

Introduced plants induce rise of a native pest and facilitate invasion in the plants' native range

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Abstract

Biological invasions are among the most serious threats to native forest ecosystems worldwide due to ever-increasing global trade and climate change. Understanding invasion processes and the ecology of invasive pests in both newly invaded and native habitats is necessary to effectively mitigate and manage the risks they pose. The effects of exotic ash tree species planted from 1900 to 2019 on distribution, occurrence, and outbreak frequency of a native pest emerald ash borer, *Agrilus planipennis* Fairmaire, were examined. The frequency and level of pest infestations gradually increased following introduction and widespread plantings of non-native host trees, and the first recorded outbreak occurred after a time lag of 30-50 years. Increased pest populations enhanced its invasion risk to other regions including the native ranges of introduced plants.

Keywords

Agrilus planipennis , native range, population dynamics, *Fraxinus* spp., invasive range, biological invasion

INTRODUCTION

With increased international trade, tourism, and global climate change, biological invasions by insect pests have become serious threats to both agricultural and forest ecosystems (Brockerhoff & Liebhold 2017; Seidl *et al.* 2018). A global approach is needed to develop effective risk mitigation and management strategies against invasive insect pests which requires understanding not only the species' ecology and invasion process in the newly invaded habitat, but also factors affecting its distribution and spatiotemporal dynamics in its native habitat (Hermes & McCullough 2014; Jones 2019).

Native to northeastern Asia (China, Russian Far East, Japan, and South Korea), the emerald ash borer (EAB), *Agrilus planipennis* Fairmaire, was accidentally introduced to North America in the 1990s via cargo crates, dunnage, or wood pallets originating from China (Siegert *et al.* 2014). Since it was first detected in southern Michigan, U.S., and Ontario, Canada in 2002 (Poland & McCullough 2006), this beetle has now spread to 35 U.S. states and five Canadian provinces (EAB Info 2020). In the process of this invasion, EAB has killed hundreds of millions of North American ash trees (*Fraxinus* spp.). More recently, this beetle has also been discovered attacking the white fringe tree, *Chionanthus virginicus* L., native to southern U.S. and commonly planted as an ornamental and landscape tree throughout the region (Peterson & Cipollini 2017; USDA NRCS 2019a). In a recent laboratory study, EAB also completed development on olive trees, *Olea europaea* L., under artificially-forced infestations (Cipollini *et al.* 2017) and thus has the potential to cause

serious economic loss to olive crops in addition to degradation of North American hardwood forest ecosystems (CFIA 2019; USDA 2019; EAB Info 2020).

All species of North American ash appear susceptible to EAB (Anulewicz *et al.* 2008); however, preference and susceptibility vary among species. Green ash (*F. pennsylvanica* Marsh.) trees were preferred and had higher levels of canopy dieback and EAB densities compared to white ash (*F. americana* L.) trees at the same sites, while white ash was preferred over blue ash (*F. quadrangulate* Michx.) trees (Anulewicz *et al.* 2007; Tanis & McCullough 2012). White and green ash cultivars had higher levels of EAB attack density and mortality than a Manchurian ash (*F. mandshurica* Rupr.) cultivar planted in a common garden trial in southeast Michigan (Rebek *et al.* 2008), suggesting that Asian ash species developed resistance mechanisms through their evolutionary history with EAB that is lacking with North American species (Rebek *et al.* 2008; Villari *et al.* 2016). Differences in susceptibility to EAB among ash species may be related to differences in host volatiles, nutrition, and defense compounds (Eyles *et al.* 2007; Whitehill *et al.* 2012; Cipollini *et al.* 2019). It was found that EAB adults preferred to feed on green, white and black ash (*F. nigra* Marsh.) leaves compared to European (*F. excelsior* L.), blue or Manchurian ash leaves, and ash species differed significantly in the relative amounts of antennally-active volatiles (Pureswaran & Poland 2009).

In China, EAB was an occasional but largely unnoticed pest of ash trees until the 1960s when North American ash species became widely introduced as plantation trees in northern China (Wei *et al.* 2004). EAB has not been recorded attacking any host plants (including *Chionanthus* spp.) other than ash trees in China and elsewhere in Asia (Valenta *et al.* 2017). Scientific literature on the biology and ecology of EAB was sparse before the 1960s, and even up to the 1980s there were only limited descriptions of its damage and life-history from anecdotal observations in books and regional publications (Wei *et al.* 2004). However, extensive field and laboratory studies of EAB and its natural enemies in northeast Asia (particularly in China) were conducted in the 2000s after this beetle became a serious invasive pest in North America. Consequently, knowledge about EAB's distribution, biology and associated natural enemies in its native (Wang *et al.* 2010; Wang *et al.* 2015) and newly invaded ranges (Duan *et al.* 2018) has greatly accumulated. In North America, EAB has established populations in warmer climate zones (as far south as 32°N) (McConnell *et al.* 2019; EAB Info 2020) than in its native range in China (as far south as 36°N) (Orlova-Bienkowskaja & Volkovitsh 2018). The cause of EAB outbreaks in China, and the apparent preference for different climate zones in its invaded range are currently unknown.

In the present study, we conducted field surveys from 2003 to 2019 and reviewed associated literature published since 1900 to gather and analyze historical data on occurrence, distribution, and outbreaks of EAB in China, and examine the role of host plants (ash species) in influencing the spatiotemporal dynamics of EAB's occurrence or outbreaks. Through analyzing historical data along with field observations of EAB occurrence and host and site characteristics, we aimed to determine the causes of EAB outbreaks and its geographic distribution in its native range. Findings from the present study should improve our understanding of EAB's geographic distribution in both its native and invaded ranges, and may contribute to development of sustainable management strategies against EAB.

MATERIALS AND METHODS

Historical and current occurrences of EAB in China

To determine the occurrence and distribution of EAB infestations in China over time, we obtained data from field surveys conducted from 2003-2019 in 11 regions of China, including seven provinces (Heilongjiang, Jilin, Liaoning, Hebei, Shandong, Henan, and Sichuan), two municipalities (Beijing and Tianjin) and two autonomous regions (Xinjiang and Guangxi) (Table S1), as well as records from the literature and reports by local faunas about the presence of EAB infestations in each province, provincial city, or region. EAB infestations were defined as areas with large numbers of emerald ash borer causing visible damage or mortality to multiple trees. We considered infestations to be at outbreak levels when emerald ash borer abundance increased in a short period of time resulting in extensive damage to more than 50% of trees. Emerald ash borer was considered present when few trees were attacked at low levels and no damage was reported.

Sample sites for field surveys included: 1) areas within the distribution of EAB with reports of EAB infestations or outbreaks; 2) areas suspected to be within the distribution of EAB with records of EAB presence but no damage reports which required verification by field investigation; and 3) areas with no historical records of EAB presence or infestation. A total of 79 1-ha sample plots were selected. Thirty ash trees were randomly selected in each plot to determine the degree of EAB infestations. When more than 50% of selected ash trees in a plot were found to be infested with EAB, the infestation level was considered to be at outbreak level.

Historical occurrence and distribution of EAB infestations were determined by searching the National Science Data of Forestry (www.lknet.ac.cn/sztsg.htm) with the term “*Agrilus planipennis* Fairmaire” from 1900 to 2019. We found a total of 218 publications of which 17 included details of EAB occurrences, host plant species, and locations in China. These publications were used to retrieve historical data on EAB infestations in China (Supplementary 1). Data retrieved from the publications included the year(s), provinces (provinces, provincial cities, or regions), and cities (prefecture-level cities or districts) of EAB occurrence, infested host plant species and the degree of EAB infestations based on the percentage of infested ash trees. Years of occurrence for each infestation reported in the literature or recorded in field surveys were categorized into six 10-year intervals from 1961 to 2019. The regions of EAB infestations were recorded as provinces, provincial cities, or regions and the exact prefecture-level cities or districts.

Variables related to EAB occurrences in China

Seven variables, including degree of EAB infestations, host tree species, host tree age, host tree size, habitat, latitude, and altitude, were recorded during field surveys in 11 regions of China from 2003 to 2019. Host tree size was measured as the diameter at breast height (DBH). The degree of EAB infestation was graded on a scale of 0-4 based on the percentage of infested ash trees: 0 = undamaged; 1 = slightly damaged, with less than 10% of ash trees infested; 2 = moderately damaged, with 10%-50% of ash trees infested; 3 = seriously damaged, with 50%-90% of ash trees infested; 4 = very seriously damaged, with over 90% of ash trees infested. Habitats were divided into three categories: (i) street trees: trees on roadsides; (ii) plantations: trees in parks, courtyards, neighborhoods, university campuses or nurseries; (iii) semi-natural conditions: trees growing in natural ecosystems or natural regenerations.

From 2012 to 2013, complementary field surveys were conducted in the Oleaceae Common Garden at the Institute of Botany, Chinese Academy of Sciences (39.99°N, 116.22°E) which contained both native and non-Asian ash species. All of the 39 native and 71 non-Asian ash trees in the 2.5 ha Oleaceae Common Garden were investigated and data were collected on the same seven variables as well as canopy condition and presence of bark splits on individual trees. Canopy condition was assigned an index on a scale with 5 levels: 1 = over 80% live crown; 2 = 60%-79%; 3 = 40%-59%; 4 = 20%-39%; 5 = below 20%. Presence of bark splits was recorded based on presence/absence: 1 = present; 0 = absent. In addition, we reviewed and extracted data on the same seven variables from the 17 recovered publications that contained detailed data about EAB infestations from 1900 to 2019. All data were analyzed to determine correlations between degrees of EAB infestation, host trees, and related environmental variables.

Spatiotemporal relationships between ash tree plantings and EAB infestations

To determine the relationship between ash tree plantings and EAB infestations in China, we gathered information on ash tree introductions and plantings from literature sources published from 1900 to 2019. We used the search terms of “*Fraxinus* and China” in Web of Science and “trees, introduction, *Fraxinus*” to retrieve publications in the National Science Data of Forestry (www.lknet.ac.cn/sztsg.htm) from 1900 to 2019. These searches generated 548 and 100 results, of which 25 publications (Table S2) included details about introduced exotic ash trees including ash tree species, planting year, name of province, provincial city or region with ash tree plantation, number of these provinces, provincial cities or regions, number of planting, and total area of plantations. Data on five variables were obtained from these 25 publications, including plantings of non-Asian ash trees; planting year; planting provinces, provincial cities, or regions; planting times; and planting areas. Planting years were divided into eight 10-year-periods from 1900 to 2019 (Table S3) and all data on ash tree species, times, and areas of plantings were accumulated for each time period.

Data on the distribution of native ash species were obtained from Flora of China (The Chinese Academy of Sciences Editorial Board of Flora 1992). Finally, we mapped the geographic distributions of native and non-Asian ash trees in China. Different non-Asian ash species were marked with different colors and ash trees native to China were marked with the green background color. The regions with EAB present were simultaneously marked to illustrate the spatial relationships between ash plantations and EAB occurrence. The planting areas of non-Asian ash species, number of provinces, provincial cities or regions with non-Asian ash plantations, and numbers of cities with EAB present were accumulated during each 10-year-period from 1900 to 2019 to determine the temporal distribution characteristics of EAB in China.

Statistical analyses

We first combined EAB presence data obtained from historical publications with the two sets of field collected data (the field surveys from 2003-2019, and the common garden field study from 2012-2013), then used a multinomial logistic regression (MLR) model to analyze the relationships between degrees of EAB infestation (as ordinal dependent variable) and host tree species, host tree age, DBH, habitat, latitude, and altitude (as independent variables) collected from different regions using the software JMP Pro 10.0.0 (SAS Institute 2012). Four variables, including latitude, altitude, DBH (continuous), and host tree age (discrete) were binned to create categories using data conversions presented in Table S3, respectively, to maintain consistency of data processing. Host tree species, habitat and bark splits were set as nominal variables, while host tree age, DBH, latitude, altitude, canopy index and degree of infestation were set as ordinal variables. One-way analysis of variance (ANOVA), followed by Tukey's means separation test, was used to evaluate effects of ash tree species and habitat (as independent variables) on level of EAB infestation (as ordinal dependent variable) in different regions using SPSS 21.0 (SPSS Institute 2012). In the Oleaceae common garden experiment, ANOVA followed by Tukey's means separation test was used to evaluate effects of ash tree species (as independent variable) on canopy index, bark splits and percentage of infested trees (as dependent variable). When determining the trend of EAB infestation level in relation to host tree age, host tree size, and host tree geographic distribution mentioned above, number of sample plots by age, DBH, and latitudinal and altitudinal distribution of ash species were plotted by EAB infestation level using OriginPro 2018 (OriginLab 2018).

RESULTS

The frequency of EAB outbreaks in China have increased since the 1960s

Data from historical literature reveal no records of EAB outbreaks on ash trees prior to 1960. The first reported outbreaks of EAB occurred on green ash in Heilongjiang and Liaoning Provinces is 1961 and 1963 respectively. The total number of cities and provinces with EAB outbreaks has increased each decade since 1961 (Table 1). By the 2010s, EAB was detected in Xinjiang-Uygur Autonomous Region and Shandong Provinces, where it caused substantial damage to exotic ash trees (green, white, and velvet ash). To date, EAB has spread to eight provinces, provincial cities, or regions in northeastern, northern and northwestern China and the numbers of cities with EAB outbreaks has increased 10-fold (Table 1).

Non-Asian ash species are much more susceptible to EAB than their native congeners in China

There was a highly significant effect of ash species on EAB infestation level based on multinomial logistic regression analysis of historical and field survey data (MLR: $df = 12, \chi^2 = 69.55, P < 0.0001$). North American and European ash species, including velvet, green, white and European ash, had significantly higher levels of EAB infestation in comparison with native ash species across China (ANOVA: $df = 7, 182, F = 10.63, P < 0.0001$) (Fig. 1). In comparison to heavy infestations on non-Asian ash species in China, EAB caused minimal damage to the three native ash species commonly used as hosts, namely *F. mandshurica*, *F. chinensis chinensis* Roxb. and *F. chinensis rhynchophylla* (Hance) A.E.Murray (Fig. 1). In addition, the other six native ash species, including *F. angustifolia syriaca* (Boiss.) Yalt., *F. baroniana* Diels, *F. bungeana* A.DC., *F. griffithii* C.B.Clarke, *F. hubeiensis* S.Z.Qu, C.B.Shang & P.L.Su and *F. platypoda* Oliv., have never been found to be attacked by EAB. There were highly significant differences in the EAB infestation indices among the nine (four exotic and five native) species of ash planted in the Oleaceae Common Garden (EAB infestation index: $df = 7, 101, F = 15.55, P < 0.0001$; Canopy index: $df = 7, 101, F = 11.59, P < 0.0001$; Bark split: df

$=7,101$, $F = 8.92$, $P < 0.0001$; with one-way ANOVA analysis); all exotic ash had much higher levels of EAB infestation than native Asian ash (Table 2). In the Oleaceae Common Garden, North American and European ash trees were heavily damaged, while native Asian ash species were only lightly or never infested.

EAB infestation levels were strongly correlated to latitudinal distribution of ash species

There was a significant positive correlation between the level of EAB infestation and latitude of ash trees (MLR: $df = 12$, $\chi^2 = 28.63$, $P = 0.0045$) with all EAB infestations occurring in northern latitudes (Fig. 2a), while there was no significant correlation between EAB infestation level and ash tree altitude (MLR: $df = 9$, $\chi^2 = 13.34$, $P = 0.1477$) (Fig. 2b). Similarly, there were no significant differences in EAB infestation levels among ash trees of different ages and sizes (MLR: $df = 4$, $\chi^2 = 4.32$, $P = 0.3650$ for ash age; $df = 3$, $\chi^2 = 2.13$, $P = 0.5457$ for ash size) (Fig. 2cd). In addition, there were no significant differences in EAB infestation levels among different habitats within ash species from the same origin category (MLR: $df = 2$, $\chi^2 = 4.05$, $P = 0.1322$ for non-Asian ash; $df = 2$, $\chi^2 = 1.43$, $P = 0.4882$ for native ash), while the EAB infestation levels in non-Asian ash trees were always more severe when compared to their native congeners within the same habitat (ANOVA: $df = 5, 184$, $F = 53.53$, $P < 0.0001$) (Fig. 3).

Spatiotemporal relationships between plantings of non-Asian ash species and EAB infestations in China

Field surveys and reports of ash species distribution, introductions, and plantings in literature sources indicated that native Asian ash species, typically Chinese (*F. chinensis*) and Manchurian ash, were widely distributed in China. However, white, green, velvet and other non-Asian ash species were also frequently found in northern China and some cities of central and southern China (Fig. 4a). In northern China, EAB infestations were detected in eight of 14 provinces, provincial cities, or regions where non-Asian ash species were present (Fig. 4a). Non-Asian ash trees have been introduced into China since the early 1900s over an increasingly wide geographic range (Fig. 4b). For example, 14,000 ha of non-Asian ash trees were planted in the 1980s and more than 20,000 ha of non-Asian ash plantations were established in the 2010s according to data collected from the literature used in this study. However, EAB outbreaks did not immediately coincide with wide-spread plantings of these non-Asian ash species; rather, there were time lags of at least 30-50 years between ash plantings and increased EAB outbreaks (Fig. 4b).

DISCUSSION

Planting exotic (non-Asian) ash trees triggered EAB outbreaks in China after several decades lag time

The type specimen of EAB was collected in Beijing and published in 1888 (Jendek 1994), while the first reported outbreak of EAB was recorded on green ash in northeastern China in the early 1960s (Wei *et al.* 2004). We conclude that the introductions and wide-spread plantings of non-Asian ash trees in northern China triggered the EAB outbreak. Our conclusion is supported by analysis of historical data and significant correlations between EAB infestation levels and exotic non-native ash species and areas where they were planted. However, there was approximately a half-century time lag between these events. For example, green ash was first introduced into northeastern China, Beijing City and Shandong Province in the late 19th and early 20th centuries. White ash was sporadically but continually planted in Beijing, Shandong, Xinjiang, Henan, and Jiangsu provinces, provincial city, or region in the early 20th century. Velvet ash was first introduced into Shandong Province in approximately 1907, and has been extensively planted in Tianjin since 1953 (Pan & You 1994). However, EAB outbreaks in these non-native ash trees were not reported in these areas until the 1960s. Subsequently, with the large number of plantings of non-Asian ash trees (Table S2), EAB outbreaks have become more severe. This suggests that there may be a threshold density for outbreaks of EAB to develop. Historically low EAB population densities in native Asian ash in China likely caused little damage initially to introduced non-Asian ash trees. Many years of planting were required for susceptible host and EAB population densities to build before outbreaks occurred. Similar time-lags of decades are common for invasive species population densities to build before new invasions are detected (Crooks & Soulé 1999; Sakai *et al.* 2001). Based on dendrochronological evidence, EAB became established

in North America in the 1990s at least 10 years before it reached high levels of infestation and was detected in 2002 (Siegert *et al.* 2014).

In China, EAB outbreaks are only associated with exotic ash trees, indicating that non-native (North American and European) ash species are more susceptible to this pest than native Asian ash species which share a co-evolutionary history. Similarly, North American birch (*Betula* spp.) species are more resistant to the North American bronze birch borer (*A. anxius* Gory) compared to European or Asian birch species planted in North America (Nielsen *et al.* 2011). Differences among ash species in resistance or susceptibility to EAB may be related to variations in host volatiles (Pureswaran & Poland 2009), composition and concentration of proteins, carbohydrates, phenolics, peroxidases, and trypsin inhibitors which are likely related to evolutionary divergence and may contribute to differences in host resistance (Eyles *et al.* 2007; Chen *et al.* 2011; Cipollini *et al.* 2011; Whitehill *et al.* 2011; Whitehill *et al.* 2012; Chakraborty *et al.* 2014). Crous *et al.* (2017) proposed that ecological disequilibrium (disruption of interactions and adaptations evolved over evolutionary time in the native range) drives the accumulation and damage by native insect pests in non-native trees.

Geographical factors contribute to variations in EAB infestation levels

We found latitudinal distributions of ash trees were positively related to EAB infestation levels rather than their habitats, altitudinal distributions, ages, and sizes. Many susceptible non-Asian ash trees have been widely planted in northern China, but these exotic species have not been widely introduced and planted in southern China as they are not tolerant of high temperatures (Pan & You 1994). In North America, the three major species of ash including green, white and black ash are distributed as far north as central Manitoba and Cape Breton Island in Canada (up to 55°N latitude) and south to Northern Texas and Florida (28°N latitude). Average temperatures range from -18°C in the winter to 27° in the summer (mean annual temperature of 5.3°C) at northern sites, and from 10°C in the winter to 33°C in the summer (mean annual temperature of 23°C) at southern sites (Burns & Honkala 1990; DeSantis *et al.* 2013; USDA NRCS 2019b). The velvet ash is primarily distributed in the southwestern and southern U.S. - from northern California (42°N latitude) where average temperatures range from 4°C in the winter and 18°C in the summer (mean annual temperature of 11°C) to southern Texas (26°N latitude) with average temperatures of 11°C in the winter to 34°C in the summer (mean annual temperature of 24°C) (USDA NRCS 2019b). In China, green, white and velvet ash trees have been mainly planted in areas from Heilongjiang in the north (45-48°N latitude) to Zhejiang (27-31°N latitude) in the south. There were also a few white and velvet ash species planted in Yunnan Province (22-26°N latitude) (Yang 2000; Zhao *et al.* 2012), which is as far south as the most southern distribution of ash species in North America. Conversely, there are only a few ash trees distributed in southern China and most of them are native and highly resistant species (Wei *et al.* 2004). In addition, non-Asian ash trees were customarily planted as street trees in northern China, whereas many native and other introduced tree species, such as *Cinnamomum camphora* Presl, *Ficus* spp., *Mangifera indica* L., and *Platanus* spp., are principally selected as street trees in southern China (Long *et al.* 2018). As a result, highly concentrated distributions of susceptible ash species in northern China might be the major reason for EAB outbreaks in these high latitude areas.

Increased populations of EAB in its native range enhanced invasion risk

Propagule pressure is perhaps the most important factor influencing the establishment of invasive species and increases with the size of species pools and higher pest populations from source regions (Brockhoff *et al.* 2014). Exotic tree species have been planted widely throughout the world as ornamental trees, for reforestation, to increase timber production, and in response to climate change; however, they may also facilitate biological invasion by associated pests (Ennos *et al.* 2019). With more extensive plantings of non-Asian ash trees in northern China since the 1970s, EAB outbreaks have become increasingly severe since the 1990s, thus elevating the risk of accidental introduction of EAB to other non-native ranges. For similar reasons, the widespread planting of exotic poplar trees since the 1950s in China might have also contributed to increases in propagule pressure of the Asian longhorned beetle (*Anoplophora glabripennis* (Motschulsky)) for accidental introduction to North America and Europe (Zhao *et al.* 2007; Hu *et al.* 2009).

Humans are important facilitators of forest insect pest spread, increasing both the frequency and severity of infestations through expanding global trade and domestic commerce (Koch & Smith 2010). The abundance of native woodboring beetles captured in traps near exporting ports was associated with nearby surrounding forests while non-native species captured within ports was associated with the volume of imports indicating that propagule pressure at exporting ports can serve as a source of species that can be potentially moved with exports (Rassati *et al.* 2018). The spread of EAB is characterized by stratified dispersal which includes both short-distance natural spread and long-distance human-assisted movement (Siegert *et al.* 2015). Most EAB adults disperse less than 100 m per flight when their host trees are close together (Barlow *et al.* 2014) but are capable of flying up to 7.2 km over a 4-day period in flight mills (Taylor *et al.* 2010). Estimated radial spread rates of infestations in North America have reached at least 13 km/year (Siegert *et al.* 2015). Long-distance dispersal of up to hundreds of kilometers usually result from human-assisted movement of host material including nursery stock, unprocessed logs, firewood, and branches trimmed from infested trees (Siegert *et al.* 2015). In North America, EAB has spread rapidly due to transportation of infested ash firewood and the abundance of susceptible host trees including green, white and velvet ash that are widely planted in south-central North America (MacFarlane & Meyer 2005; Herms & McCullough 2014). On the other hand, few susceptible exotic non-Asian ash trees have been introduced and planted in the central and southern regions of China and human activities such as transportation of ash firewood are not common. Consequently, differences in spread and distribution of EAB in North America and China may be related to the distributions of susceptible host plants and human activities.

In conclusion, our study demonstrated that widespread planting of non-Asian ash trees in northern China was significantly correlated to increasing outbreaks of EAB, ultimately resulting in accidental introduction of this invasive species to North America via commercial trade. The distribution, occurrence, and frequency of EAB outbreaks from 1960 to 2019 in China also suggest that native insect pests must reach a threshold population density before outbreaks occur on non-native host trees. Further, EAB infestation level was positively correlated with northern latitudes where more non-Asian ash trees were planted. Increased populations of pests in their native range along with increasing international trade may elevate the risk of invasion to non-occurrence regions. Historical analyses of the spatiotemporal dynamics and outbreaks of native insect pests can provide useful information on effective management in both native and invaded regions.

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AUTHOR CONTRIBUTIONS

Y.D. and K.W. contributed equally to this work. X.W. designed experiments. Y.D., K.W. and X.W. collected and analyzed the data and wrote the manuscript. J.D., D.J. and T.P. contributed to the substantial editing of later versions. All authors participated in preparation of this manuscript.

CONFLICT OF INTEREST

The authors declare no competing interest.

DATA AVAILABILITY STATEMENT

Ash species and site characteristics for field sites with EAB occurrences in China, and planting information of non-Asian ash trees in China are available from Supplementary Information. Other datasets generated and analyzed during this study are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

Supplementary 1 Table S1-S3 References in Table S2

Figures and Tables

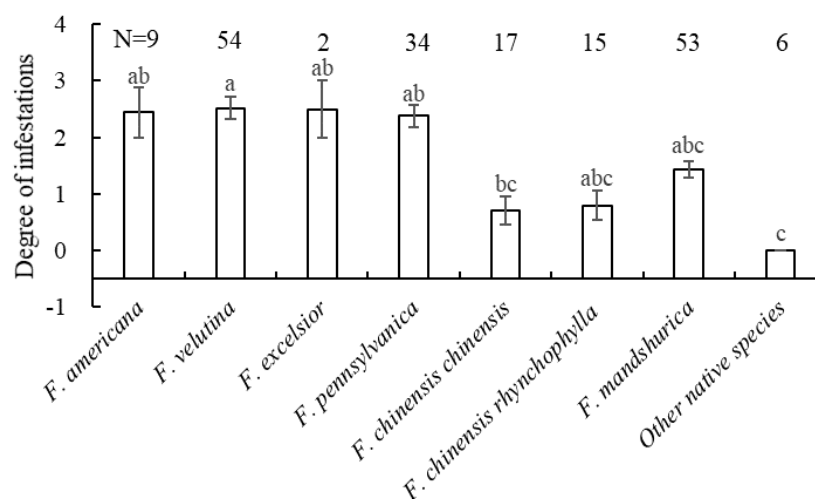
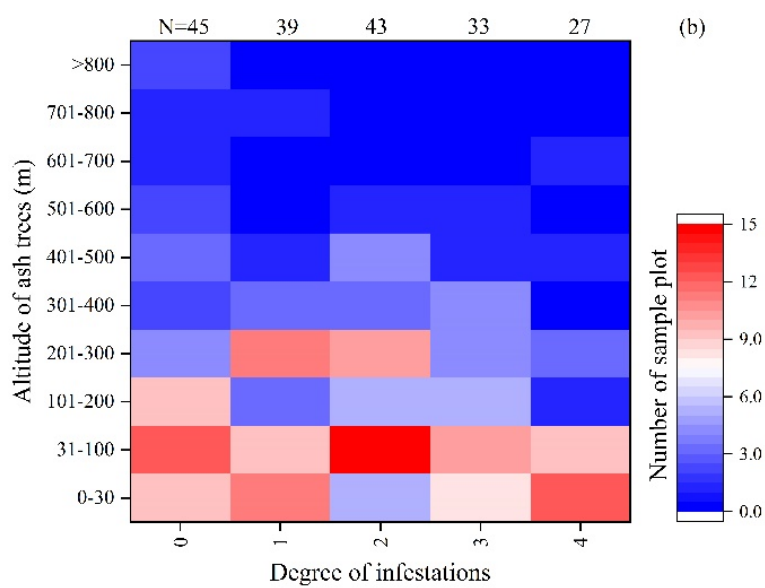
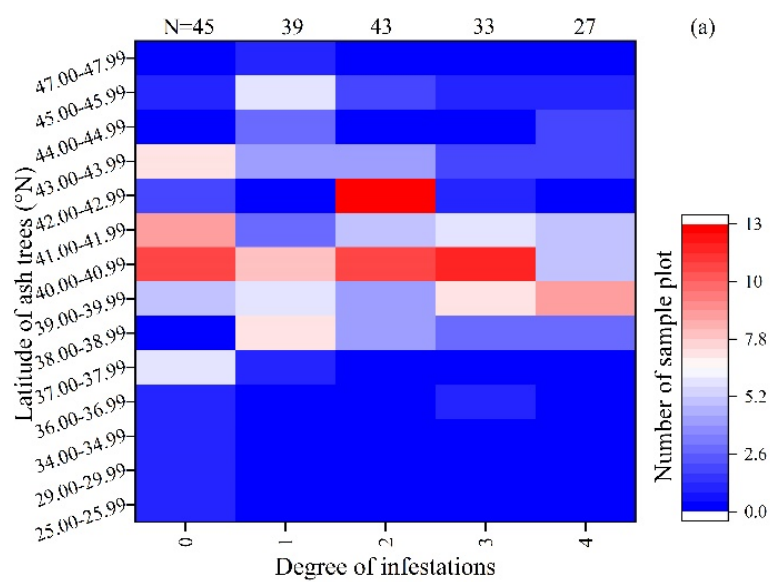


Figure 1 Degrees of EAB infestation for different species of ash trees in China. Bars with different lowercase letters indicate significant differences (Tukey test, $P < 0.05$), while the numbers above the bars represent the number of sample plots in which each ash species presented. The level of EAB infestation were graded on a scale of 0-4 according to the percentage of ash trees infested with EAB (0 = undamaged; 1 = slightly damaged, with less than 10% of trees infested; 2 = moderately damaged, with 10%-50% of trees infested; 3 = seriously damaged, with 50%-90% of trees infested; 4 = very seriously extremely damaged, with over 90% of trees infested). EAB was not detected in other native ash species including *F. angustifolia syriaca*, *F. baroniana*, *F. bungeana*, *F. griffithii*, *F. hubeiensis* and *F. platypoda*. These six ash species were combined as other native species for one-way ANOVA analysis since there was only one site for each species. The minimum ordinate value was set as -1 to highlight the degree of infestation level 0.



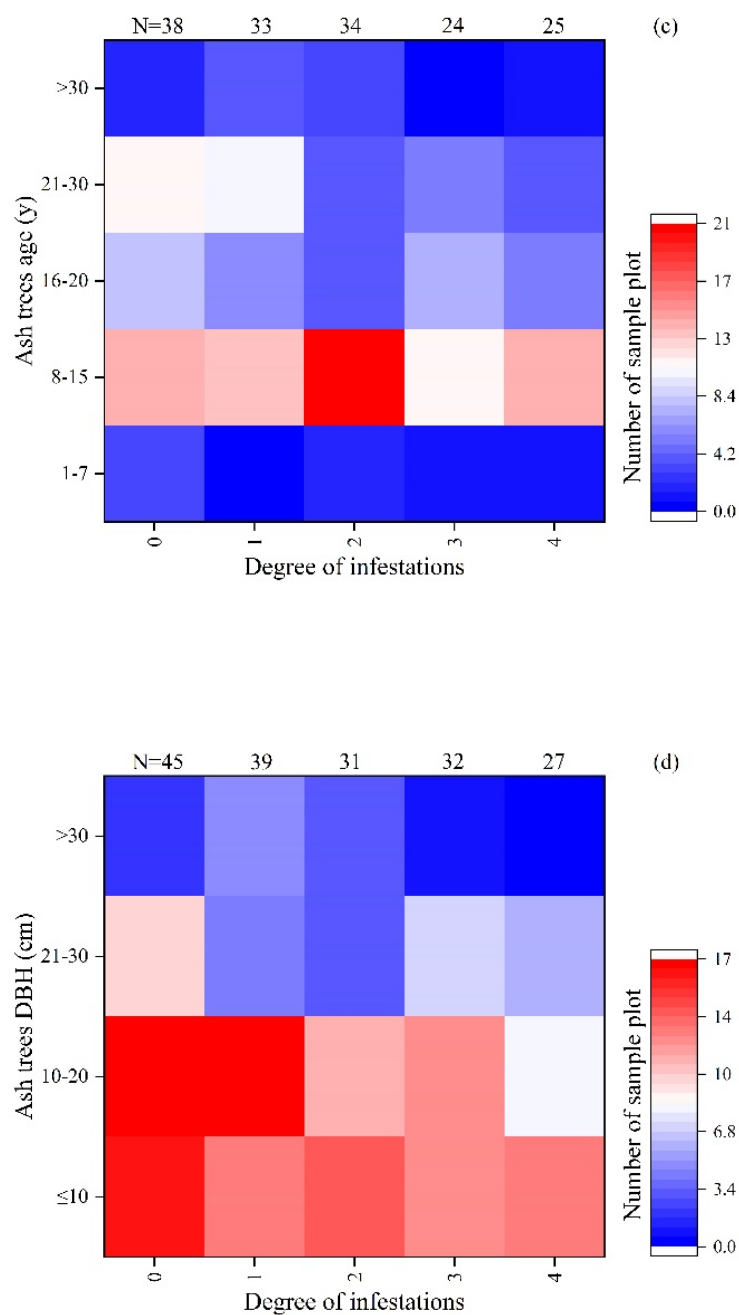


Figure 2 Number of sample plots of ash trees (all ash species combined) within each EAB infestation degree category by (a) latitudinal range, (b) altitudinal range, (c) age class, and (d) DBH class. The numbers of sample plots of ash trees in each EAB infestation degree category are given above the heat maps. (See **Figure 1** legend for explanation of degrees of EAB infestation).

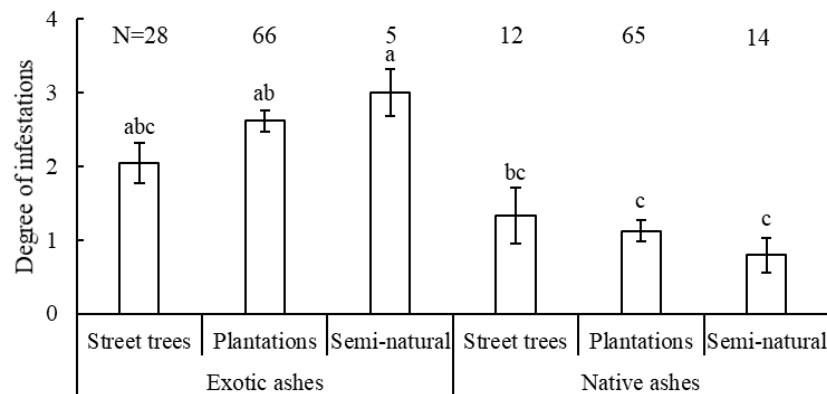
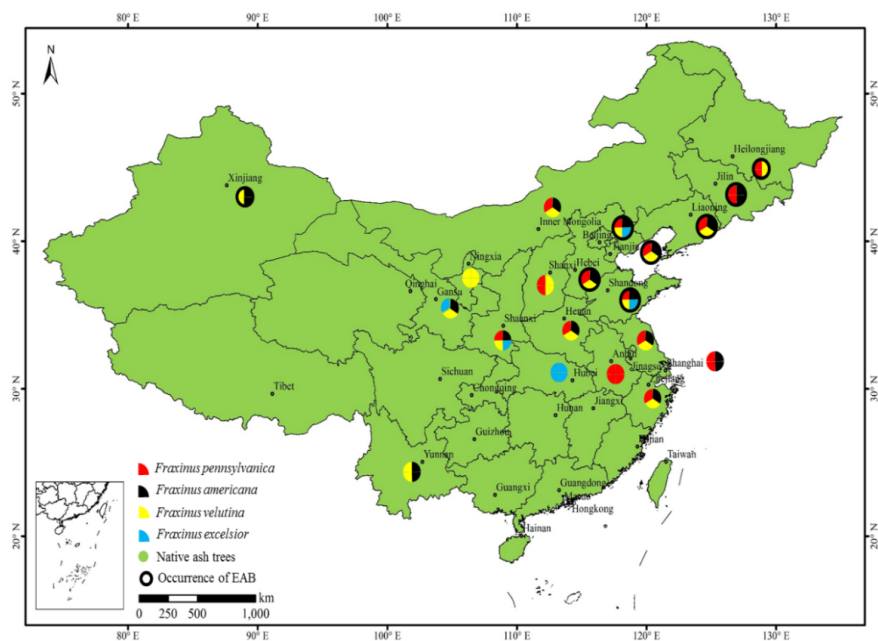


Figure 3 Degree of EAB infestation for ash trees growing different habitats in China. Habitats were divided into three categories: (i) street trees: trees on roadsides; (ii) plantations: trees in parks, courtyards, neighborhoods, university campuses or nurseries; (iii) semi-natural conditions: trees growing in natural ecosystems or natural regenerations. (See **Figure 1** legend for explanation of degrees of EAB infestation, ordinate value, statistical analysis).



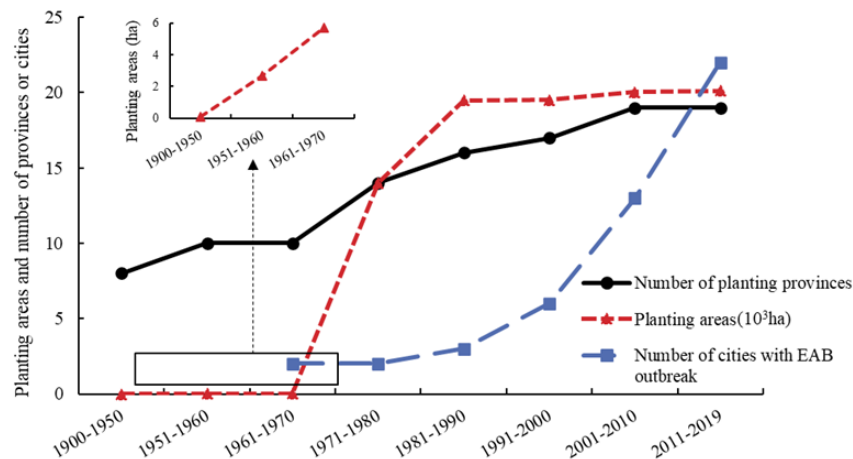


Figure 4 Ash tree distribution and EAB presence in China from 1900 to 2019. (a) The green background indicates the range of native Asian ash species which are widely distributed in all 34 provinces, provincial cities, or regions in China. Red, black, yellow, and blue quadrants indicate locations where exotic green, white, velvet, or European ash trees were planted, respectively. Black circles indicate the presence of EAB infestations. (b) Relationships between the plantings of non-Asian ash trees and EAB outbreak in China from 1900 to 2019. The insert figure represents an enlarged display of ash plantings from 1900 to 1970.

Table 1 Historical outbreaks of EAB in China

Years	Host plants	Provinces, provincial cities or regions with E
1961-1970	<i>F. pennsylvanica</i> ¹	Heilongjiang and Liaoning
1971-1980	<i>F. pennsylvanica</i> ¹	Heilongjiang and Liaoning
1981-1990	<i>F. pennsylvanica</i> , <i>F. velutina</i>	Heilongjiang, Liaoning and Tianjin
1991-2000	<i>F. pennsylvanica</i> , <i>F. velutina</i>	Heilongjiang, Liaoning, Tianjin, and Beijing
2001-2010	<i>F. pennsylvanica</i> , <i>F. velutina</i> , <i>F. americana</i> , <i>F. excelsior</i>	Heilongjiang, Liaoning, Tianjin, Beijing, Jilin, and L
2011-2019	<i>F. pennsylvanica</i> , <i>F. velutina</i> , <i>F. americana</i> , <i>F. excelsior</i>	Heilongjiang, Liaoning, Tianjin, Beijing, Jilin, Hebe

1 Introduction records of exotic ash trees in China, suggest that *F. americana* was not introduced into northeast China before the 1960s (Pan & You 1994). *F. pennsylvanica* nursery trees were probably planted there at that time, but called American ash and sold by Shenyang Xingnongyuan Seedling Company. **2** Details for locations and sampling for field surveys are provided in Table S1.

Table 2 Species of ash trees sampled and mean (\pm SE) canopy index, bark split ranking, and percentage of trees infested with EAB for each species at the Institute of Botany, Chinese Academy of Sciences, Beijing, 2012-2013.

Scientific name	Common name	Geographic distribution	Number of trees
<i>F. americana</i>	White ash	Eastern North America	22
<i>F. pennsylvanica</i> ¹	Green ash	Eastern North America	25
<i>F. velutina</i>	Velvet ash	Western and southwestern North America	17
<i>F. excelsior</i> ²	European ash	Western Palearctic (Europe, north Africa and southwest Asia)	7
<i>F. mandshurica</i>	Manchurian ash	Eastern Palearctic (central and east Asia)	13
<i>F. chinensis</i> ³	Chinese ash	Eastern Palearctic (central and east Asia)	17

Scientific name	Common name	Geographic distribution	Number of trees
<i>F. hubeiensis</i>	Hubei ash	Eastern Palearctic (central and east Asia)	3
<i>F. baroniana</i>	Narrow-leaf ash	Eastern Palearctic (central and east Asia)	5
<i>F. bungeana</i> ⁴	Small-leaf ash	Eastern Palearctic (central and east Asia)	1

1 *F. pennsylvanica* var. *lanceolata* (Borkh.) Sarg. (syn. var. *subintegerrima* (Vahl) Fern. was combined with *F. pennsylvanica* Marshall. **2** *F. excelsior* var. *aurea* was combined with *F. excelsior* L. **3** *F. rhynchophylla* Hance and *F. chinensis rhynchophylla* (= *F. chinensis* Roxb. subsp. *rhynchophylla* (Hance) A. E. Murray) were combined with *F. chinensis* Roxb. **4** The sample size was too small to be included in one-way ANOVA. **5** Canopy index: 1 = over 80% live crown; 2 = 60%-79%; 3 = 40%-59%; 4 = 20%-39%; 5 = below 20%. **6** bark splits: 0 = absent; 1 = present; 5-7. Means within a column followed by different lowercase letters are significantly different (Tukey test, $\alpha=0.05$).