Current Forestry Reports (2026) 12:7
https://doi.org/10.1007/s40725-025-00258-4

FOREST ENTOMOLOGY (B CASTAGNEYROL, SECTION EDITOR)

New Insights on the Ecology, Economics, and Management of *Anoplophora* Longhorned Beetles (Coleoptera: Cerambycidae: Lamiinae)

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Received: 8 October 2025 / Accepted: 10 October 2025

Abstract

Purpose of Review The genus *Anoplophora* includes 52 species, of which three are known to be invasive and a fourth has recently been identified as a potential international high-risk invasive. One species, the Asian longhorned beetle (*Anoplophora glabripennis* (Motschulsky)), has been called one of the 100 worst global invasive species. Here, we present an overview of available information regarding members of the genus *Anoplophora* at risk of spreading beyond their native ranges, including summaries of their ecology, economic impacts, management, and taxonomy, with an emphasis on information that has been made available in the last decade.

Recent Findings This updated review shows that since the revision of the genus by Lingafelter and Hoebeke (2002) the number of recognized species has increased from 36 to 52, and we have a wealth of new information on the invasion history, phenology of the high-risk species, knowledge of pheromones, assessments of host-range, and the exploration of trapping methods. Efforts have been made to identify potentially useful natural enemies to help manage invasive populations if eradication efforts are unsuccessful.

Summary The species of *Anoplophora* that have established outside their native range have native distributions that cover larger geographic areas and feed on more tree species from multiple genera than do the species that have not dispersed internationally. While infestations of *A. glabripennis* continue to be detected and the risk of significant ecological and economic impacts remains high, limited economic information has been developed, and methods for management have changed little since the first detections of *A. glabripennis* outside its native range in New York, U.S. in 1996. Many research gaps remain for the invasive species of *Anoplophora* and more information on the other *Anoplophora* species is needed to prevent their movement and improve early detection.

Keywords Chemical ecology · Invasive pest management · Invasive species · Phenology · Thermal responses · Woodborers

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Published online: 17 February 2026

Introduction

The genus *Anoplophora* contains 52 species (Table 1), all of which are herbivores that feed on tree foliage and tender bark as adults and within the tree itself (i.e., on phloem and xylem) as larvae. Adult feeding rarely causes significant damage to host trees, but larval feeding can create large galleries that interfere with water movement and reduce the structural integrity of limbs and trunks, often causing breakage and endangering people and property. Many *Anoplophora* species are large and visually striking, yet most are infrequently observed in their native ranges, thus basic biology, habits and host plants are known for less than one-fourth of the species in this genus.

Four *Anoplophora* species are known to be invasive (establish outside the native range and cause economic and/or ecological harm) and have been transported internationally in solid wood packaging materials or live host plants. Most available information is based on research focused on *A. glabripennis* (Motchulsky) (commonly called the Asian longhorned beetle), *A. chinensis* (Forster) (commonly called the citrus longhorned beetle), *A. malasiaca* (Thomson), and recently, *A. horsfieldii* (Hope) (Table 1; Fig. 1). While past work suggested that *A. malasiaca* and *A. chinensis* are variants of the same species [2], recent genetic information suggests they are distinct lineages [1] (discussed in detail later); thus, for the purposes of this review we treat them as distinct species. Along with *A. macularia* (Thomson) these four species are considered the most economically important species in both native and invaded habitats [2]. Because of variation in economic and ecological impact, the intensity of research varies substantially among species, with research focused heavily on species that have moved internationally or are economically impactful (Fig. 2).

Anoplophora glabripennis is documented as the most economically and ecologically impactful species of *Anoplophora* in the world, with non-native populations established in Europe, Asia, and North America. In 1996, an infestation of *A. glabripennis* was found in urban trees growing in Brooklyn, NY, U.S [18]. Although live beetles had previously been found in warehouses containing imported products in both the U.S. and Canada, the infested trees in Brooklyn represented the first detection of an established breeding population of *Anoplophora* outside its native range in Asia. Since that first detection, additional infestations have been found in Europe and North America [19] (Fig. 3), as well as in Japan [20].

Anoplophora glabripennis has a broad host range that includes trees such as *Acer*, *Populus*, *Salix*, *Ulmus* and at least 18 additional genera [21]. The combination of this broad host range and the economic and ecological importance of this species in both natural and managed wooded landscapes in North America and Europe has led members of the European and Mediterranean Plant Protection Organization (EPPO), the United States, and Canada to adopt policies of eradication when populations are detected. These policies of eradication have been extended to other invasive members of the genus including *A. chinensis*, *A. malasiaca* and *A. horsfieldii*, a species that recently established in South Korea [22]. Other members of the genus, for which limited information is available, are generally considered high risk of eventually being introduced and impacting forests outside their native range.

When the Brooklyn, NY infestation of *A. glabripennis* was detected, limited information was available for this or any *Anoplophora* species in general. Efforts to fill this knowledge gap led to a revision of the genus *Anoplophora* by Lingafelter and Hoebeke [2] that included a description of 36 known and described species, all distributed in eastern Asia. Since the publication of Lingafelter and Hoebeke (2002) [2], continued taxonomic and phylogenetic research, including the use of molecular tools, has led to the revision of the genus, identification of new *Anoplophora* species, and the consolidation of some species as synonymous [1]. The current review of the literature shows that the number of recognized species has increased from the 36 described by Lingafelter and Hoebeke [2] to 52, with all members of the genus still native to East and South-East Asia [1, 3–17, 23] (Table 1). The pace of research on this genus is represented by the history of species discovery which remained relatively constant from 1842 until the last decade (Fig. 4).

Much of the research conducted since the detection of *A. glabripennis* in North America has generally focused on the ecology of this species, the management and eradication of introduced populations, and the economic impacts of the invasion. Previous reviews of *Anoplophora* have focused on the systematics [2] or evolutionary ecology of the genus [1], and there have been specific reviews of *A. glabripennis* and/or *A. chinensis* (including *A. malasiaca*) that include general reviews [21, 24, 25], host range and preferences [26–29], chemical ecology [30, 31], natural enemies [32–36], and management [19, 37, 38]. Here, we review information on the ecology, economics, and management of *Anoplophora* within the context of past research syntheses [2, 21, 37] and with an emphasis on information published in the last 5 years for both high-risk species and for members of the genus *sensu lato*. We also highlight knowledge gaps and ongoing research needed to improve the management of known invasive *Anoplophora* and to assess the potential of other species to become invasive.

Table 1 Currently recognized *Anoplophora* species, including their native range, relatedness, and larval hosts

Species	Native Range	Sister Species Groups [1]	Hosts	References
Anoplophora albopicta (Matsushita, 1933)	Taiwan	Not mentioned		[2–5]
Anoplophora amoena (Jordan, 1895)	Indonesia (Java, Sumatra) and Malaysia (Borneo)	Elegans group		[1, 2]
Anoplophora ankangensis (Chiang, 1981)	China (Henan, Hunan, Shaanxi, Guangxi)	Not mentioned	*Prunus persica* (L.) Batsch	[1, 6, 7]
Anoplophora asuanga Schultze, 1923	Philippines (Mindanao, Sorsogon, Dinagat, Luzon, Stargao, Leyte, Samar), Malaysia, Indonesia	Lucipor group		[1–4]
Anoplophora beryllina (Hope, 1840)	China (Hubei, Jiangxi, Zhejiang, Fujian, Guangdong, Hunan, Guangxi, Sichuan, Yunnan), Sri Lanka, Vietnam, Myanmar, India (Assam, Sikkim), Laos, Thailand, Korea	Beryllina group	*Castanea mollissima* Blume, *Castanea seguinii* Dode, *Castanea sativa* Miller, *Juglans*, *Quercus dealbata* Hook.f. & Thomson x Miq., *Quercus glaucus* Thunb.	[1–4, 8, 9]
Anoplophora birmanica Hildepohl, 1990	India, Myanmar, Thailand	Horsfieldii group		[1, 2, 4, 10]
Anoplophora bowringii (White, 1858)	India (Assam), Vietnam, Laos, Myanmar, and China (Hubei, Jiangxi, Zhejiang, Fujian, Guangdong, Guangxi, Yunnan, Hong Kong)	Beryllina group		[1, 2, 9]
Anoplophora cheni Bi & Ohbayashi, 2015	China (Yunnan, Guizhou), Vietnam (Yên Bái)	Wusheana group, Questionable lumping		[1, 4, 7]
Anoplophora chiangi Hua and Zhang, 1991	China (Hunan, Guizhou)	Not mentioned		[3, 7, 11, 12]
Anoplophora chinensis (Forster, 1771)	China (Jilin, Liaoning, Hebei, Henan, Shandong, Shanxi, Shaanxi, Gansu, Hubei, Anhui, Jiangsu, Jiangxi, Zhejiang, Fujian, Guangdong, Hong Kong, Hainan, Guangxi, Hunan, Guizhou, Sichuan, Yunnan), Korea, Japan, Vietnam, Taiwan, Indonesia, Philippines, Malaysia (Borneo), Thailand, Myanmar, Cambodia, Laos	Chinensis group	*Acacia*, *Acer*, *Aesculus*, *Aleurites*, *Alnus*, *Aralia*, *Betula*, *Broussonetia*, *Cajanus*, *Camelia*, *Carpinus*, *Carya*, *Castanea*, *Castanopsis*, *Casuarina*, *Citrus*, *Corylus*, *Cotoneaster*, *Elaeagnus*, *Eriobotrya*, *Ersoniana*, *Fagus*, *Ficus*, *Fortunella*, *Hedera*, *Hibiscus*, *Ilex*, *Juglans*, *Lagerstroemia*, *Lindera*, *Litchi*, *Mackia*, *Mallotus*, *Malus*, *Melia*, *Morus*, *Olea*, *Ostrya*, *Persea*, *Pholina*, *Pinus*, *Platanus*, *Poncitrus*, *Populus*, *Prunus*, *Psidium*, *Pyrocantha*, *Pyrus*, *Quercus*, *Rhus*, *Robinia*, *Rosa*, *Rubus*, *Salix*, *Sapium*, *Schinia*, *Sophora*, *Stransvaesia*, *Stylurus*, *Styrax*, *Tectorum*, *Ulmus*	[1–4, 8]
Anoplophora coeruleoantennata (Breuning, 1946)	China (Sichuan)	Glabripennis group but not sampled		[1–3, 13]
Anoplophora decemmaculata Pu, 1999	China (Hubei, Hunan)	Elegans group		[1–3]
Anoplophora elegans (Gahan, 1888)	China (Henan, Guangdong, Hainan, Guizhou, Yunnan), Vietnam, Laos, Myanmar, Thailand	Elegans group		[1, 2, 4, 8, 12]
Anoplophora species novo	Vietnam	Elegans group		[1]
Anoplophora fanjingensis Yang, Yang & Tian, 2020	China (Guizhou)	Glabripennis group, presumed a synonym of *A. freyi*		[1, 11]
Anoplophora flavomaculata (Gressitt, 1935)	Taiwan, China	no sister species		[1, 2, 7]

Table 1 (continued)

Species	Native Range	Sister Species Groups [1]	Hosts	References
Anoplophora glabripennis (Motschulsky, 1854)	China (Heilongjiang, Jilin, Liaoning, Inner Mongolia, Beijing, Hebei, Shandong, Shanxi, Ningxia, Shaanxi, Gansu, Henan, Hubei, Anhui, Jiangsu, Jiangxi, Zhejiang, Fujian, Hunan, Guangxi, Guizhou, Sichuan, Yunnan, Xizang), Korea	Glabripennis group, *A. freyi* may be close to becoming a separate species	*Acer*, *Aesculus*, *Alnus*, *Betula*, *Carpinus*, *Cerasus*, *Citrus*, *Corylus*, *Cotoneaster*, *Cryptomeria japonica* (Thunb. ex L.f.) D.Don, *Fagus*, *Lagerstroemia*, *Malus*, *Melia*, *Morus*, *Ostrya*, *Platanus*, *Populus*, *Prunus*, *Pyrus*, *Rosa*, *Salix*, *Ulmus*	[1, 2, 4, 8]
Anoplophora granata Holzschuh, 1993	Thailand (Wiang Papao, Chiang Rai), China (Guangxi), Laos	Imitator Group		[1–3, 8, 14]
Anoplophora gressitti Ohbayashi and Bi, 2014	Thailand, China, Myanmar, India	no sister species		[1, 15]
Anoplophora guerryi (Pic, 1903)	Laos, China	Beryllina group	*Quercus*, *Castanopsis fargesii* Franch	[1, 8]
Anoplophora horsfieldii (Hope, 1842)	China (Henan, Shaanxi, Hubei, Anhui, Jiangsu, Jiangxi, Zhejiang, Fujian, Guangdong, Hunan, Guangxi, Guizhou, Sichuan, Yunnan), Taiwan, Vietnam, India, Loas	Hosfieldii group	*Celtis sinensis* Pers., *Celtis formosana* Hayata, *Citrus*, *Ulmus pumila* L., *Camellia oleifera* Abel, *Camellia sinensis* (L), *Melia azedarach* L., *Quercus glauca* Thunberg, *Ulmus pumila* L.	[1–4]
Anoplophora huangjianbini Wang & He, 2021	China (Fujian, Guangxi)	Not mentioned		[12]
Anoplophora iadina Wang, He and Huang, 2023	China (Yunnan)	Not mentioned	*Acer*	[9]
Anoplophora imitator (White, 1858)	China (Shaanxi, Hubei, Jiangsu, Jiangxi, Zhejiang, Fujian, Guangdong, Hainan, Hunan, Guangxi, Guizhou, Sichuan, Yunnan)	Imitator Group	*Castanea mollissima* Blume, *Populus*	[1, 2, 4, 12]
Anoplophora irregularis (Aurivillius, 1924)	Malaysia (Borneo, only in one catalogue 1961, no type specimens found)	Not mentioned		[2]
Anoplophora jianfenglingensis Hua, 1989	China (Hainan) may be synonymous with *A. granata*.	Not mentioned		[2]
Anoplophora leechi (Gahan, 1888)	China (Beijing, Hebei, Henan, Jiangsu, Zhejiang, Hubei, Jiangxi, Hunan, Guangxi), Indonesia, Vietnam	Imitator Group	*Castanea mollissima* Blume	[1–3, 11, 16]
Anoplophora longehirsuta Breuning, 1968	Laos, Myanmar, China (Guangxi), Thailand and Vietnam	Stanleyana group		[1, 2]
Anoplophora lucipor Newman, 1842	Philippines (Luzon)	Lucipor group		[1, 2, 4]
Anoplophora lurida (Pascoe, 1857)	China (Hebei, Henan, Gansu, Hubei, Jiangsu, Jiangxi, Zhejiang, Hunan, Guangxi, Sichuan), Taiwan	Beryllina group	*Castanea crenata* Siebold & Zucc., *Sophora japonica* L.	[1–3, 8]
Anoplophora malasiaca (Thomson, 1865)	China (Henan, Jiangsu, Zhejiang, Fujian, Guangdong, Hainan, Guangxi, Sichuan), Taiwan, Japan (Is. Ishigaki-jima, Is. Miyako-jima, Is. Okinawa), Korea, Malaysia	Chinensis group	*Acer oblogum* Wall. ex DC., *Castanopsis*, *Citrus*, *Distylium racemosum* Siebold & Zucc., *Melia azedarach* L., *Rosa rigosa* Thunb., *Ziziphus mauritiana* Lam.	[1–4, 8]
Anoplophora malasiaca (Thomson, 1865)	Japan (Hokkaido, Honshu, Shikoku, Izu Isls., Is. Tsushima, Is. Yakushima, Is. Amami-ôshima, Is. Okinawa), Korea, Taiwan	Chinensis group	*Alnus*, *Casuarina*, *Citrus*, *Litchi*, *Melia*, *Morus*, *Platanus*, *Pyrus*, *Rosa*, *Salix*	[1, 2, 4, 8]
Anoplophora mamaua Schultze, 1923	Philippines (Mindoro & Mindanao)	Lucipor group		[1, 2, 4]
Anoplophora medenbachii (Ritsema, 1881)	Indonesia (Java, Sumatra), Malaysia, Myanmar, Thailand (Chiang Mai, Chiang Rai)	Chinensis group		[1, 2, 4, 10]

Table 1 (continued)

Species	Native Range	Sister Species Groups [1]	Hosts	References
Anoplophora millegranus (Bates, 1891)	China	Beryllina group	*Castanea mollissima* Blume	[1, 8]
Anoplophora multimaculata (Xie & Wang, 2015)	China (Hubei, Zhejiang)	Not mentioned		[6, 7]
Anoplophora ogasawarensis Makihara, 1976	Japan (Ogasawara (Bonin) Is)	Not sampled		[1, 2]
Anoplophora puxian Wang & He, 2021	China (Sichuan)	Glabripennis group, presumed to be a synonym of *A. coeruleoantennata*		[1, 9, 13]
Anoplophora quadrifasciatus (Breuning, 1961)	Vietnam, China (Guangxi)	Wusheana group		[3]
Anoplophora rubidacorpora Xie, Shi & Wang, 2012	China (Guizhou)	Not mentioned		[17]
Anoplophora rugicollis Wang, Xie & Wang, 2022	China (Yunnan), Vietnam (Lào Cai)	Glabripennis group		[1, 5, 9]
Anoplophora ryukyuensis Breuning & Ohbayashi, 1964	Vietnam, China, Japan (Yonaguni-jima Is, Ishi-gaki-jima Is)	Not sampled		[1, 4, 8]
Anoplophora sameshimai (Ohbayashi, 2001)	Japan	Grouped with other *Dolichoprosopus* that was moved to *Anoplophora*	*Lithocarpus edulis* (Makino) Nakai	[1]
Anoplophora sebastieni Duranton 2004	Philippines (Luzon)	Not mentioned		[4]
Anoplophora siderea Bi, Chen & Ohbayashi, 2020	China (Guangxi, Guangdong)	Not mentioned		[7]
Anoplophora similis (Gahan, 1900)	China (Fujian, Guangdong, Hainan, Sichuan)	Imitator Group		[1, 2, 7, 12]
Anoplophora stanleyana Hope, 1839	India (Assam, Meghalaya, Sikkim), Bhutan, Vietnam, Myanmar, Thailand (Nan), China (Guangxi)	Stanleyana group		[1–4, 8, 10]
Anoplophora wusheana Chang, 1960	Taiwan	Wusheana group		[1, 3, 4]
Anoplophora xuei Lin & Wen, 2024	China (Guizhou, Guangxi)	Not Mentioned		[16]
Anolpophora yokoyamai (Gressitt, 1937)	Japan	Grouped with other *Dolichoprosopus* that was moved to *Anoplophora*		[1, 8]
Anoplophora zhiyuani Wang, Xie & Wang, 2025	China (Yunnan), Vietnam (Yên Bái)	Not mentioned		[5]
Anoplophora zibroides Wang, He & Huang	China (Hunan and Guangxi)	Not mentioned	*Symplocos*	[9]

Ecology

Invasion History of *Anoplophora*

Anoplophora Glabripennis

Reconstructing the invasion history of *A. glabripennis* requires understanding the native context of this species. *Anoplophora glabripennis* has long been considered an important forest pest in China [39] but it became particularly prominent with the development of the Three-North Shelter Forest Program [24]. This monumental 75-year afforestation project was formally initiated in 1978 to slow desertification and limit the expansion of the Gobi Desert by planting a green belt or "Great Green Wall" around the southern and eastern edges of the desert. As of 2003 the program had planted more than 150 million hectares of trees spanning more than 4,700 km along the desert margin. However, large portions of these regions were planted as monocultures of poplar (*Populus*) and poplar hybrids [37, 40] that were subsequently discovered to be highly susceptible to *A. glabripennis* [24]. As a result, *A. glabripennis* populations

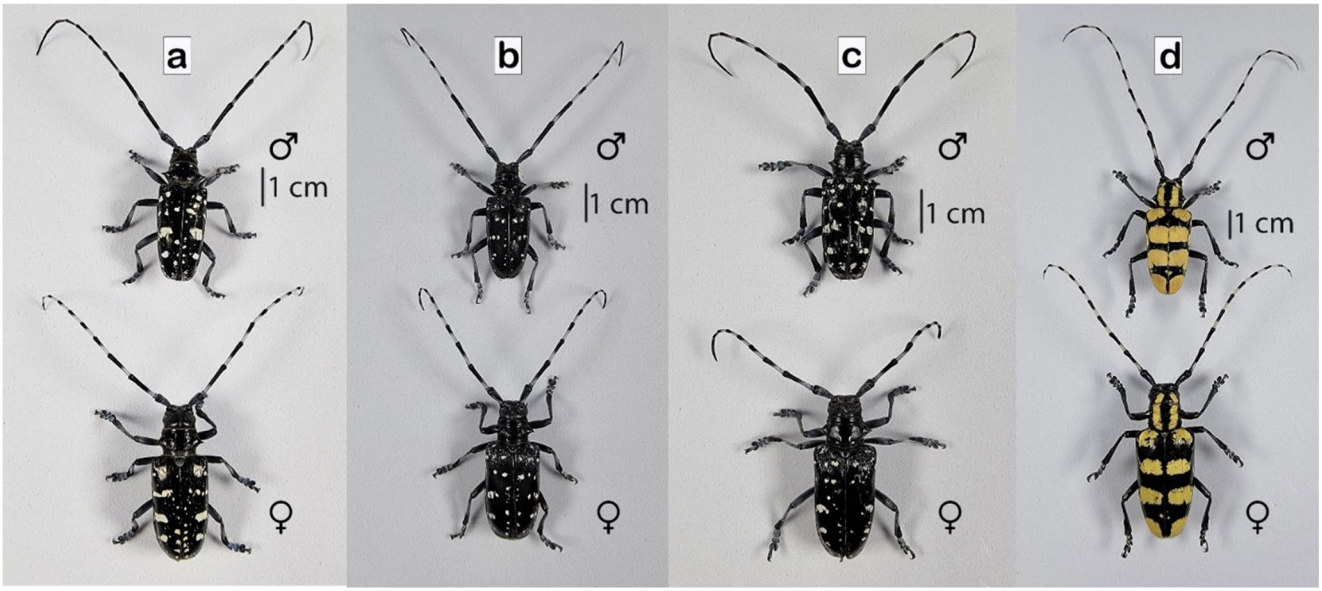

Fig. 1 The four species of *Anoplophora* that have established outside their native range are *A. glabripennis* (**a**), *A. chinensis* (**b**), *A. malasiaca* (**c**), and *A. horsfieldii* (**d**). Specimens along the top are male, those along the bottom are female. A 1 cm line is shown for each species to facilitate size comparisons. Photos by Melody Keena

grew rapidly in these stressed, susceptible stands leading to high population densities, significant feeding damage, and loss of millions of trees. Larval feeding reduces wood quality; thus, some of the infested trees were harvested and processed into solid wood packaging materials, such as pallets and crates (which are typically constructed out of lower quality material). As populations grew and infested material was transported to neighboring provinces within China, *A. glabripennis* spread and widespread damage was recorded in new regions [41, 42]. The international transport of solid wood packaging material led to the inadvertent movement of *A. glabripennis* to North America and Europe, leading to both interceptions and establishments at many different locations (Table 2). Recent infestations of *A. glabripennis* have been reported in 2021 in Japan and 2020 in South Carolina, U.S., emphasizing the continued threat this species poses to global forest ecosystems [20, 43].

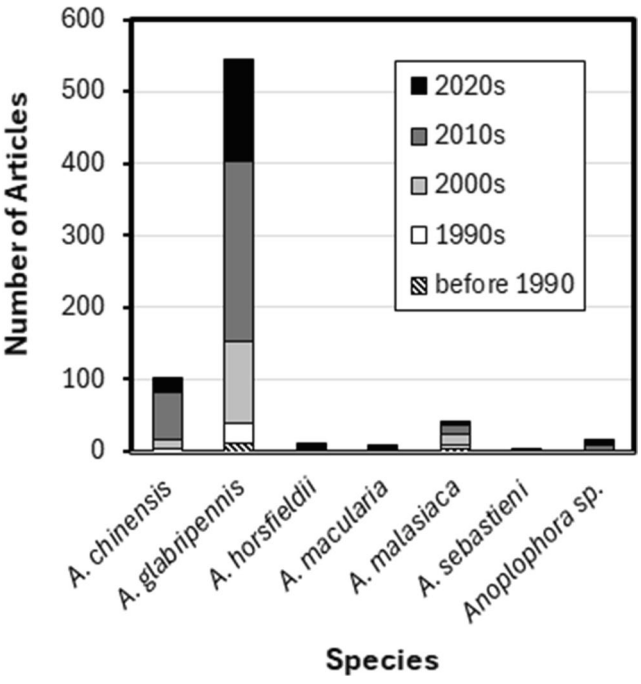

Fig. 2 Number of publications on *Anoplophora* species by decade, based on Web of Science and Scopus for all occurrences through January 2025

Source of information on infestations, eradications, and pathways EPPO Global Database for each species https://gd.eppo.int/taxon/ANOLGL/distribution, https://gd.eppo.int/taxon/ANOLCN/distribution, https://gd.eppo.int/taxon/ANOLHO/distribution. Note *A. malasiaca* included *A. chinensis* in EPPO but separated based on Strangi et al. [44]. Part of tree infested obtained from review articles [2, 19, 22].

Molecular analyses of native populations and non-native infestations of *A. glabripennis* provide even greater insight into its invasion history. Native populations show significant population structure, with clearly defined northern and southern populations that were revealed with high resolution genome-wide markers [45]. Sampling in the native range revealed the occurrence of cryptic invasions of *A. glabripennis*, likely linked with human-assisted transport of infested wood products within the native range [46]. Incursions of *A. glabripennis* in North America and Europe were not limited to a single native source region, rather multiple

geographic locations in the native range contributed to different infestations [47–50]. Secondary spread within the invaded range was also detected in both North America and Europe, with evidence of introduced populations serving as a source or bridgehead for another infestation [50]. The functional significance of these different source regions is still unknown and is an area of future study.

Anoplophora Chinensis/Malasiaca

Like *A. glabripennis*, *A. chinensis* and *A. malasiaca* are both recognized as important tree pests in their native range [37]. However, live plants and bonsai are the predominant invasion pathway for these species [37] rather than solid wood packing material. Repeated interceptions of *A. chinensis* were first reported in the Netherlands in 1980, and infestations have since become established throughout Europe (Table 2). Only a single infestation was reported in Washington state, U.S., which was eradicated in 2017 [37]. An initial genetic analysis with mitochondrial DNA barcode variation of three Italian infestations suggests that the multiple independent introductions occurred in Italy from different parts of the native range [44]. A global molecular analysis of *A. chinensis* or *A. malasiaca* has not been conducted, nor has the population structure of the native range been fully described. An in-depth molecular analysis on native and non-native populations of *A. chinensis*/*A. malasiaca* with genome-wide markers would provide valuable information on the invasion history of these species. Furthermore, a population genomic analysis of *A. chinensis* and *A. malasiaca* would help delimit the species and permit a comparative analysis of the invasion histories across *Anoplophora*.

Anoplophora Horsfieldii

An infestation of *A. horsfieldii* in South Korea was recently described [22, 51] and represents a new invaded region for another species of *Anoplophora*. This new infestation was first reported in September 2019 but has grown considerably with over 1,000 beetles collected at the invasion site in 2023 by professional and citizen scientists combined [22, 51]. The source of this infestation and the pathway of introduction is unknown. Further investigations into the invasion history of *A. horsfieldii* are warranted, given the continued risk the genus *Anoplophora* poses to the global forest community.

The Effects of Environment and Climate on *Anoplophora* Life History, Geographic Distribution, and Potential Range

The native climatic niches of most *Anoplophora* species are subtropical and tropical (Fig. 3), given the region of greatest species diversity in China. However, the primary source regions of the four invasive species (*A. glabripennis*, *A. chinensis*, *A. malasiaca*, and *A. horsefeldii*) are temperate and in regions with relatively low *Anoplophora* diversity [2] (Figs. 3 and 5). Within their native ranges in China, the distributions of *A. glabripennis*, *A. chinensis*, and *A. horsefeldii* include substantial geographic overlap, albeit with some key interspecific differences (Fig. 5).

The distribution of *A. chinensis* spans the largest latitudinal range of the four focal species, with species records within the tropics north to 43.42 N (based on Global Biodiversity Information Facility www.gbif.org, records accessed 5/29/2025, https://doi.org/10.15468/dl.qrvj5w, https://doi.org/10.15468/dl.5naa73, https://doi.org/10.15468/dl.ctfyvz, https://doi.org/10.15468/dl.6nwbss). This contrasts with *A. glabripennis* whose native distribution extends further north (43.63 N) where populations are found both inland and at higher altitudes than other species [24], but its distribution does not extend into the tropics (although this region has not been as thoroughly sampled). The northern, cool-temperature distribution of *A. glabripennis* may provide exaptations that have allowed this species to successfully invade cooler climates in North America or Europe [52]. *Anoplophora chinenis* and *A. glabripennis* also show the broadest longitudinal distribution. The capacity to tolerate diverse abiotic conditions large correlates with geographic ranges and may reflect both developmental plasticity and population-level variation that has made these the most successful invaders in the genus to date. Compared with the three other invasive species, *A. malasiaca* shows the most restricted distribution with populations known primarily from Japan and South Korea. These data suggest the species in this genus that have been most successful at establishing outside their native range are those with the broadest native ranges. However, the rate of invasion for these species may also be driven by the widely distributed source populations, with broadly distributed populations being more likely to be transported in shipped materials.

Winter survival, flexibility in voltinism, and development rate are likely key traits that have allowed *A. glabripennis* to invade regions well north of its native range. Exploration of *A. glabripennis* winter physiology in both native and introduced populations has shown that there is substantial spatial, temporal, host-associated, and life stage plasticity in cold tolerance [53–55]. Larvae are the predominant overwintering stage and were found to be partially freeze-tolerant and had a lower lethal temperature of −25 °C after a two-hour exposure [55]. It is thought that larval freeze tolerance is increased by elevated levels of cryoprotectants, such as glycerol, which would increase hemolymph osmolality and provide protection against stressful lower temperatures [55]. Larvae also enter a temperature-independent developmental

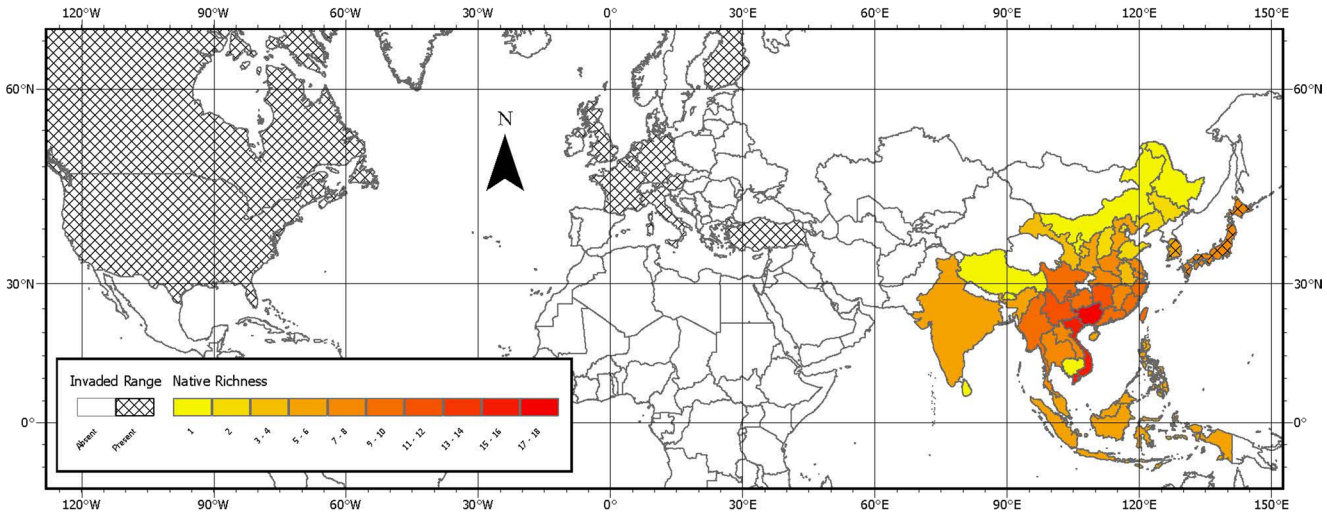

Fig. 3 The number of documented native *Anoplophora* species are shown for the countries (and provinces if known) of east Asia. The cross hatched regions represent countries where invasive *Anoplophora* have established breeding populations (several of which have been eradicated, see Table 2). Both Japan and South Korea have invasive *Anoplophora* populations present along with the native species

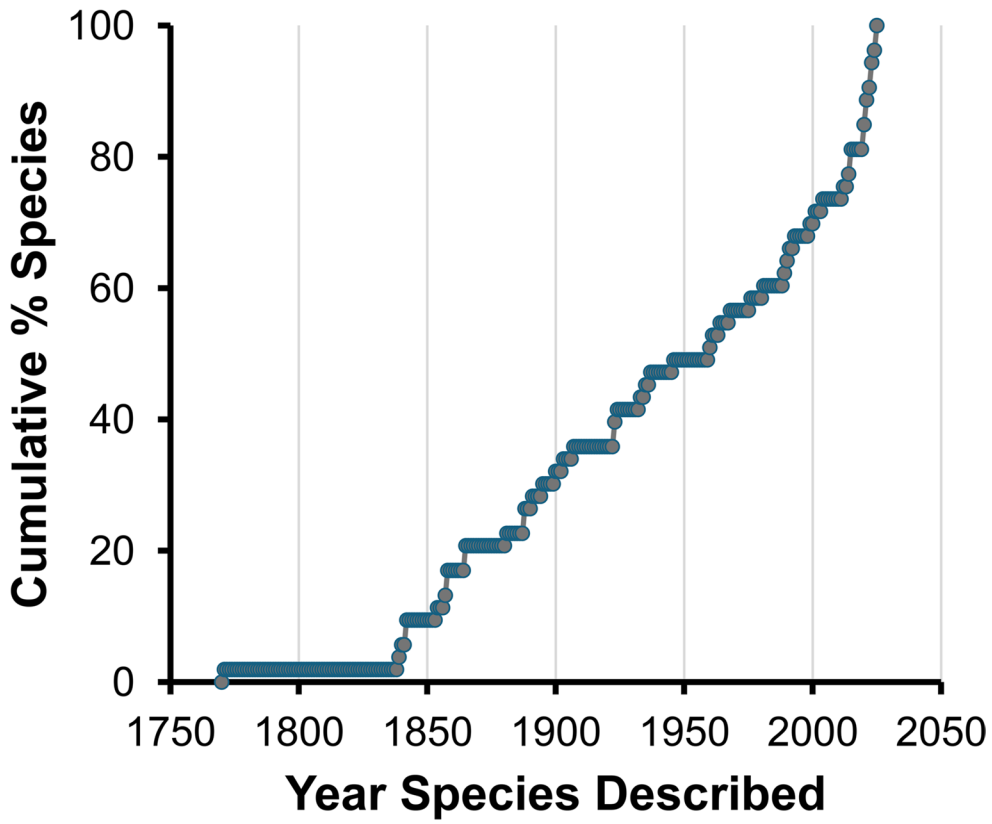

Fig. 4 Rate of new descriptions of *Anoplophora* species by year through 2024 based on when each species was described in the literature

arrest, which is indicative of a diapause period [55]. Cool temperatures were required for larvae to resume development, which suggests that this developmental stage is obligate. Compared with *A. chinensis* larvae, *A. glabripennis* have a higher metabolic rate after exposure to cold and are better able to maintain metabolic activity during low temperatures [56], which could help explain the distribution of these species in their native ranges. Underlying phenotypic plasticity or selection on existing variation in cold tolerance traits may have allowed native *A. glabripennis* populations to effectively exploit dense stands of susceptible hosts in the cold climates of China where the Three-North Shelter Forest program took place [24, 25]. This exceptional cold

Table 2 Current and previous *Anoplophora* infestations reported outside their native range up to 2025, with notes on pathways of introduction and part of host used

Species	Invaded Range (years new infestations detected)	Infestations Eradicated as of Jan. 2025	Pathway of Introduction	Part of tree they infest
Anoplophora chinensis (Forster)	Established: Croatia (2007, 2014), Italy (2014, 2017-18), Turkey (2014, 2016), Intercepted (beetles emerged from imported live trees): Canada (1997), Denmark (2011), France (2003, 2018), Germany (2008), Netherlands (2007, 2009), Switzerland (2014), United Kingdom (2005, 2008, 2010-11) United States (1999, 2001, 2002)		Live plants for planting	Lower trunk (< 50 cm), root collar and exposed roots.
Anoplophora glabripennis (Motschulsky)	Established: Austria (2001, 2012-13), Canada (2003, 2013), Finland (2015), France (2002-3, 2008, 2013 2016), Germany (2004-5, 2012, 2014-16) Italy (2007, 2009, 2013, 2015-19), Japan (2021), Montenegro (2015), Netherlands (2010, 2012), Switzerland (2011-12, 2014-15), United Kingdom (2012), United States (1996, 1998–2000, 2008, 2010, 2011, 2020) Intercepted: Australia, Belgium (2008), Canada (1992–2019) Czechia (2006), Denmark (2008), Lebanon (2015-16)	Austria, Canada, Finland, France (most infestations), Italy (some infestations), Montenegro, Netherlands, Switzerland (most infestations), United Kingdom, United States (majority of infestations)	Solid wood packaging materials and occasionally live plants for planting	Upper part of the trunk and main branches
Anoplophora horsfieldii (Hope)	Established: South Korea (2019) Intercepted: Canada (2022)		Live plants for planting and solid wood products made from its hosts	Upper part of the trunk and main branches
Anoplophora malasiaca (Thomson)	Established: Italy (2000, 2004, 2006-8)		Live plants for planting	Lower truck (50 cm), root collar and exposed roots.

tolerance was further demonstrated by the successful establishment of a breeding population of *A. glabripennis* in Finland in 2015 (60° N), the most northern latitude of any previously recorded *Anoplophora* population [52]. Similarly, the tolerance of the species for warmer semitropical conditions (or the availability of source populations adapted to warmer conditions) may foster the ability of *A. glabripennis* to invade locations with warmer climates, as highlighted by the recent detection of a breeding population in coastal South Carolina, U.S [43].

Anoplophora glabripennis, *A. chinensis*, and *A. malasiaca* all show substantial plasticity in larval development and phenology. This includes the ability to develop across a wide range of temperatures, key life history cues that synchronize pupation. This synchronization ensures that adults complete development during the warmest part of the year and can successfully find mates [52, 57]– [58]. This plasticity includes a high level of flexibility in the number of instars larvae can complete before pupation in artificial diet, ranging from a minimum of 5 [59] to an observed maximum of 23 [60], with seasonality, temperature profiles, and pupal weight determining whether the larvae will molt to another instar or pupate. For example, laboratory data from *A. glabripennis* suggests the presence of a temperature profile that acts as a developmental gate and prevents pupae that are over the minimum weight of 0.5 g from progressing to pupation if temperatures exceed 25 °C for several days or if temperatures have peaked and have been declining [60]. This delay in pupation under high temperatures may help avoid pupal development under detrimental conditions, and the delay under declining temperatures may help prevent pupation and adult emergence from occurring too late in the season for successful reproduction for both *A. glabripennis* and *A. malasiaca* [60, 61]. Larvae experiencing decreasing temperatures will also continue to grow and molt as long as temperatures remain high enough to allow development in artificial diet [60, 61]. A diapause (which not all larvae require [60, 61]) and chill period during the winter season

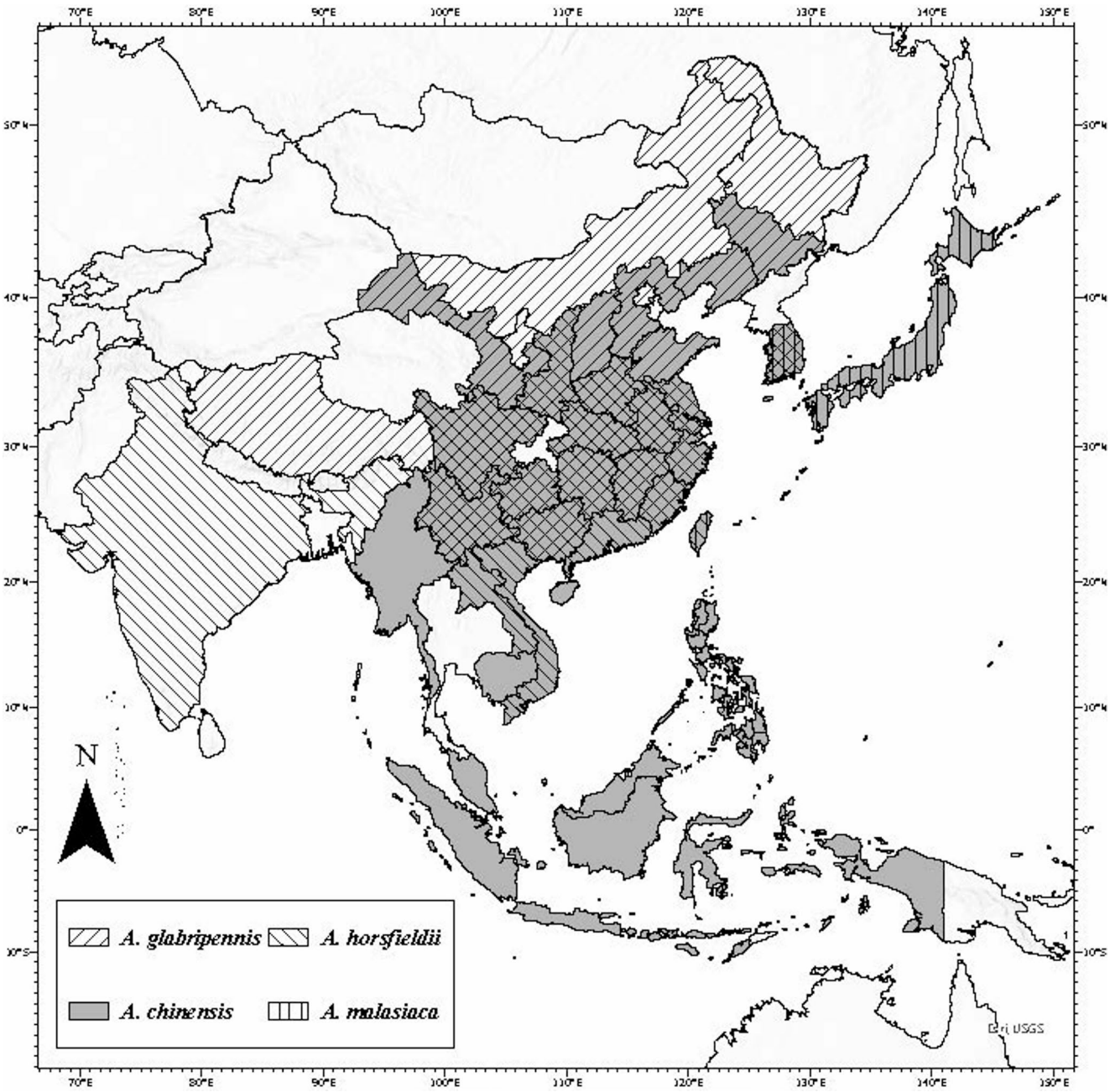

Fig. 5 Native distributions for the four species of *Anoplophora* that have established outside their native range. Only countries and administrative regions with survey data that confirm the presence of these species are included. Some countries have not been surveyed

help to further synchronize *A. glabripennis* larval development and pupation with climate [62]. Less is known about *A. chinensis* development, but pupation appears to be cued by changes in host quality [58]. Reductions in artificial diet moisture content also appear to cue larvae that the growing season is coming to an end, so larvae that have reached the minimum pupation weight (~ 0.8 g) delay pupation until moisture content (and temperatures) rise again in the spring [58]. Of these three invasive *Anoplophora* species, *A. chinensis* has the broadest thermal tolerance and can complete development at temperatures ranging from 10 to 35 °C in artificial diet. Its larvae also grow faster and to larger sizes than the those of the other two species [58].

Existing developmental rate and life table data in both artificial diet and under field conditions provide the knowledge needed to develop a phenology model for *A. glabripennis* [52]. This model has been run under a wide range of conditions including the semitropical conditions found in the most recently discovered breeding population in South Carolina, U.S [59]. The results highlight the

wide range of voltinism displayed in this species when exposed to extremely distinct climates within the invaded range. For example, in Toronto, Canada, beetles completed development in 1–4 years, while 2–8 years were required in Paddock Wood, United Kingdom; 1–3 years in Bethel, OH and Chicago, IL U.S.; and 3–10 years in Helsinki, Finland [52, 59, 63]. A recent assessment of *A. glabripennis* phenology in South Carolina suggests the beetle completes development within 1 year, with some limited evidence that the beetle may complete development in as few as 8 months [59, 64]. Similar models and information for other species of *Anoplophora* would be valuable for managing other invasions and would improve our understanding of these species.

Species distribution models (SDMs) and ecological niche models have been used to evaluate the risk of establishment and spread of *Anoplophora* under current and future climates. Although *A. glabripennis* has a broad geographic distribution in its native range (21–45° N latitude), SDMs suggest that its niche has expanded to include warmer and more humid areas in the invaded range [65]. Distribution modelling of the recently introduced population of *A. horsfieldii* in South Korea has shown that this species has the potential to spread throughout Jeju Island and to other subtropical areas in South Korea and Japan, including coastal regions with major ports [66]. Since invasive *Anoplophora* infestations are universally targeted for eradication, populations have not become widespread or occupied all potentially suitable habitats in the introduced range, based on species distribution and phenology modeling [52, 65, 67, 68]. Species distribution and CLIMEX modeling also suggest that *A. glabripennis* will be able to expand its range northward as areas that are presently too cold grow warmer and that the warmest parts of the current range become less suitable [69–71]. CLIMEX modeling for *A. chinensis'* potential range in China suggests there may be areas in all provinces of China that may be suitable and that if temperatures increase, *A. chinensis* population expansion to the northeast and northwest would be possible [72].

Dispersal behaviors in *Anoplophora* have predominantly been studied in *A. glabripennis*. While adults are capable of flight, walking is the primary method of movement for these beetles as they move within and among host trees to feed, oviposit, and find mates [73]. Flight appears to be temperature limited (>15 °C) and often occurs to escape disturbance or to find suitable mates or hosts [74]. Dispersal distance in *A. glabripennis* varies among populations and is strongly influenced by landscape and climate. Forest structure will alter dispersal distances, with longer dispersal distances in low tree density stands and reduced dispersal in high density stands [75, 76]. In mark-recapture field studies, a small number of individuals dispersed more than two kilometers, while laboratory studies using flight mills suggest that they can fly 14 km in their lifetime [77, 78]. Modeling based on invasive population spread dynamics suggests that rare, longer range dispersal events (2–8 km) occur when beetle populations reach higher densities [79, 80]. Human-aided movement has also been implicated in secondary spread within invaded regions [47–49, 81], emphasizing the value in proactive management of firewood or other potentially infested material [82].

Host Plant Interactions and Gut Microbials

Anoplophora species have a broad host breadth. Members of this genus feed on and damage at least 38 genera of hardwood trees across 20 families in 9 orders, including both angiosperms and a few gymnosperms (Table 1). Most *Anoplophora* species, for which host preference is known, are polyphagous though a few are monophagous. Females oviposit under the bark in healthy trees or those weakened by stress. Larvae take one or more years to complete development, feeding initially on the phloem and cambial region of the host and then tunneling through the sapwood and heartwood. Adults typically emerge in summer through a circular exit hole (Fig. 6).

In the invaded range, diet breadth decreases for invasive *Anoplophora* species relative to their native range. For example, in China, *A. glabripennis* completes development in 34 tree species (from 14 genera in 10 families) and has been reported on >100 tree species worldwide [24]. In the invaded range in North America and Europe there are usually only 5–11 genera of known host trees (in 3–8 families) available at the invaded sites and complete development only occurred on at most 7 genera (*Acer*, *Aesculus*, *Betula*, *Fraxinus*, *Salix*, *Sorbus*, and *Ulmus*) [83–86]. *Acer* species are disproportionally attacked in most infestations that occur outside the native range [28, 43, 83, 85–87], however the reason for this clear preference is unknown. Less is known about *A. chinensis*, but it appears that a similar narrowing of diet breadth also occurs. In the native range *A. chinensis* is reported to complete development in 26 genera of hosts while in Europe it completed development primarily in *Acer* followed by *Betula* and *Corylus* [37]. The polyphagous nature of the invasive *Anoplophora* species likely plays a major role in their ability to successfully establish in novel habitats and often on novel species within preferred genera.

Host switching during invasion is a key trait underlying the successful establishment of *Anoplophora* in new habitats. *Anoplophora glabripennis*' ability to degrade lignocellulose on its own and augmented by its symbiotic fungus, *Fusarium solani* (*Mart.*) *Sacc.*, which it carries, may also aid in sterol synthesis and detoxification of plant allelochemicals [88–90]. Other *A. glabripennis* gut microbes

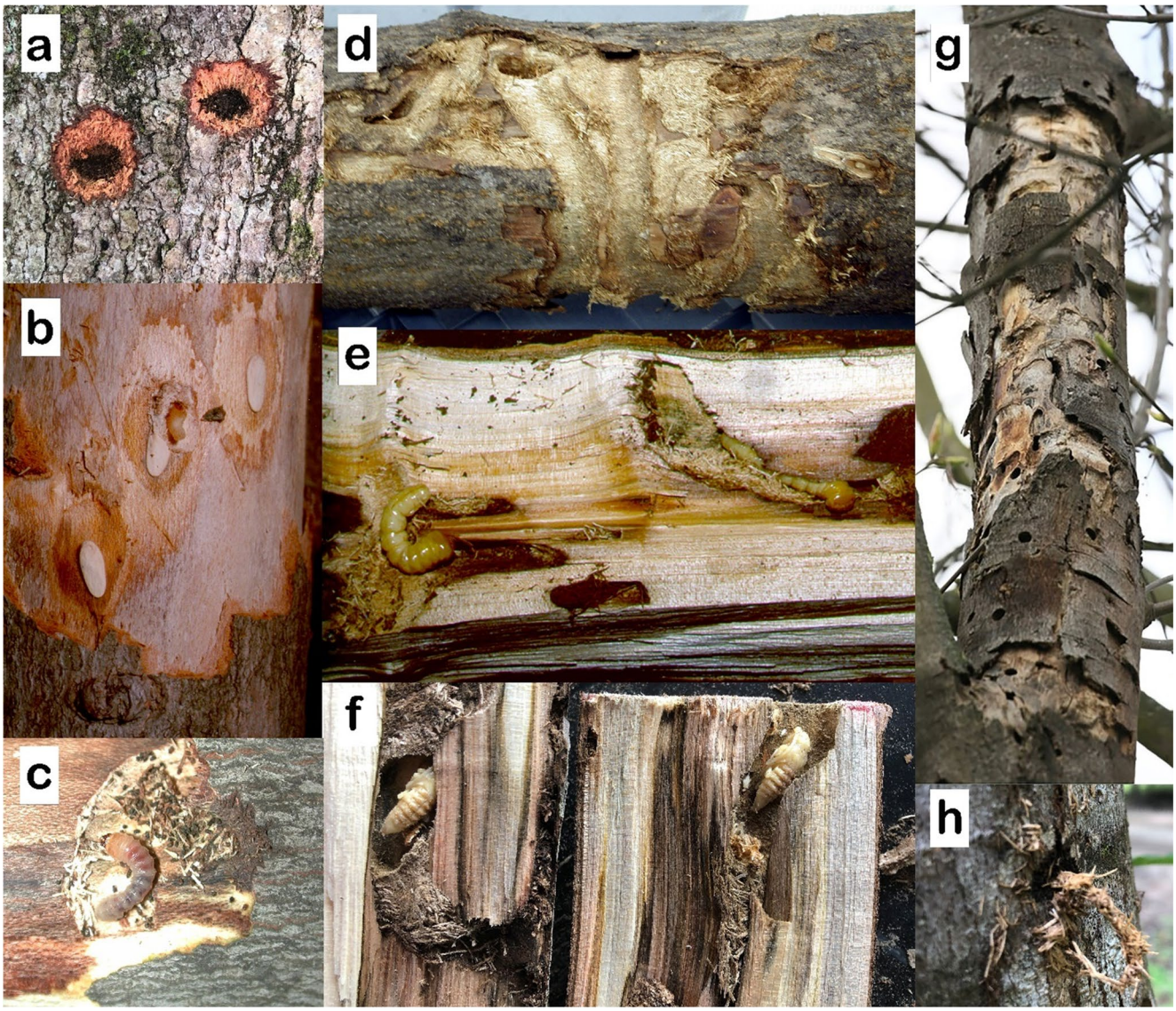

Fig. 6 *Anoplophora glabripennis* immature stages and the damage they cause: **a** oviposition pits (~ 1 cm in diam.) in red maple (**b**) egg and hatchling under the bark, (**c**) small larva tunneling just under the bark, (**d**) larval tunneling under the bark and entrance holes into the sapwood, (**e**) large larvae tunneling the heart wood, (**f**) pupae in their chambers inside the wood, (g) exit holes and bark falling off where larvae tunneled, and h)frass being pushed out through the oviposition pit. Photos by David Coyle, Melody Keena, and Hannes Lemme

also collaborate with the host to digestion carbohydrates and convert released sugars and amino acid intermediates into essential nutrients otherwise lacking from their woody host plants [91]. These gut microbes allow *A. glabripennis* to utilize healthy trees and could contribute to this species' successful use of novel species in its preferred genera. Some recent research also has shown host produced salincoids could confer resistance to *A. glabripennis* by reducing adult feeding and egg production [92]. Identifying possible resistance compounds or traits that could be used to select for resistant cultivars of high priority hosts that are planted in monoculture plantations to produce wood could be a long-term management option.

Chemical Ecology and Reproductive Behaviors

Of the 52 described species of *Anoplophora*, the chemical ecology and mating behaviors have only been studied for the invasive species (excluding *A. horsfieldii*). *Anoplophora glabripennis* uses both visual cues and a complex blend of host volatile attractants (from susceptible hosts) and repellents (from non-hosts) to find suitable host plants [73, 93, 94]. Both *A. glabripennis* and *A. malasiaca* also release sexually active sesquiterpenes that are likely derived from their hosts [95, 96]. These three species have male-produced pheromones: 4-(n-heptyloxy) butanal (*A. glabripennis* only), 4-(n-heptyloxy) butanol (all three species), nonanal

(*A. malasiaca* only), and (3E,6E)-α-farnesene (*A. glabripennis* only) [96–99]. These male-produced pheromones vary in attractiveness to both sexes. For example, the *A. glabripennis* male-produced compounds are primarily attractive only to virgin females that are reproductively mature [100]. Females of all three species also produce contact pheromones (blends of cuticular hydrocarbons) that elicit mounting and copulation following male antennal contact [101, 102]. In addition, *A. glabripennis* female contact pheromones can photo-oxidize and produce volatile aldehydes that are attractive to males [103] and females also lay down a trail pheromone that males follow to find mates [104]. It is also suspected that a female *A. glabripennis* marks her oviposition sites in some way [73]. Further research to find effective lures is still ongoing and research to find lures for detecting *A. horsfieldii* which has only recently established outside its native range and the other *Anoplophora* species is needed to detect new invasions and monitor existing populations.

There has been concern about the potential for hybridization between *A. glabripennis*, *A. malasiaca*, and *A. chinensis* since they are sympatric in parts of China, share male pheromone components, and feed on several of the same hosts. In addition, *A. chinensis* and *A. malasiaca* have been suggested to be synonymous and not separate species [2]. However, recent phylogenomic work based on targeted enrichment has validated and revised the taxonomic limits of these two species [1]. Molecular analysis proved that intermediate morphotypes in areas of sympatry were *A. glabripennis* variants rather than interspecific hybrids [105]. Recent mating studies have also shown that *A. glabripennis* and *A. chinensis* cannot produce viable offspring, although some *A. chinensis* males will copulate with *A. glabripennis* females (but not the reverse) [106, 107]. However, *A. malasiaca* males could copulate with *A. glabripennis* females and some viable offspring resulted [106]. *Anoplophora chinensis* and *A. malasiaca* were able to successfully mate and produce offspring in both reciprocal crosses and hybrid eggs were also viable, so these may be distant subspecies that are currently geographically isolated and genetically distinct [106]. Should the species that can successfully mate (or at least attempt matings) become sympatric, the reproductive interference could influence fitness and blur the lines delimiting these species, complicating detection and monitoring efforts.

Economics and Impacts

Anoplophora species have caused significant economic and ecological damage because they attack and kill healthy trees. Larval feeding can compromise the tree's vascular system, damage the structural integrity of the wood, render the timber unmarketable, and eventually lead to tree death, particularly after years of feeding or high numbers of individuals per tree. Most *Anoplophora* species that have successfully established outside their native range cause economic damage in their native countries as well as in invaded areas. *Anoplophora glabripennis* has caused annual losses of approximately $1.5 billion in China [24]. In heavily infested areas, 80–100% of the preferred host trees can be infested; this resulted in nearly 200 million trees being cut and destroyed by 2005 to prevent further spread in the Three North region of China alone [25]. The greatest economic losses caused by *A. malasiaca* and *A. chinensis* have occurred in fruit-tree production, especially in citrus orchards [36]. In Japan, 50–94% of citrus trees in an area can be infested, even in managed orchards [108].

Eradication is universally used to manage established invasive *Anoplophora* infestations. Although resource intensive, the cost of not eradicating these species is extremely high. Eradication programs are expensive [e.g., $20 million Euros (2008-13) in Lombardy, Italy for *A. malasiaca*; $537 million USD (1996–2013) in the U.S. (Illinois, Massachusetts, New Jersey, New York, and Ohio) for *A. glabripennis*; and $500 million CDN in Ontario, Canada for *A. glabripennis* [108–110]. An added cost to eradication is the cost of replanting or compensating growers and homeowners for tree losses. For example, in Turkey in 2021, 539 hazel nut growers were compensated a total of $2 million for the loss of entire *A. chinensis* infested orchards that had to be removed [111]. Despite these costs, the benefits still outweigh the potential economic impact of not eradicating these species. For example, the costs of not eradicating *A. glabripennis* in the United States are staggering: 1.2 billion urban trees, valued at $669 billion USD, would be at risk if an invasion were left unmanaged and if lost could lead to a 35% loss of canopy cover [112]. Outside of an urban environment, there would be additional projected losses to U.S timber, the maple syrup industry, nurseries, fruit production, and tourism, costing at least another $143 billion USD [113]. Furthermore, an unmanaged *A. glabripennis* infestation in the Canadian province of Ontario could destroy $1.6 billion CDN in timber and $358 million CDN in maple products if all *Acer* trees were killed, with an additional cost of $12.2 billion CDN to remove and replace damaged trees [114].

Management Options

Prevention and Eradication of Invasive *Anoplophora*

Prevention is the first and most cost-effective approach for invasive species management. However, despite on-going

efforts to eliminate invasion pathways and prevent incursions, four *Anoplophora* species have become established outside their native ranges. International trade in live plants and as a biotic stowaway in solid wood packaging materials were primary pathways for these invasions (Table 2). In response to these introductions, International Standards for Phytosanitary Measures (ISPM) No. 15 (which requires that all solid wood packaging materials be treated to kill woodboring insects) was developed by the International Plant Protection Convention (IPPC) and adopted in 2002. Since its development, ISPM 15 has been adopted by more than 130 countries (https://www.ippc.int/static/media/files/publication/en/2019/02/ISPM_15_2018_En_WoodPackaging_Post-CPM13_Rev_Annex1and2_Fixed_2019-02-01.pdf, Accessed 6/25/2025). Last revised in 2018, ISPM 15 is meant to significantly reduce the risk of introducing or spreading woodboring insects like *Anoplophora*. There is evidence that since implementation of ISPM 15 detections of live *Anoplophora* larvae in solid wood packaging material have decreased (i.e. the treatments are killing the larvae), though some are still being intercepted [115]. ISPM 36 was subsequently adopted in 2012 to provide integrated measures for international trade in live plants. ISPM 36 requires that pest risk management measures be applied during production and distribution to reduce the risk of moving associated pests (including *Anoplophora*) when live plants are moved. Current versions of both ISPM standards are available at www.ippc.int. Some countries have their own more stringent rules that target *Anoplophora* species. For example, the European Union has a regulation that was implemented in 2019 that bans the import of high-risk plants from countries outside the European Union [116]. Collectively, these preventive measures have reduced interception rates of *Anoplophora* species in Europe and North America [19, 37].

Once an infestation of an invasive *Anoplophora* species is found in either North America or Europe, an eradication program is initiated [19, 37, 117]. Ideally the infested area is found early while it is still small and few trees are involved, but that is not always the case. All established populations of the four invasive *Anoplophora* species have been initially detected in urban or sub-urban sites and are often reported by the public rather than being found during an official survey [19, 81]. The following is a summary of the eradication programs in North America and Europe as outlined in the published protocols [113, 117, 118]. Once an infestation is found, it is delimited, then a regulated area is declared that includes all known infested trees plus a buffer zone of ~ 2 km (up to 4 km if a cluster of heavily infested trees are found), and movement of potentially infested material out of the area is restricted. Visual surveys (i.e. ground, bucket truck and climber) are the primary detection methods used to find signs of infestation, but trapping, sniffer dogs, trap trees, and acoustic methods have also been used [19, 117]. Visual surveys have been estimated to find on average 81% of the trees with oviposition pits and 74% of those with exit holes of *A. glabripennis* [119]. There are currently no semiochemical-based trap lures which can be effectively used to detect, monitor, and potentially replace the expensive and time-consuming visual surveys used by eradication programs to locate and delimit infestations. The lack of a volatile blend that is highly attractive to one or both sexes of *Anoplophora* species may be due in part to the complex chemical ecology of these species [73]. Although systemic insecticides were initially used to try and prevent trees from becoming infested in some US locations, they are no longer being used because of questionable efficacy and public concern over their use.

Once an infestation is detected and delimited, all infested trees identified during surveys are cut and chipped. If the infestation is caused by *A. chinensis* or *A. malasiaca* then additional treatments to the stump and exposed roots are applied [120]. Adjacent known hosts are often removed within the regulated area and in Europe a 100-m-wide clear-cut is required when a larger, more dispersed infestation is found. Eradication is only declared when no new infested trees are found after a minimum of 3–4 years and two complete life cycles. Public awareness campaigns are a vital part of these eradication programs and include alerting the public to the threat posed by these invasive pests and establishing a reporting framework so members of the public can report sightings of beetles or signs of damage. These campaigns were critical for the early detection by the public and then rapid response to infestations of *A. glabripennis* in North America [81]. In addition, future-proofing eradicated areas may involve selecting non-host trees for replanting and can even extend to prohibiting the planting of any possible hosts, as is done in affected areas in Europe.

More than 45% of known infestations of *Anoplophora* species have been declared eradicated and several other populations are nearing that point [19]. Despite these successes, *Anoplophora* continues to pose significant invasion risks. For example, *A. horsfieldii* has emerged as a new invader with an unknown invasion pathway and has invaded a novel, warmer climate. While a small infestation of *A. horsfieldii* was first discovered on Jeju Island, South Korea in September 2019, the extensive scope of the infestation was not fully quantified until 2023 when more than 1,000 specimens were collected from the area. The scale of this infestation suggests a rapidly growing infestation [22, 51]. Currently, little is known about this species' biology and ecology and management options are in their infancy. The discovery of an infestation of *A. glabripennis* in South Carolina in May 2020 [43] is another example of the continued

risks posed by *A. glabripennis*. The South Carolina infestation is further south than any previous U.S. infestations and *A. glabripennis* has been shown to complete its development in a year or less in this warm environment [59]. Given the rate of development in this habitat, the South Carolina infestation has greater growth potential than infestations eradicated in northern climates. In addition to the potential for rapid population increase, many infested trees in South Carolina are located in expansive wetlands, areas with standing water and dangerous wildlife. This poses significant challenges to performing visual surveys and removing infested trees. However, recent pest management research has discovered new ways to manage *A. glabripennis* infestations in these challenging environments. For example, a fell and leave is a novel approach can be used that cuts infested trees in swampy areas and leaves them on the ground where they will rapidly decay and kill all developing insects. This approach permits host destruction without the need for whole-tree removal and chipping [121], thus meeting the demands for *Anoplophora* management under challenging environmental conditions.

Recently, several tools have been developed to aid forest managers and eradication programs. A suite of them is available within a package called Asian Longhorned Beetle Eradication and Risk Tracking (ALBERT) that help track and inform eradication efforts [40. This tool reconstructs beetle dispersal and estimates a locally based direction-explicit dispersal kernel from infestation records that document the timing, location, and approximate level of infestation for each infested tree. This dispersal kernel is then applied to each of the known infested trees to build a spatially explicit estimate of the distribution and intensity of risk on the landscape at an annual time scale. By combining this estimate of spatial risk due to beetle dispersal, with reductions in risk driven by eradication activities (i.e., surveys and host removal), the tool can provide a temporal estimate of how spatial risk changes through time. The tool can be used to evaluate proposed eradication activities to optimize eradication efficacy and/or minimize costs [122], and the tool has proved quite accurate when compared to an actual isolated infestation [123]. A spatial decision support system was also developed to guide surveillance in Canada that helped guide surveyors to residual pockets of infested trees and helped the eradication effort reach the pest-free goal [124]. Another example uses tree infestation records to both look at species attacked and the special utilization individual hosts to assess hosts on which to concentrate surveys [81].

Biological Control

Eradication programs for *Anoplophora* are successful and necessary, but costly. The programs require significant financial and labor investments, years of effort, and substantial tree removal [117]. In some cases, traditional eradication methods may be unfeasible or impossible. Furthermore, with new invasions still occurring and the difficulties in eradicating established populations plus ensuring adequate financial support to complete multi-year eradication programs, concerted effort has been put into finding natural enemies that could be used to reduce *Anoplophora* populations and support eradication efforts. This has involved both classical biological control, which involves finding natural enemies in the native range, and finding novel associations where natural enemies of other insects in the invaded areas have used the introduced *Anoplophora* species as hosts. A diverse range of natural enemies have been documented (there are likely many more undocumented species) for *Anoplophora* species [33–35, 125–142]. There are 7 fungal species that attack adults and larvae, 3 nematodes that attack all stages, 2 birds and one beetle that prey on larvae, and 35 hymenopteran species in 7 families that attack larvae, with only a single recorded egg parasitoid. Table 3 provides information on the identified species that attack *Anoplophora* species except for *A. glabripennis* for which there are recent reviews [34]– [35]. Two fungal pathogens have been developed into commercially available products, *Beauveria asiatica* S.A. Rehner & Humber in Japan and *Metarhizium brunneum* Petch. in the U.S., both of which can cause high beetle mortality [33, 35, 141].

Among the identified parasitoids of *A. glabripennis*, two of the most common in the native range that are thought to have narrower host ranges have been imported to the U.S. for further evaluation: *Spathius anoplophorae* Yang (Braconidae) and *Oxysychus glabripennis* Yang (Pteromalidae) [34]. Unfortunately, the primary natural enemies used for pest management in China [*Dastarcus helophoroides* (Fairmaire) (Bothrideridae) and *Sclerodermus* spp. (Bethylidae)] have unacceptably broad host ranges and thus are not suitable for classic biological control on other continents. The most promising parasitoid for use against *A. chinensis* is the egg parasitoid *Aprostocetus fukutai* Miwa & Sonan (Eulophidae), an adventive biological control agent that was detected in Italy 2004 (initially mis-identified as *Aprostocetus anoplophoreae* n. sp.) [127, 128]. *Aprostocetus fukutai* has parasitism rates of up to 72% in the field, is specific to *A. chinensis*, is gregarious, and develops in synchrony with its host [19], making it a promising biological control agent against *A. chinensis*. Like many other biological control programs, rearing large numbers of parasitoids in laboratory conditions is time and labor intensive, as well as costly.

Table 3 Natural enemies of *Anoplophora* species, excluding *A. glabripennis*

Order: Family	Species	Regions reported from or laboratory evaluation	Anoplophora Hosts	Stage Attacked	References
Hypocreales: Cordycipitaceae	*Beauveria asiatica* S.A. Rehner & Humber (formerly *B. brongniartii*)	Japan, China	*A. chinensis*, *A. malasiaca*	Adults	[33, 35]
Hypocreales: Cordycipitaceae	*Beauveria bassiana* (Balsamo) Vuillemin	Laboratory	*A. chinensis*	Adults	[33]
Rhabditida: Steinernematidae	*Steinernema feltiae* Filipjev	China	*A. chinensis*	Larvae, Pupae, Adults	[33]
Rhabditida: Steinernematidae	*Steinernema carpocapsae* Weiser	China	*A. chinensis*	Larvae, Pupae, Adults	[33]
Coleoptera: Bothrideridae	*Dastarcus helophoroides* Fairmaire	China, Japan	*A. chinensis*	Larvae	[33]
Hymenoptera: Bethylidae	*Sclerodermus brevicornis* (Kieffer)	Laboratory	*A. chinensis*	Larvae	[125]
Hymenoptera: Bethylidae	*Sclerodermus* spp.	Italy	*A. chinensis*	Larvae	[33]
Hymenoptera: Braconidae	*Ontsira anoplophorae* Kusigemati & Hashimoto	Japan	*A. chinensis*	Larvae	[33]
Hymenoptera: Braconidae	*Spathius erythrocephalus* Wesmael	Italy	*A. chinensis*	Larvae	[33]
Hymenoptera: Braconidae	*Spathius ibarakius* Belokobylskij & Maetô	Korea	*A. chinensis*	Larvae	[126]
Hymenoptera: Eulophidae	*Aprostocetus fukutai* (Miwa & Sonan)	China, Japan, Italy	*A. chinensis*	Egg	[127, 128]
Hymenoptera: Eupelmidae	*Calosota vernalis* Curtis	Italy	*A. chinensis*	Larvae	[33]
Hymenoptera: Eurytomidae	*Eurytoma melanoneura* Walker	Italy	*A. chinensis*	Larvae	[33]
Hymenoptera: Formicidae	*Oecophylla smaragdina* Fabricius	Asia	*A. chinensis*	Larvae	[33]
Hymenoptera: Pteromalidae	*Cleonymus brevis* Boucek	Italy	*A. chinensis*	Larvae	[33]
Hymenoptera: Pteromalidae	*Trigonoderus princeps* Westwood	Italy	*A. chinensis*	Larvae	[33]

Rearing *Anoplophora* species themselves was estimated to cost >$20 USD per beetle when costed 20 years ago [143]. Additional research and development is needed to expand and mature potential biological control programs to diversify management options for invasive *Anoplophora* species.

Conclusions

Eradication has proven to be successful for three of the four invasive *Anoplophora* species. Ongoing eradication programs are expensive and require substantial human and financial resources, and these costs are high in part due to the lack of effective traps and lures. Other management options, such as biological control may be needed if resources for eradication programs continue to decline or new infestations exceed resources available for eradication. The recent invasion of *A. horsfieldii* into South Korea also highlights the possibility that other *Anoplophora* species could arise as the next invasive species from this genus, causing unforeseen economic and ecological impacts. Therefore, continued investment in research on *Anoplophora* is required. Rapid identification tools for the less common species would provide valuable support for early detection and rapid response efforts. This would also include expanding our knowledge of the basic biology and ecology of these understudied species. A few additional *Anoplophora* species currently occupy more temperate regions in their native range; thus, the likelihood of additional species invasions into more northern latitudes may be low – but the higher *Anoplophora* diversity in subtropical areas of Asia suggests the potential for an increased risk of invasions into warmer environments.

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Acknowledgements We thank R. Haack and A. Hajek for reviewing earlier versions of the paper and offering helpful suggestions. We thank Z. Qin for help in verifying the species present in China. The work was partially funded by USDA Forest Service Northern Research Station.

Author Contributions MK and RTT drafted the first version of the manuscript and prepared all the figures. ADR and DRC reviewed and provided additions to sections of the final draft. All authors reviewed the manuscript.

Funding USDA Forest Service appropriated base funds. Funding to ADR from Natural Resources Canada.

Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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