walker), Tortricidae, oak leafroller	5	–	–
Bucculatrix ainsliella Murtfeldt, Bucculatricidae, oak skeletonizer	–	–	1
Erannis tiliaria (Harris), Geometridae, linden looper	–	3	–
Lochmaeus manteo Doubleday, Notodontidae, variable oakleaf caterpillar	–	–	2
Lymantria dispar (L), Erebidae, gypsy moth	1	–	1
Malacosoma disstria Hübner, Lasiocampidae, forest tent caterpillar	2	8	6
Symmerista canicosta Franclemont, Notodontidae, redhumped oakworm	–	–	1
Symmerista leucitys Franclemont, Notodontidae, orangehumped mapleworm	–	–	1
Phasmida			
Diapheromera femorata (Say), Diapheromeridae, northern walkingstick	–	–	3
***Agrilus granulatus liragus*, bronze poplar borer**			
Drought	7	8	2
Lepidoptera			
Choristoneura conflictana (Walker), Tortricidae, large aspen tortrix	4	–	1
Malacosoma disstria Hübner, Lasiocampidae, forest tent caterpillar	4	7	1

bilineatus (58 times), and *A. granulatus liragus* (17 times; Table 2). Other weather events listed as inciting factors for population increases of these *Agrilus* (mostly for *A. bilineatus*) included late spring frosts, hail, ice storms, and strong wind events (Table 2). Several of the reports also mentioned tree age (i.e., overmaturity) as well as sandy soils and shallow soils as predisposing factors that increased tree vulnerability to *Agrilus* infestation, especially during periods of drought.

The greatest diversity of defoliators listed as inciting factors for population increases of the three *Agrilus* species was associated with *A. bilineatus* (13 defoliator species, representing 8 families in 3 orders), followed by *A. anxius* (3 defoliators in 3 families and 2 orders), and *A. granulatus liragus* (2 defoliators in 2 families in 1 order; Table 2). The top two defoliators mentioned as inciting factors for each *Agrilus* species were, in decreasing order, *Fenusa pumila* Leach [formerly *F. pusilla* (Lepeletier)] and *Malacosoma disstria* Hübner (both tied) for

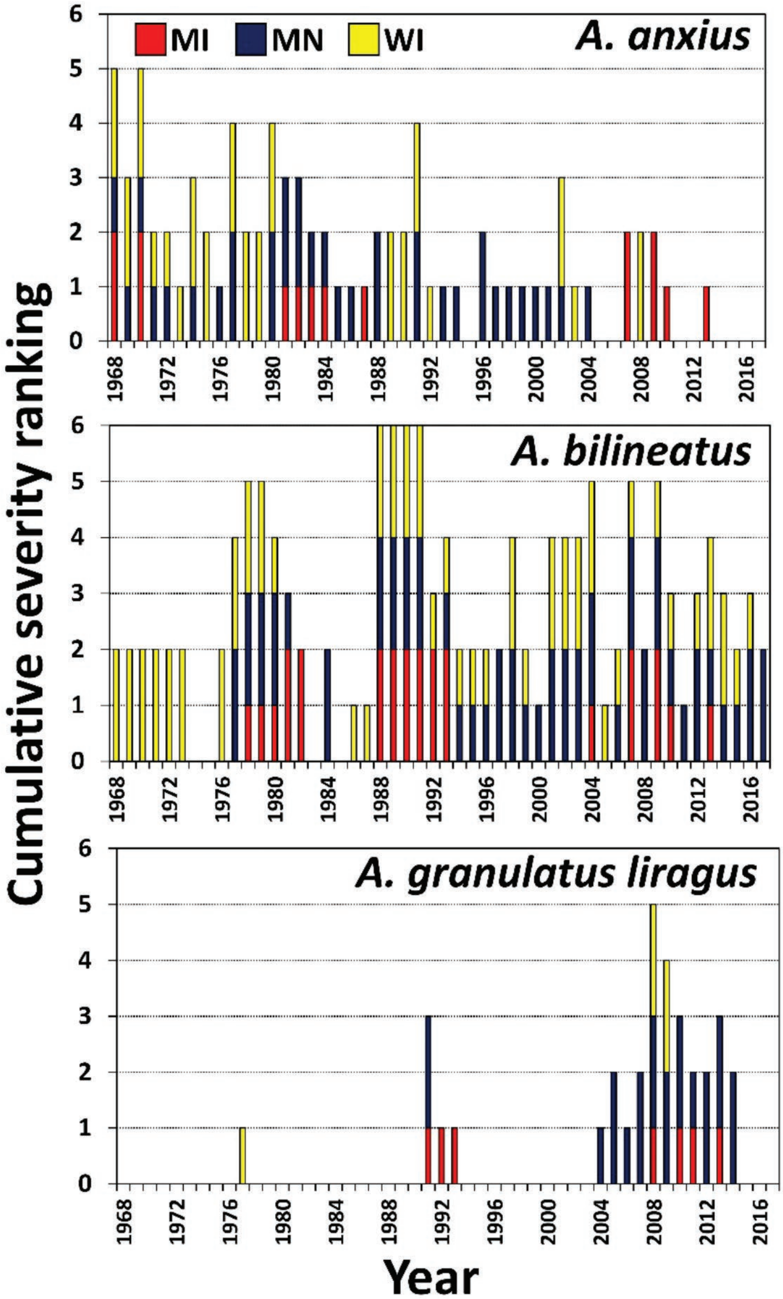

Figure 1. Stacked bar graph (within years) showing the cumulative severity rankings (0–2 for each state by year) of *Agrilus anxius*, *A. bilineatus*, and *A. granulatus liragus* infestations in Michigan, Minnesota, and Wisconsin during 1968–2017 based on annual forest pest reports from each state. A value of 0 signifies that the insect was not reported as a pest, 1 represents an infestation ranked low, and 2 represents an infestation ranked moderate to severe within each state by year. See text for more details.

A. anxius; *Alsophila pometaria* (Harris) and *M. disstria* for *A. bilineatus*; and *M. disstria* and *Choristoneura conflictana* (Walker) for *A. granulatus liragus*. The insect order, family and common name for each defoliator are listed in Table 2. *Malacosoma disstria* was the only defoliator listed as an inciting factor for all three *Agrilus* species (Table 2).

The historic timeline of *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* reaching pest status in the Lake States is depicted for the 50-year period during 1968–2017 in Fig. 1. For the years not shown in Fig. 1 (1950–1967), there were no reports for any of the three *Agrilus* species in Michigan, six reports for *A. anxius* in Minnesota (1951, 1955, 1958–59, 1961, and 1964), and eight reports for *A. anxius* (1953, 1959–62, and 1965–67) and two reports for *A. bilineatus* (1966–67) in Wisconsin. *Agrilus anxius* was reported as a pest in all three states in the same year only twice, in 1968 and 1970 (incited by drought and late frost), and only once for *A. granulatus liragus* in 2008 (incited by drought and *C. conflictana* and *M. disstria* defoliation; Fig. 1). By contrast, there were 12 years when *A. bilineatus* was reported as a pest in all three states: 1978–80, 1988–91, 1993, 2004, 2007, 2009, and 2013; usually with drought and various combinations of defoliators listed as the inciting agents (Fig. 1). Moreover, during the 3-yr period 1988–1990, *A. bilineatus* infestations were reported as moderate to severe in all three states, with drought and defoliation listed as the main inciting factors (Fig. 1).

Four additional native *Agrilus* species were mentioned in the 197 reports we reviewed and all in Wisconsin, including *A. otiosus* Say, which was reared from dying hickory (*Carya*) trees that were also infested with the bark beetle *Scolytus quadrispinosus* Say (Curculionidae: Scolytinae) and the canker fungus *Ceratocystis smalleyii* Johnson and Harrington (WI DNR 2005). The other three *Agrilus* species were *A. arcuatus* (Say), *A. cliftoni* Knull, and *A. transimpressus* Fall, all of which were reared in 2012 from dead and dying branches of declining black walnut trees (*Juglans nigra* L.) (WI DNR 2012; Andrea Diss-Torrance and Michael Hillstrom, pers. comm.). Two of these three walnut-infesting species (*A. cliftoni* and *A. transimpressus*) were recognized recently as new state records for Wisconsin (Hoftiezer 2011). Collections of the above hickory- and walnut-infesting *Agrilus* species resulted from targeted surveys of declining hickory and walnut stands in Wisconsin (WI DNR 2005, 2012).

Discussion

It is not surprising that *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* were the most commonly reported *Agrilus* species in the Lake States, given that their respective hosts, *Betula*, *Populus* and *Quercus*, are among the most common hardwood trees (i.e., broadleaf trees, dicots) in the region (MN DNR 2017, Pugh et al. 2017, WI DNR 2018), and that these three *Agrilus* species are the most damaging *Agrilus* species that infest these host trees in the Lake States (Millers et al. 1989, Solomon 1995). As background, consider that the land areas of the Lake States are heavily forested (56% of MI, 32% of MN, and 49% of WI), and that hardwood forest types dominate the forestland in each state (73% in MI, 69% in MN, and 80% in WI) (MN DNR 2017, Pugh et al. 2017, WI DNR 2018). The aspen-birch forest type is the most common forest type in Minnesota, it ranks second in Michigan and third in Wisconsin. By contrast, the oak-dominated forest types rank first in Wisconsin, second in Minnesota, and third in Michigan. The most common forest type in Michigan is the sugar maple/beech/yellow birch type (Pugh et al. 2017).

There are also many conifers (e.g., softwood trees, gymnosperms) in the Lake States, but none serve as larval hosts for any *Agrilus* species in this region (Jendek and Poláková 2014). In fact, the only *Agrilus* species worldwide to be reared from a conifer host is *A. schwerdtfegeri* Schwerdtfeger, which emerged from a dead branch of *Pinus maximinoi* Moore (= *P. tenuifolia* Bentham) in Guatemala (Jendek 2013b).

The relationship of defoliation and drought with population increases of *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* in the Lake States (Table 2), has been documented for many other *Agrilus* species worldwide (Ohgushi 1978, Vansteenkiste et al. 2004, Sever et al. 2012, Sallé et al. 2014, Chamorro et al. 2015). Tree responses to defoliation and drought can be highly variable, depending on factors such as seasonality of the stress event (early summer vs. late summer), severity (mild vs. severe), and duration (one year vs. multi-year) (Kulman 1971, Kozlowski et al. 1991). Some typical early responses to defoliation include a reduction in tree carbon balance, fine root growth, and water uptake, followed by mobilization of stored reserves to develop and expand replacement foliage, which often reduces subsequent stem growth and concentrations of various defensive compounds present in stem tissues (Kulman 1971, Wright et al. 1979, Ericsson et al. 1980, Heichel and Turner 1983, Herms and Mattson 1992, Wargo 1996, Krokene 2015). Similarly, the response of phytophagous insects to drought-stressed trees can vary widely by feeding guild, with borers usually being favored by drought (Mattson et al. 1988, Larsson 1989, Huberty and Denno 2004, Rouault et al. 2006, Haavik et al. 2015, Showalter et al. 2018). For example, severe drought can reduce a tree's ability to develop callus tissue, which can engulf and kill young wood-boring larvae such as *Agrilus* larvae (Sallé et al. 2014).

The greater frequency of *A. bilineatus* outbreaks in the Lake States as compared with *A. anxius* and *A. granulatus liragus* (Table 1, Fig. 1) may reflect differences in xylem structure of their host trees, with *A. bilineatus* infesting *Quercus* with ring-porous xylem, while *A. anxius* infests *Betula* and *A. granulatus liragus* infests *Populus*, which both have diffuse-porous xylem. This is an important difference, given that water moves primarily in the outermost annual ring of xylem in ring-porous trees, compared with several annual rings in the outermost sapwood in diffuse-porous trees (Kozlowski 1961, Wiant and Walker 1961, Kozlowski and Winget 1963). This difference also helps explain why ring-porous trees are more vulnerable to girdling insects like *Agrilus* larvae as well as pathogens that invade the outer xylem and cause wilt diseases such as chestnut blight, Dutch elm disease, and oak wilt (Zimmermann and McDonough 1978). As an example consider the study in Wisconsin by Haack and Benjamin (1982) where the current-year annual ring of xylem along the main trunk of mature red (*Q. rubra* L.) and black (*Q. velutina* Lam.) oaks measured 0.8–1.8 mm in width, whereas the average width (measured at the widest point between the dorsal and ventral surfaces of the enlarged prothorax, Chamorro et al. 2015) of third instar *A. bilineatus* larvae measured 0.9 mm and fourth (last) instars measured 1.3 mm, indicating that late-instar *A. bilineatus* larvae could easily girdle the outermost annual ring of xylem in many host trees.

Differences in xylem structure also influence the within-tree attack pattern of *Agrilus* species as well as the ease in detecting infested trees. For example, in ring-porous trees, once the xylem tissue of a portion of a branch or the trunk is completely girdled, all foliage above the girdled area usually wilts and dies that same year. For *A. bilineatus*, this usually happens in late summer when most larvae are last instars and their feeding galleries are sufficiently deep to girdle the outer annual-ring of xylem (Haack and Benjamin 1982, Haack and Acciavatti 1992). Since *A. bilineatus* females apparently lay eggs only on live portions of a host tree, the area of current-year infestation moves downward from the crown to the lower trunk in each subsequent year of attack (Haack and Benjamin 1982, Haack et al. 1983, Petrice and Haack 2014). By contrast, the first appearance of wilting foliage and dieback on birch and aspen, which have diffuse-porous xylem, usually requires multiple years of infestation by *A. anxius* and *A. granulatus liragus* before enough annual rings of the outer conducting xylem have been effectively girdled to reduce translocation and cause dieback (Barter 1957, 1965, Solomon 1995, Muilenburg and Herms 2012). Moreover, given that dieback is more gradual in birch and aspen, infestation can occur throughout the entire tree as well as in the same area of a tree for several consecutive years until that portion of the tree dies (Loerch and Cameron 1984). As an example of the difference in timing of crown dieback in response to a stress event, consider the widespread severe drought that occurred in 1988 throughout the Lake States (Trenberth et al. 1988, Haack and Mattson 1989, Jones et al. 1993), with widespread oak mortality reported in all three Lake States in 1988 and continuing through to 1991 (Fig. 1), compared with fewer and more delayed infestations reported for *A. anxius* or *A. granulatus liragus* (Fig. 1).

In recent years, most aerial surveys for forest pests in the Lake States occur in early summer, which enhances detection of current-year, early-season defoliators. However, given that foliar wilting and discoloration of *Agrilus*-infested trees usually does not occur until late summer, this practice would usually lead to an undercount of the number of areas infested with species of *Agrilus*, and therefore the outbreak history depicted in Fig. 1 should be considered as an underestimate of the actual number of *Agrilus* infestations that took place in the Lake States. Another difference between ring-porous and diffuse-porous trees that can influence the results of early-season aerial surveys is that ring-porous trees tend to leaf out later than diffuse-porous trees in any given area (Panchen et al. 2014). This occurs because in ring-porous trees, current-year earlywood xylem, which contains mostly large-diameter vessels that transport the bulk of the water, is produced before budburst, whereas in diffuse-porous trees, most current-year xylem is produced after leaf elongation (Umebayashi et al. 2008, Takahashi et al. 2013, Foster 2017).

Nonetheless, even in situations where late-summer aerial surveys are conducted, it would be easiest to detect first-season infestations of *A. bilineatus* because foliage will wilt and discolor during the first year of attack if the infested portion of the tree is completely girdled. By contrast, *Agrilus*-infested birch and aspen usually require multiple years of infestation before showing dieback and if infestations only occur for one or two years the trees may callus-over old galleries and recover (Balch and Prebble 1940, Anderson 1944, Barter 1957, 1965). Given this situation, it is likely that *Agrilus* infestations of birch and aspen occur more often than depicted in Fig. 1.

Many species of *Agrilus*, as well as other borers, preferentially infest overmature trees, especially during periods of stress (Balch and Prebble 1940, Kozlowski 1969, Dunbar and Stephens 1976, Solomon 1995, Williams et al. 2013, Brown et al. 2015). Such a relationship, along with the forest history of the Lake States, is important to consider when viewing the pattern of *Agrilus* outbreaks depicted in Fig. 1. Consider that most of the virgin forests in the Lake States were logged during the late 1800s and early 1900s, with many large-scale forest fires soon following (Stearns 1997, Dickmann and Leefers 2003). Much of the cut-over land was soon abandoned, or farmed for short periods of time and then abandoned. Many of these degraded lands were then colonized by "pioneer" tree species, such as aspen (*P. grandidentata* Michx. and *P. tremuloides* Michx.) and paper birch (*B. papyrifera* Marshall), which are short-lived trees that reach physiological maturity at 50-70 years (Burns and Honkala 1990). Although some oaks in the Lake States are relatively short-lived (*Q. ellipsoidalis* E.J. Hill), most oaks are moderate to long-lived species (Loehle 1988, Burns and Honkala 1990, Barnes and Wagner 2004). Forest surveys conducted in the Lake States in the early 1990s indicated a skewed distribution with a large "wave" of forest stands then 55–75 years old (Stone 1997). More recent forest surveys in the Lake States (2014 for MI, 2016 for MN, and 2015 for WI) indicate sharp reductions in aspen and birch acreage, especially in older age classes, compared with increases in acreage of oak-dominated forests, especially in older age classes (Pugh et al. 2017, MN DNR 2017, WI DNR 2018). Such shifts in the species composition and age structure of forests in the Lake States may explain, in part, the decline in *A. anxius* outbreaks in recent years, the recent spike in the early 2000s of *A. granulatus liragus* activity, and the near steady activity of *A. bilineatus* over the past several decades (Fig. 1).

The defoliators listed in Table 2 are common throughout the Lake States as well as in much of eastern North America, and a few also occur in the West (e.g., *C. conflictana*, *F. pumila*, and *M. disstria*; Drooz 1985). At times, outbreaks of *C. conflictana* and *M. disstria* cover millions of hectares and can continue for multiple years before subsiding (Prentice 1955, Drooz 1985, Ciesla and Kruse 2009, Schowalter 2017). Of the defoliators listed in Table 2, only two are exotic to North America (*F. pumila* and *Lymantria dispar* (Linnaeus)), and both are far less outbreak prone today than in the past as a result of introduced natural enemies: mostly parasitoids for *F. pumila* (Kirichenko et al. 2019), and a fungus and virus for *L. dispar* (Solter and Hajek 2009). In addition, all of the defoliators listed in Table 2 initiate larval feeding in early summer, with the exception of the two *Symmerista* species, which are late-season defoliators (Drooz 1985). Early-season defoliation typically reduces same-year tree growth more than late-season defoliation because trees often use stored reserves to refoliate after early-season defoliation, but seldom refoliate after late-season defoliation (Kulman 1971, Ericsson et al. 1980). However, severe late-season defoliation can have a greater impact on stem growth the following year, compared with early season defoliation (Mattson et al. 1988). With respect to *Agrilus* adult activity, early-season defoliation would usually occur prior to peak *Agrilus* oviposition, whereas late-season defoliation would usually occur after most *Agrilus* oviposition had ended for the year. Outbreaks of many defoliators are also favored during periods of drought (Mattson and Haack 1987, Millers et al. 1989), and drought plus defoliation would likely even more significantly weaken trees, which would further increase tree susceptibility to borer infestation (Thomas et al. 2002).

Now that *A. bilineatus* has become established in Turkey (Hızal and Arslangündoğdu 2018, EPPO 2019a), it is difficult to predict how damaging this species will be to European chestnut and oak trees. Drought and widespread defoliation of hardwood trees are also common in Europe (Gibbs and Greiggi 1997, Moraal and Hilszczanski 2000, Thomas et al. 2002, Sallé et al. 2014, Tiberi et al. 2016) and will likely make European host trees susceptible to *A. bilineatus* attack. However, throughout Europe there are several native species of *Agrilus* that utilize chestnut and oak trees as larval hosts (Jendek and Poláková 2014). Among these, *A. biguttatus* Fabricius is considered the most destructive, especially on oaks, which also commonly reaches outbreak levels in response to defoliation and drought (Moraal and Hilszczanski 2000, Sallé et al. 2014). Therefore, if European host trees are not highly susceptible to *A. bilineatus*, then *A. bilineatus* will likely encounter high levels of competition from native European *Agrilus* for hosts and consequently *A. bilineatus* may only become a minor pest in Europe. On the other hand, if some European chestnut and oak species are highly susceptible to *A. bilineatus* infestation, such as was the case when European *Quercus robur* L. trees were planted in Michigan (Haack 1986, Haack and Petrice 2020), then *A. bilineatus* could become a major pest in Europe. Nonetheless, given that drought is predicted to increase in frequency and severity in the future, outbreaks of *Agrilus* species and many other forest insects are expected to become more common in the United States and worldwide (Allen et al. 2010, Kolb et al. 2016).

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