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RESEARCH ARTICLE

Introduced plants induce outbreaks of a native pest and facilitate invasion in the plants' native range: Evidence from the emerald ash borer

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Abstract

1. Biological invasions are among the most serious threats to native forest ecosystems worldwide due to ever-increasing international trade and global change. Understanding the invasion processes and ecology of invasive pests in both newly invaded and native habitats is necessary to effectively manage the risks they pose.
2. The emerald ash borer (EAB), *Agrilus planipennis*, is one of the most devastating invasive forest insect pests in North America and has also invaded European Russia and parts of Europe. Through synthesizing historical data spanning >100 years and contemporary field observations in China, we examined EAB's distribution, occurrence and outbreak frequency in its native range in relation to historical introductions and plantings of non-Asian ash trees in China.
3. The frequencies and levels of EAB infestations in China gradually increased from 1900 to 2021 after a time-lag of 30–50 years following introductions and widespread plantings of non-Asian ash trees from North America. Increased frequencies of EAB outbreaks following the planting of North American ash trees in China may have increased the risk of EAB invading North America and other novel regions.
4. *Synthesis*. Our findings demonstrated that planting susceptible non-native host plants can induce outbreaks of a native insect pest in its native range, which, in turn, may enhance risks of invading novel regions via human-assisted activities (e.g. international trade). In addition, our findings suggest that lag-times of several decades between planting susceptible hosts and initial pest outbreaks may pose challenges in predicting the true risk of invading novel regions. Consequently, comprehensive risk assessment for invasive insect pests should consider the role of non-native plants introduced or planted in the pest's native range.

KEYWORDS
Agrilus planipennis, ash trees, biological invasion, insect–plant interactions, native range, population dynamics, risk assessment

Yingqiao Dang and Ke Wei contributed equally.

1 | 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 (Herms & McCullough, 2014; Jones, 2019).

Native to northeastern Asia, the emerald ash borer (EAB), *Agrilus planipennis*, 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, 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.; Herms & McCullough, 2014). More recently, this beetle has also been discovered attacking the white fringe tree, *Chionanthus virginicus*, native to the southern U.S. and commonly planted as an ornamental and landscape tree throughout the region (Peterson & Cipollini, 2017). In a recent laboratory study, EAB also completed development on olive trees, *Olea europaea*, 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 (EAB Info, 2020).

All species of North American ash appear susceptible to EAB (Anulewicz et al., 2008); however, preference and susceptibility vary among species. *Fraxinus pennsylvanica* (green ash) trees were preferred and had higher levels of canopy dieback and EAB densities compared to *F. americana* (white ash) trees at the same sites, while *F. americana* was preferred over *F. quadrangulata* (blue ash) trees (Anulewicz et al., 2007; Tanis & McCullough, 2012). *Fraxinus pennsylvanica* and *F. americana* cultivars had higher levels of EAB attack density and mortality than a *F. mandshurica* (manchurian ash) 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 defence compounds (Whitehill et al., 2012). For instance, EAB adults appeared to prefer feeding on *F. pennsylvanica*, *F. americana* and *F. nigra* (black ash) leaves compared to *F. excelsior* (European ash), *F. quadrangulata* or *F. mandshurica* 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, 2015) and newly invaded ranges (Duan et al., 2018) has greatly increased. In North America, EAB has established populations in warmer climate zones (as far south as 32°N; EAB Info, 2020; McConnell et al., 2019) than in its native range in China (as far south as 36°N; Orlova-Bienkowskaja & Volkovitsh, 2018). Although anecdotal observations suggest EAB outbreaks in China arose after widespread planting of non-Asian ash trees, empirical data on tree planting and development of EAB infestations have never been gathered and analysed to determine any relationship, including the role of potential contributing factors such as tree species and geographical location. Hence, the cause of EAB outbreaks in China, and the apparent broader distribution in more southern and warmer climate zones in its invaded range are currently unknown.

In the present study, we conducted field surveys from 2003 to 2021 and reviewed associated literature published since 1900 to gather and analyse historical data on EAB occurrence, distribution and outbreaks in China, and examined the role of host plants (ash species) in influencing the spatiotemporal dynamics of EAB occurrence or outbreaks. Through analysing historical data along with field observations of EAB occurrence and host tree and site characteristics, we aimed to determine the causes of EAB outbreaks and EAB's geographical distribution in its native range. Furthermore, we sought to investigate the possible link between increased EAB outbreaks in its native range with the invasion of North America and other regions. Findings from the present study should improve our understanding of EAB's geographical distribution in both its native and invaded ranges, and would contribute to the development of sustainable management strategies against EAB.

2 | MATERIALS AND METHODS

2.1 | Current and historical occurrences of EAB in China

To determine the recent occurrence and distribution of EAB infestations in China, we obtained data from field surveys conducted from 2003 to 2021 in 13 regions of China (Table S1), as well as records from literature and reports of local faunas about the presence of EAB infestations. An EAB infestation was defined as an area with visibly damaged ash trees that displayed characteristic signs of EAB attack including D-shaped emergence holes or bark splits that form

over larval galleries as a potential tree defence mechanism to expose larvae to unfavourable weather conditions or natural enemies. We considered an infestation to be at outbreak level when EAB abundance increased within a period of 1–3 years resulting in more than 50% of trees being infested.

Sample sites for field surveys included the following: (a) areas within EAB's distribution with reports of EAB infestations or outbreaks, (b) areas suspected to be within EAB's distribution with records of EAB presence which required verification by field investigation but no damage reports and (c) areas with ash tree species but no historical records of EAB presence or infestation. Sample habitats were divided into three categories: (i) street trees: trees on roadsides; (ii) plantations: trees in parks, courtyards, neighbourhoods, university campuses or nurseries; and (iii) semi-natural conditions: trees growing in natural ecosystems or natural regenerations. A total of 83 sample plots (1-ha plantation or semi-natural site, or a site with at least 400 street trees) were arbitrarily selected (Table S1). In all, 30 ash trees were then randomly selected in each plot to determine the percentage of infested ash trees (n, where n = number of infested ash trees /30 × 100). The degree of EAB infestation was graded on a scale of 0–4 based on the percentage of infested ash trees (n): 0 = undamaged, with $n = 0$; 1 = slightly damaged, with $0 < n < 10\%$; 2 = moderately damaged, with $10\% \leq n < 50\%$; 3 = seriously damaged, with $50\% \leq n < 90\%$; 4 = extremely damaged, with $n \geq 90\%$.

The process of collecting and analysing different data types (especially for old records) can be challenging as the target species received little attention for many years. To overcome limitations and determine the historical occurrence and distribution of EAB infestations, we searched the National Science Database of Forestry (www.lknet.ac.cn/sztsg.htm) using all synonyms for EAB, that is, scientific name '*Agrilus planipennis*' or '*Agrilus marcopoli*' as well as Chinese common names 'Bai La Zhai Ji Ding' and 'Hua Qu Liu Zhai Ji Ding', as search terms, respectively. Additionally, other non-internet resources such as books and reports of local faunas were also searched (Supplementary References). We found a total of 225 publications of which 17 included details of EAB occurrences, host plant species and their locations in China (listed in Supplementary References), from 1900 to 2021. These publications were used to retrieve historical data on EAB infestations in China. Data retrieved from the publications included the year(s), provinces and cities (prefecture-level cities or districts) of EAB occurrence, infested host plant species and the degree of EAB infestation 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 2021. The regions of EAB infestations were recorded as provinces and the exact cities.

2.2 | Variables related to EAB occurrences in China

Seven variables, including degree of EAB infestation, host tree species, age, and size, habitat, latitude and elevation, were recorded during field surveys in 13 regions of China from 2003 to 2021. Host tree size was measured as diameter at breast height (DBH). The degree of EAB infestation was graded as described above.

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. *Fraxinus pennsylvanica* var. *lanceolata* (Borkh.) Sarg. (syn. var. *subintegerrima* (Vahl) Fern.) was combined with *F. pennsylvanica* Marshall. *Fraxinus excelsior* var. *aurea* was combined with *F. excelsior* L. *Fraxinus rhynchophylla* Hance and *F. chinensis rhynchophylla* (=*F. chinensis* Roxb. subsp. *rhynchophylla* (Hance) A. E. Murray) were combined with *F. chinensis* Roxb. All of the 39 native and 71 non-Asian ash trees in the 2.5 ha Oleaceae Common Garden were investigated and the data were collected on the same seven variables as well as canopy condition, presence of bark splits and presence of EAB infestation on individual trees. Canopy condition was assigned an index on a scale with five levels based on the percentage of live crown (m): (1) $m \geq 80\%$, (2) $60\% \leq m < 80\%$, (3) $40\% \leq m < 60\%$, (4) $20\% \leq m < 40\%$ and (5) $m < 20\%$. Both presence of bark splits and EAB infestation were 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 2021. All data were used to determine differences between the response variable degree of EAB infestation and the independent variables in the tree host and environmental categories.

2.3 | 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 in formal databases and other informal reports especially for non-English publications (e.g., local fauna reports) from 1900 to 2021 (Supplementary References). We used the search terms '*Fraxinus* and China' in Web of Science and 'tree and introduction and Bai La' (Bai La: Chinese common name of *Fraxinus*) in the National Science Database of Forestry (www.lknet.ac.cn/sztsg.htm) to retrieve publications from 1900 to 2021. These searches generated 655 and 105 results, respectively, of which 27 publications (Table S2) included details about introduced non-Asian ash trees including ash tree species, planting year, name of province with ash tree plantation, number of these provinces, number of plantings and total area of plantations. Data on five variables were obtained from these 27 publications, including plantings of non-Asian ash trees, planting year, planting provinces, planting times and planting areas. Planting years were divided into eight time periods from 1900 to 2021 (1900–1950 as the first period followed by 10-year periods) and all data on ash tree species, times and areas of plantings were summed for each time period. Data on the distribution

of native ash species were obtained from Flora of China (CAS-EBF, 1992). Finally, we mapped the geographical distributions of native and non-Asian ash trees in China. The planting areas of non-Asian ash species, number of provinces with non-Asian ash plantations and numbers of cities with EAB present were summed during each time period from 1900 to 2021 to determine the temporal distribution characteristics of EAB in China.

EAB is not native to North America and had never been reported on the continent prior to 2002 (Herms & McCullough, 2014). Molecular analyses of AFLP fingerprints, alleles at two microsatellite loci and mtDNA cytochrome oxidase subunit I gene (COI; 439 bp) sequences revealed North American populations of EAB originated from China and were most closely related to populations from Hebei and Tianjin (Bray et al., 2011). Thus, based on the information on EAB infestations and ash tree distributions in China mentioned above, we then collected data on the occurrence of EAB and planting records of its susceptible host trees in North America (the United States and Canada) prior to 2021 to further explore the impact of EAB infestations and its host plants in its native ranges on EAB population dynamics in its invasive ranges. Occurrences and spread of EAB in North America were obtained from the literature (Siegert et al., 2014) and EAB timelines in http://www.emeraldashborer.info/about-eab.php. The geographical distribution (at the level of states or provinces) of ash trees susceptible to EAB (*F. pennsylvanica*, *F. americana*, *F. velutina* (velvet ash), *F. quadrangulata*, *F. nigra*, *F. excelsior* and *F. uhdei* (tropical ash)) in North America were collected from GBIF (https://www.gbif.org/). Finally, the temporal relationship between ash plantings and EAB infestations in China and North America from 1900 to 2021 was explored using the number of both states/provinces/cities with EAB infestations and states/provinces with susceptible host trees in these two regions. All these data were summed during each time period from 1900 to 2021.

2.4 | Statistical analyses

Under a completely randomized design, we first combined EAB infestation data obtained from historical publications with the two sets of field collected data (the field surveys 2003–2021, and the common garden field study 2012–2013). Then, we used a generalized linear mixed model (GLMM) with the multinomial distribution and the cumulative logit link function to analyse the relationships between degree of EAB infestation (as an ordinal dependent variable) and host tree species, habitat, latitude, elevation, host tree age and DBH. Host tree species and habitat were set as nominal variables, while latitude, elevation, host tree age and DBH were set as continuous variables. We tested for multicollinearity among the continuous variables (latitude, elevation, host tree age and DBH) using multiple linear regression based on the variance inflation factor (VIF) and tolerance (TOL) prior to including them in the final GLMM. We found no strong evidence of multicollinearity among these variables as indicated by our models VIF < 1.6 and TOL > 0.6 (Allison, 1999). For nominal (tree species and habitat type) variables with significant effects on the degree of EAB infestation based on GLMM, differences between species or habitats were determined using post-hoc pairwise chi-square analyses or Fisher's exact tests. Fisher's exact test was selected over chi-square analyses when more than 20% of the expected counts for each cell was less than five (Campbell, 2007).

Similarly, using EAB infestation data obtained from the common garden field study in 2012–2013, GLMM with the multinomial distribution and the cumulative logit link function was used to evaluate the effects of ash tree species (as an independent variable) on canopy index (as an ordinal dependent variable). If significant effects of ash species were detected via GLMM, we then conducted pairwise chi-square tests and Fisher's exact test (with the Bonferroni adjustment) to detect the significance of difference between ash species. Additionally, GLMMs with the binomial distribution and the logit link function were also used to evaluate the effects of ash tree species (as an independent variable) on bark splits, and EAB infestations (as binomial dependent variables), respectively.

All these analyses were conducted using SAS software version 9.4 (SAS Institute Inc., 2013). When determining the trend of EAB infestation levels in relation to host tree age, size and geographical distribution, box plots with number of sample plots by age, DBH, and latitudinal and elevational distributions of ash species were plotted by EAB infestation levels using OriginPro 2018 (OriginLab, 2018).

3 | RESULTS

3.1 | The frequency of EAB outbreaks in China has increased since the 1960s

Data from historical literature reveal no records of EAB outbreaks on ash trees in China prior to 1960. The first reported outbreaks of EAB occurred on *F. pennsylvanica* in Heilongjiang and Liaoning provinces in 1961 and 1963, respectively. The total numbers of cities and provinces with EAB outbreaks have increased each decade since 1961 (Table S3). Since the 2010s, EAB was detected in Inner Mongolia and Xinjiang-Uygur Autonomous regions, and Shanxi and Shandong provinces, where it has caused substantial damage to non-Asian ash trees (*F. pennsylvanica*, *F. americana* and *F. velutina*). To date, EAB outbreaks have been recorded in 10 provinces in northeastern, northern and northwestern China and the numbers of cities with EAB outbreaks have increased 10-fold (Table S3).

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

There was a significant effect of ash species on EAB infestation levels based on historical and field survey data (Table 1). North American and European ash species, including *F. velutina*, *F. pennsylvanica*, *F. americana* and *F. excelsior*, had significantly higher levels of EAB infestations in comparison with native ash species across China (Figure S1).

In comparison to heavy infestations on non-Asian ash species in China, EAB caused minimal damage to the four native ash species commonly used as hosts, namely *F. mandshurica*, *F. chinensis chinensis* (Chinese ash), *F. chinensis rhynchophylla* (Korean ash) and *F. angustifolia syriaca* (Syrian ash). In addition, the other five native ash species, including *F. baroniana* (Baron's ash), *F. bungeana* (Bunge ash), *F. griffithii* (Griffith ash), *F. hubeiensis* (Hubei ash in Chinese) and *F. platypoda* (Xiang La tree in Chinese), have never been found to be attacked by EAB (Figure S1).

There were significant differences in the EAB infestation indices among the nine (four non-Asian and five native) species of ash planted in the Oleaceae Common Garden, all non-Asian ash had much higher levels of EAB infestations 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.

3.3 | EAB infestation levels were strongly influenced by the latitudinal distribution of ash species in China

There were significant differences in the levels of EAB infestations among different latitudes of ash trees in China with all EAB infestations occurring in northern latitudes (Figure 1A; Table 1), while there

TABLE 1 Statistical details of the generalized linear mixed model analyses used in exploration of the effects of ash tree species, latitude, elevation, host tree age and diameter at breast height (DBH), and habitats on the degree of emerald ash borer infestation

	Statistics			
Independent variable	***N***	***df***	***F***	***p***
Ash tree species	135	9, 116	3.64	0.0005
Latitude of ash trees	135	1, 116	7.81	0.0061
Elevation of ash trees	135	1, 116	0.18	0.6725
Ash tree age	135	1, 116	0.06	0.8039
Ash tree DBH	135	1, 116	0.72	0.3986
Habitats without considering the origin of ash species	135	2,116	0.67	0.5141
Habitats considering the origin of ash species	195	5, 186	10.22	<0.0001

TABLE 2 Species of ash trees sampled and mean (± *SE*) canopy index, bark split ranking and percentage of trees infested with emerald ash borer (EAB) for each species in the Oleaceae common garden study at the Institute of Botany, Chinese Academy of Sciences, Beijing, 2012–2013

Scientific name	Common name	Geographical distribution	Number of trees sampled	Canopy index[6]	Bark splits[7]	Percentage of infested trees (%)[8]
F. americana	White ash	Eastern North America	22	2.09 ± 0.33 bc	0.59 ± 0.11 ab	59.09 ± 0.11 ab
F. pennsylvanica[1]	Green ash	Eastern North America	25	3.72 ± 0.32 ab	0.84 ± 0.07 ab	84.00 ± 0.07 a
F. velutina	Velvet ash	Western and southwestern North America	17	4.35 ± 0.28 a	0.88 ± 0.08 a	100.00 ± 0.00[5]
F. excelsior[2]	European ash	Western Palearctic (Europe, north Africa and southwest Asia)	7	3.71 ± 0.52 ab	0.86 ± 0.14 ab	85.71 ± 0.14 a
F. mandshurica	Manchurian ash	Eastern Palearctic (central and east Asia)	13	1.31 ± 0.17 c	0.15 ± 0.10 b	7.69 ± 0.08 b
F. chinensis[3]	Chinese ash	Eastern Palearctic (central and east Asia)	17	1.71 ± 0.38 c	0.29 ± 0.11 b	17.65 ± 0.10 ab
F. hubeiensis[4]	Hubei ash	Eastern Palearctic (central and east Asia)	3	1.00 ± 0.00	0.00	0.00
F. baroniana[4]	Baron's ash	Eastern Palearctic (central and east Asia)	5	1.00 ± 0.00	0.00	0.00
F. bungeana[4]	Bunge ash	Eastern Palearctic (central and east Asia)	1	1.00 ± 0.00	0.00	0.00

Notes: [1]*Fraxinus pennsylvanica* var. *lanceolata* (Borkh.) Sarg. (syn. var. *subintegerrima* (Vahl) Fern.) was combined with *F. pennsylvanica* Marshall. [2]*Fraxinus excelsior* var. *aurea* was combined with *F. excelsior* L. [3]*Fraxinus rhynchophylla* Hance and *F. chinensis rhynchophylla* (=*F. chinensis* Roxb. subsp. *rhynchophylla* (Hance) A. E. Murray) were combined with *F. chinensis* Roxb. [4]These ash trees were not included in generalized linear mixed model (GLMM) as there was no EAB infestation among them. [5]The infestation GLMM did not include *F. velutina* as all these sample trees showed the same values without standard error. [6]Canopy condition was assigned an index on a scale with five levels based on the percentage of live crown (*m*): (1) $m \geq 80\%$, (2) $60\% \leq m < 80\%$, (3) $40\% \leq m < 60\%$, (4) $20\% \leq m < 40\%$, (5) $m < 20\%$. [7]Bark splits: 0 = absent, 1 = present. [8]Percentage of infested trees was calculated from presence of EAB infestation on individual trees, 0 = absent, 1 = present. [6–8]Means within a column followed by different lowercase letters were significantly different ($n = 101$, $df = 5, 92$, $F = 7.39$, $p < 0.0001$ for canopy index; $n = 101$, $df = 5, 95$, $F = 4.97$, $p = 0.0004$ for bark splits; and $n = 84$, $df = 4, 79$, $F = 5.90$, $p = 0.0003$ for presence of EAB infestation; with GLMM).

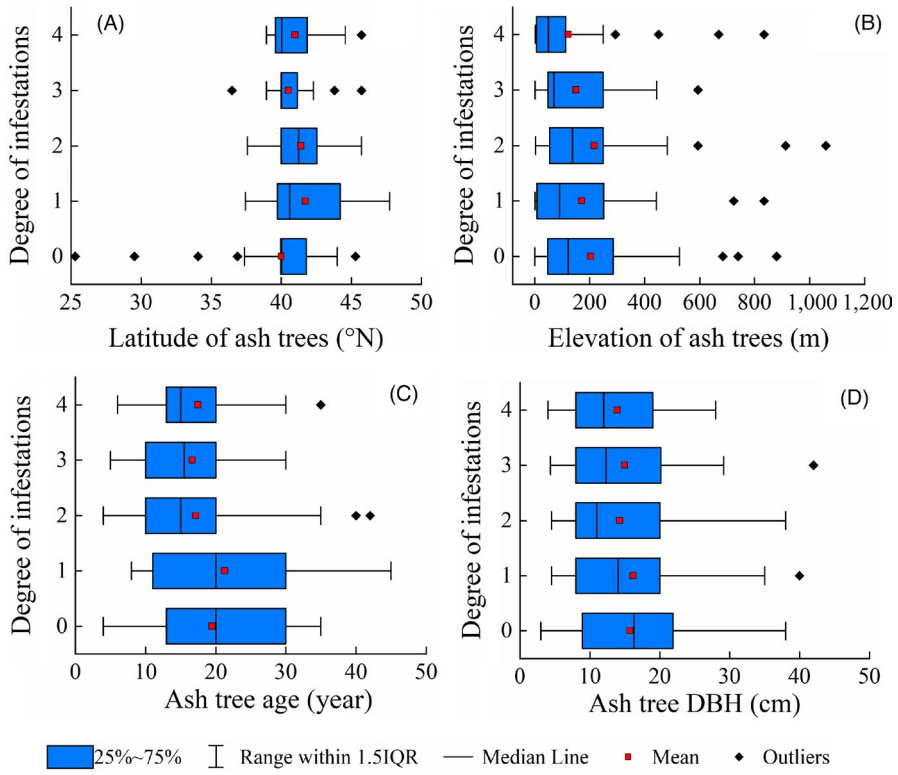

FIGURE 1 Effects of (A) latitude, (B) elevation, (C) ash tree age and (D) diameter at breast height (DBH) on the degree of emerald ash borer (EAB) infestation. A total of 83 plots were surveyed across 13 regions in China from 2003 to 2021, and historical literature was reviewed from 1961 to 2021. The degree of EAB infestation was graded on a scale of 0–4 according to the percentage of ash trees infested with EAB (*n*) (0 = undamaged, with $n = 0$; 1 = slightly damaged, with $0 < n < 10\%$; 2 = moderately damaged, with $10\% \le n < 50\%$; 3 = seriously damaged, with $50\% \le n < 90\%$; 4 = extremely damaged, with $n \ge 90\%$). Significantly more sample plots with EAB infestations were found at higher latitudes, while there was no significant difference in degrees of EAB infestations among different elevations, ash ages or ash DBH

was no significant difference in EAB infestation levels by ash tree elevation (Figure 1B; Table 1). Similarly, there were no significant differences in EAB infestation levels among ash trees of different ages and sizes (Figure 1C,D; Table 1). In addition, there were no significant differences in EAB infestation levels among different habitats without considering the origin category of ash species (Table 1), while EAB infestation levels in non-Asian ash trees were always more severe when compared to their native congeners within the same habitat (Figure 2; Table 1).

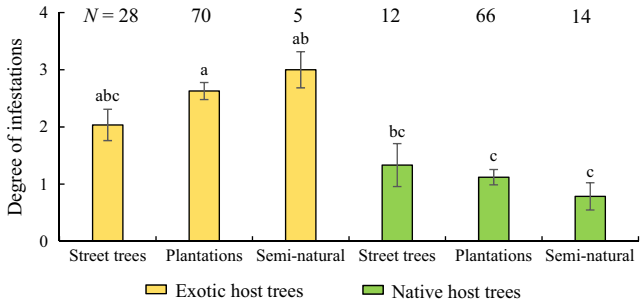

FIGURE 2 Degree of emerald ash borer (EAB) infestation for exotic (yellow bars) and native (green bars) ash trees growing in different habitats in China. Habitats of 83 sample plots surveyed from 2003 to 2021 along with those obtained from historical literature from 1961 to 2021 were divided into three categories: (i) street trees: trees on roadsides; (ii) plantations: trees in parks, courtyards, neighbourhoods, university campuses or nurseries; and (iii) semi-natural conditions: trees growing in natural ecosystems or natural regenerations. Bars with different lowercase letters indicate significant differences, while the numbers above the bars represent the number of sample plots within each habitat category (see Figure 1 legend for explanation of degree of EAB infestation)

3.4 | EAB outbreaks did not immediately coincide with widespread plantings of non-Asian ash trees

Field surveys and reports of ash species distribution, introductions and plantings in literature sources indicated that native Asian ash species, typically *F. chinensis* and *F. mandshurica*, were widely distributed in China. However, *F. americana*, *F. pennsylvanica*, *F. velutina* and other non-Asian ash species were also frequently found in northern China and some cities of central and southern China (Figure 3A). In northern China, EAB infestations were detected in 10 of 14 provinces where non-Asian ash species were present (Figure 3A). Non-Asian ash trees have been introduced into China since the early 1900s over an increasingly wide geographical range (Figure 3B). 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 since the 2010s according to historical data analysis. However, EAB outbreaks did not immediately coincide with widespread 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 (Figure 3B).

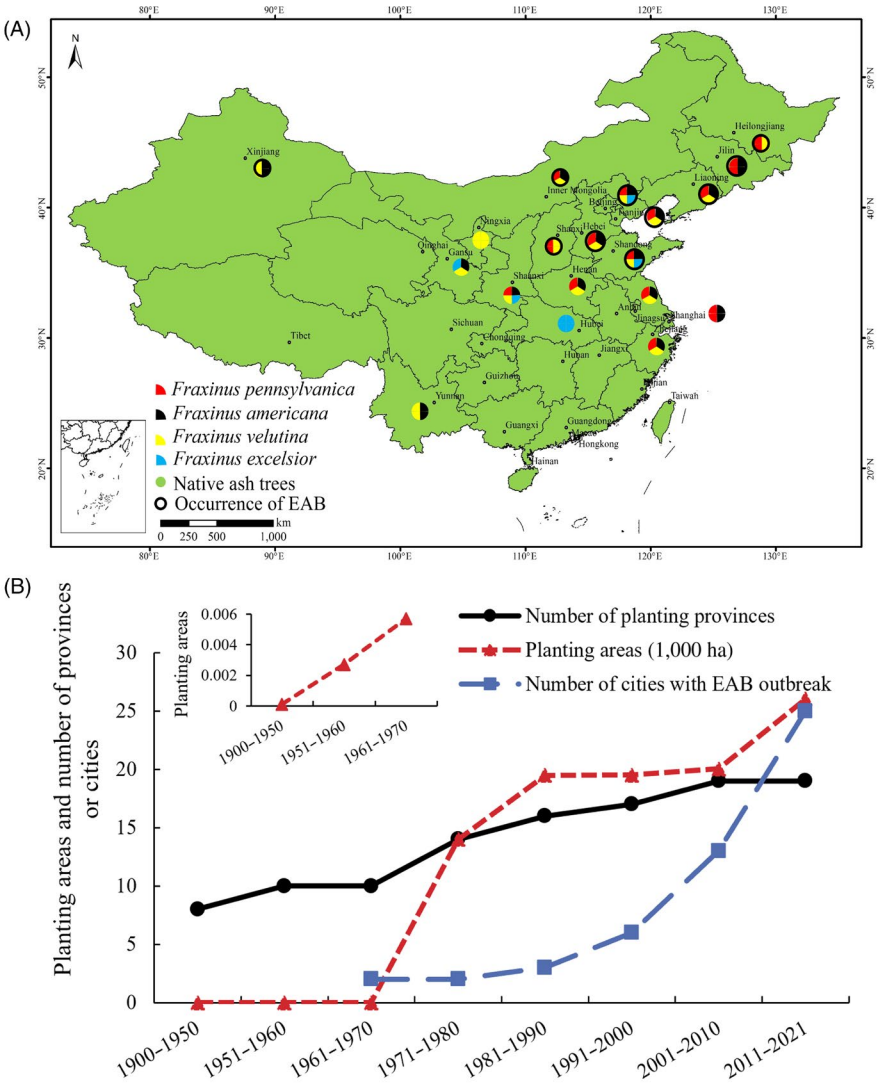

FIGURE 3 Ash tree distribution and emerald ash borer (EAB) presence in China based on historical literature from 1900 to 2021 and field surveys from 2003 to 2021. (A) The green background indicates the range of native Asian ash species across the entire period from 1900 to 2021 which are widely distributed in all 34 provinces in China. Red, black, yellow and blue symbol quadrants indicate locations where *F. pennsylvanica*, *F. americana*, *F. velutina* and *F. excelsior* (non-Asian ash species) were planted, respectively. Symbols outlines with black circles indicate the presence of EAB infestations. (B) Relationships between the number and area of non-Asian ash tree plantings and EAB outbreaks over time in China from 1900 to 2021. The insert figure represents an enlarged display of ash plantings from 1900 to 1970

3.5 | Widespread plantings of North American ash trees and subsequent EAB outbreaks in China preceded the EAB outbreak in North America

Based on genetic analysis of EAB populations in its native and invaded regions, North American EAB populations are thought to have been introduced from Hebei or Tianjin, China (Bray et al., 2011). This conclusion is also supported by timelines of EAB infestations and ash plantings in both regions. At least 16 species of ash trees are native and widely distributed in natural forests of North America. In addition, cultivars of *F. pennsylvanica* and *F. americana* have been commonly planted as landscape trees in urban areas since the 1940s (MacFarlane & Meyer, 2005). EAB was detected in North America in 2002 (Figure 4; Herms & McCullough, 2014) and based on dendrochronological reconstruction of infestation, it was likely introduced in the 1990s (Siegert et al., 2014). Widespread plantings of North American ash trees and subsequent EAB outbreaks in China preceded the EAB outbreak in North America. While the outbreak in North America was correlated with increasing North American ash plantings and EAB populations in China, the outbreaks in China began at least 2–4 decades before those in North America (Figure 4).

4 | DISCUSSION

4.1 | Planting 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), yet the first reported outbreak of EAB was recorded on *F. pennsylvanica* in northeastern China in the early 1960s (Wei et al., 2004). We conclude that introductions and widespread plantings of non-Asian ash trees in northern China triggered the EAB outbreak. Our conclusion is supported by analysis of historical data and significant findings between EAB infestation levels and non-Asian ash species and areas where they were planted. However, there was approximately a 50-year time-lag between these events. For example,

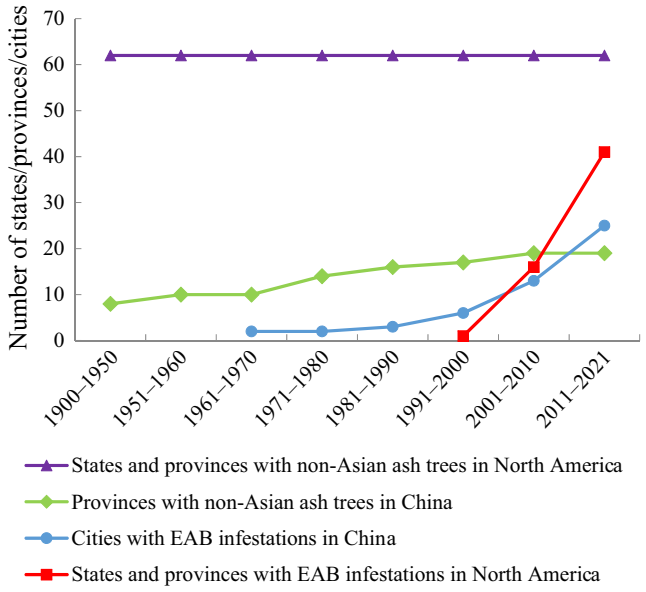

FIGURE 4 Non-Asian ash trees and emerald ash borer (EAB) infestations in China and North America from 1900 to 2021

F. pennsylvanica was first introduced into northeastern China, Beijing City and Shandong Province in the late 19th and early 20th centuries. *Fraxinus americana* was sporadically but continually planted in Beijing, Shandong, Xinjiang, Henan and Jiangsu provinces in the early 20th century. *Fraxinus velutina* 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-Asian 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 it may take a substantial amount of time for EAB population density to increase sufficiently to cause outbreaks in its native ranges.

Insect pests often take some time to adapt to new host species or a new habitat (Evans & Dooley, 2013). For EAB, adaptation to non-native hosts may have occurred in China prior to the invasion of North America given the 30- to 50-year time-lags between ash plantings and EAB outbreaks in China, as well as the rapid spread of EAB populations in its invaded ranges. EAB population densities were historically low in native Asian ash in China, and it may have taken some time for planted non-Asian ash trees to grow to a susceptible size, for EAB to adapt to the newly introduced species, and then for EAB populations to build to outbreak levels, which likely explains the relatively low damage initially caused to these non-Asian ash trees. 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 sufficiently high levels of infestation to be detected in 2002 (Siegert et al., 2014).

In China, EAB outbreaks are only associated with non-Asian ash trees, indicating that those (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* 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 (Chakraborty et al., 2014; Chen et al., 2011; Whitehill et al., 2012). Increased susceptibility of North American and European ash compared to Asian species allows for greater EAB survival and reproduction resulting in higher tree mortality (Rebek et al., 2008), and consequently potential for development of EAB outbreaks. In addition, EAB larvae may develop faster in more susceptible or stressed trees compared to resistant trees (Tluczek et al., 2011) which can impact population dynamics and increase infestations. 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.

4.2 | Geographical factors contribute to variation in EAB infestation levels

We found latitudinal distributions of ash trees were positively related to EAB infestation levels rather than their habitats, elevational distributions, ages and sizes without considering the effect of time. Although changes over time would likely impact these model results, temporal differences were not significant in our present research. Although degrees of EAB infestations were not significantly different among different habitats for either non-Asian or native ash trees (Figure 2), there was a trend for non-Asian ash to have a higher degree of infestation in semi-natural habitats compared to street tree habitats, while native ash species tended to have a higher degree of infestation when planted as street trees compared to semi-natural habitats. It is possible that native trees were less stressed and thus had higher levels of resistance as well as increased prevalence of natural enemies in natural settings compared to roadside plantings. On the other hand, non-Asian ash trees, which have no coevolutionary history with EAB, have no resistance and may not be as attractive to native natural enemies; hence they, may be more susceptible in natural ecosystems where endemic populations of EAB are present.

Climate may be one of the factors influencing EAB outbreaks in introduced ranges. However, climatic factors would likely have similar effects on both native ash trees and non-Asian ash trees in the pest's native range. We believe that lack of coevolutionary history and host resistance in non-Asian ash species was the major factor resulting in EAB outbreaks in China. In fact, our recent species distribution modelling using MaxEnt showed that in addition to climatic factors, the presence of susceptible host tree species plays a major role in delineating EAB's distribution (Dang, Zhang et al., 2021).

The fact that susceptible non-Asian ash trees have been widely planted in northern China, yet are comparatively rare in southern China may explain latitudinal variation in EAB infestation levels. Additionally, previous research has demonstrated that non-Asian ash species are not especially tolerant of high temperatures (Pan & You, 1994). In North America, the three major species of ash including *F. pennsylvanica*, *F. americana* and *F. nigra* are distributed as far north as central Manitoba and Cape Breton Island in Canada (up to 55°N), and south to Northern Texas and Florida (28°N). Average temperatures range from −18°C in the winter to 27°C 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; USDA NRCS, 2019). *Fraxinus velutina* is primarily distributed in the southwestern and southern U.S.—from northern California (42°N) 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) with average temperatures of 11°C in the winter to 34°C in the summer (mean annual temperature of 24°C; USDA NRCS, 2019). In China, *F. pennsylvanica*, *F. americana* and *F. velutina* have been mainly planted in areas from Heilongjiang in the north (45–48°N) to Zhejiang (27–31°N) in the south. There were also a few *F. americana* and *F. velutina* planted in Yunnan Province (22–26°N; 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*, *Ficus* spp., *Mangifera indica* 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.

4.3 | Increased populations of EAB in its native range enhanced invasion risk and likely facilitated the invasion of North America and other regions

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 (Brockerhoff et al., 2014). Non-native 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, thus elevating the risk of accidental introduction of EAB to other non-native ranges. For similar reasons, the widespread planting of non-Asian poplar trees since the 1950s in China might have also contributed to increases in propagule pressure of the Asian long-horned beetle for accidental introduction to North America and Europe (Hu et al., 2009; Zhao et al., 2007).

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). For example, in Italy, the abundance of native wood boring beetles captured in traps near exporting ports was associated with nearby surrounding forests while non-native species captured within ports were 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). Based on genetic analysis of different EAB populations, introductions in North America originated from Hebei or Tianjin, China (Bray et al., 2011). 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 <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 kilometres usually results 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 (Herms & McCullough, 2014) that are widely planted in eastern and central North America (https://www.gbif.org/). On the other hand, few susceptible 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.

As there are relatively few historical records on the invasion of EAB in Eastern Europe (Valenta et al., 2017), our discussion mostly focuses on comparisons with EAB in North America. With low host resistance due to a lack of coevolutionary history, planting of non-Asian ash trees (both North American and European species) can trigger EAB outbreaks in China and subsequently increase the invasion risk to novel regions. While it may be that the EAB invasion of Eastern Europe has followed a similar pattern to North America, the degree to which planting of European ash trees in China may have contributed to EAB invasion in Europe is currently unknown.

5 | CONCLUSIONS

Our study demonstrated that EAB infestation in China was associated with northern latitudes where more susceptible non-native

ash trees were planted. The widespread planting of non-native ash trees in northern China was significantly correlated to increasing outbreaks of EAB there. With time-lags of 30–50 years between the planting of non-Asian ash trees and EAB outbreaks, the increased populations of pests in their native ranges along with increasing international trade may enhance the risk of invasion to North America and other novel regions. Historical analyses (>100 years) of the spatiotemporal dynamics and outbreaks of native insect pests provide valuable information on EAB host interactions and invasion dynamics that contribute to our understanding of invasion ecology and effective management of EAB in both its native and invaded regions.

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CONFLICT OF INTEREST

The authors declare no competing interest.

AUTHORS' CONTRIBUTIONS

X.W. designed the experiments; Y.D., K.W. and X.W. collected and analysed the data and wrote the manuscript; J.J.D., D.E.J. and T.M.P. contributed to the substantial editing of later versions. All authors contributed critically to drafts and gave approval for publication.

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

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