Title

Preventing invasions of Asian longhorn beetle and citrus longhorn beetle: Are we on the right track?

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Abstract

Two Asian longhorn beetles, *Anoplophora glabripennis* and *Anoplophora chinensis* are among the most serious alien invasive species attacking forest and urban trees, both in North America and Europe. Major efforts have been put into preventing further entry and establishment of the two species as well as promoting their successful eradication. Here we review these efforts, their progress and outcome, and scientific advancements in monitoring and control methods. The combined international activities and harmonizing legislative changes in detection and eradication methods have proven worthwhile, with more than 45% of eradication programmes successful in the last 12 years. Some countries were able to completely eradicate all populations and others managed to reduce the area affected. Although the costs of the eradication programmes can be very high, the benefits outweigh inaction. Attempts to eradicate *A. chinensis* have been more challenging in comparison with those targeting *A. glabripennis*. For both species, efforts are hampered by the ongoing arrival of new beetles, both from their native regions in Asia and from other invaded regions via bridgehead effects. The methods used for eradication have not changed much during the last decade, and host removal is still the method most commonly used. On the other hand, detection methods have diversified during the last decade with advances in semiochemical research and use of detection dogs. The next decade will determine if eradications continue to be successful, particularly in the case of *A. chinesis*, which has been targeted in some countries for containment instead of eradication.

Keywords: Biological invasions; *Anoplophora* spp.; eradication; management strategies; pest detection; surveillance

Declarations

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Key Message

- *Anoplophora glabripennis* and *Anoplophora chinensis* are invasive wood borers native to Asia
- Both species are serious pests in their invaded range, attacking healthy forest and urban trees
- We analyze data from 2008-2020, regarding interceptions, establishments and eradications
- In Europe and North America more than 45% of eradication programmes were successful
- Innovations on management strategies and recent scientific achievements are reviewed

Author Contribution Statement

MB and HJ had the idea for the review. MB, HJ, EB and ND set the main structure of the work. SB, MF and GR conducted the literature search. SB conducted the data analysis and drafted the manuscript. All authors contributed to writing the final version of the manuscript and critically revised the work.

1. Introduction

In the last decades, increasing international trade resulting from globalisation has facilitated the introduction of non-native species to new environments and thus boosted the problems with biological invasions worldwide (Brockerhoff and Liebhold 2017; Liebhold and Kean 2019; Lesieur et al. 2019; Zhao et al. 2020). Invasive species have considerable ecological and economic impacts on agricultural, urban and forest systems, compromising their sustainability and the ecosystem services they provide (e.g., Boyd et al. 2013; de la Vega et al. 2020; Gugliuzzo et al. 2021). The Asian longhorn beetle (ALB) *Anoplophora glabripennis* (Motschulsky) and the citrus longhorn beetle (CLB) *Anoplophora chinensis* (Förster) (synonym *Anoplophora malasiaca* (Thomson)) (Lingafelter and Hoebeke 2002) are two emblematic examples of such alien invasive species.

Both ALB and CLB are highly polyphagous wood borers developing in dozens of deciduous tree species, with CLB having a wider host range than ALB (Lingafelter and Hoebeke 2002; Haack et al. 2010; Van der Gaag et al. 2010; Van der Gaag and Loomans 2014; Sjöman et al. 2014; EFSA et al. 2019a,b). In Europe, *Acer* is the most commonly attacked genus by both species (e.g. EFSA et al. 2019a,b). However, the two species differ regarding plant part on which oviposition and larval development take place. In ALB, oviposition and larval development occur on the upper trunk and main branches, whereas CLB mainly oviposits on the lower trunk, root collar region and on exposed roots, and larvae develop in the lower trunk and roots. This crucial difference translates into different pathways of introduction. ALB introductions are largely associated with the use of solid wood packing material (WPM) in international trade of goods, whereas CLB is rarely introduced with cut wood. CLB introductions are mainly associated with imports of live plants such as small maple trees and bonsais (e.g. Hérard and Maspero 2019).

ALB is native to China and the Korean Peninsula (Lingafelter and Hoebeke 2002; Williams et al. 2004a). Non-native breeding populations of ALB have been reported in many locations in the USA, Canada, Europe and Japan (Makihara 2002; Takahashi and Ito 2005; Hu et al. 2009; Haack et al. 2010), making ALB one of the most successful and most feared invasive insect species worldwide. CLB is native to eastern Asia, where it is widely distributed in China, Korea, and Japan. CLB has also been reported from Indonesia, Malaysia, Philippines, Taiwan, and Vietnam (Lingafelter and Hoebeke 2002; EFSA et al. 2019a). Contrary to ALB, established populations of CLB outside its native range have only been reported in a few countries in Europe. Both species have accidentally arrived in North America and Europe several times independently as documented by molecular genetic studies, numerous interceptions, and infestation hotspots (e.g., Haack et al. 2010; Hérard and Maspero 2019). These successive arrivals may hamper eradication attempts in a given region. Due to their potential impacts on ecosystems and many economically important tree species, these two species have been regulated as priority quarantine pests in Europe, the United States and other countries (EU 2019; USDA-APHIS 2020a).

Haack et al. (2010) reported an extensive analysis of interceptions, establishments, eradications and management strategies used to deal with ALB and CLB in the invaded range, covering the period up to 2008. The authors also challenged the scientific community to respond to the needs identified by the difficulties associated with mitigating the threat posed by these beetles and with eradicating local established populations. Since then, 12 years have passed, but the two beetles still remain a menace for an increasing number of countries, and a large number of eradication programmes are still in progress. The aims of the present work are (i) to update the interception records which indicate ongoing transport with international trade, (ii) to review the eradication programmes carried out during the last 12 years, and (iii) to analyse the current status at the country level in order to understand the successes and failures of measures to mitigate invasions by the two beetles. Further objectives are to analyse the scientific achievements that occurred in the last 12 years, especially with regard to efforts in developing novel tools and methods for detection, monitoring and control, and to understand how the scientific community and managers have dealt with the challenges posed by these two species

1.1. Terminology and data sources

Interception. We follow the definition of interception provided in Haack et al. (2010), which further differentiates *entry interceptions* from *post-entry interceptions*. For the period prior to 2008, data from Haack et al. (2010) were used. After this period, interception data were retrieved from EPPO via Europhyt for Europe, thus representing the EU member states and Switzerland (data kindly provided by Françoise Petter, assistant director of EPPO) and for North America via USDA-APHIS (see Turner et al. 2020, 2021).

Establishment. The International Standard for Phytosanitary Measures (ISPM) No. 5 definition of establishment was adopted (FAO 2019). We consider a new establishment when located at least 5 km distant from infested trees detected in previous delimiting surveys or when findings occurred in a previously infested area, but where the population was officially declared eradicated by the relevant authorities (e.g., Toronto in 2013).

Demarcated area. The *demarcated area* corresponds to the area legally established by each national plant protection organization (NPPO) as subject to eradication and containment measures, and usually comprises an infested zone, where the pest is present, and a buffer zone around the infested zone (FAO 2019).

In order to obtain the temporal and geographical data of ALB and CLB establishments, demarcated areas and buffer zones, the main sources consulted were the EPPO Global Database (https://gd.eppo.int), GERDA - Global Eradication and Response DAtabase (Kean et al. 2015) and the USDA-APHIS website (https://www.aphis.usda.gov/). This information was complemented by a search of the scientific and grey literature, including works published in scientific journals, conference proceedings, presentations, and eradication reports and other technical reports of national and regional plant protection organisations. When only distribution maps were available, affected areas were extrapolated using ArcGis online tools. For data regarding the period up to 2008, this information was retrieved from Haack et al. (2010).

For most analyses we used two similar twelve-year periods, comparing data from 1997 to 2008 and from 2009 to 2020. For interceptions we used data from 1998 until 2019 (i.e., two eleven-year periods).

2. Interceptions and preventive measures

2.1 Regulation and legislation

In international trade, the International Standards for Phytosanitary Measures No. 15 (ISPM-15), which was adopted in 2002 and revised in 2009, provides treatment standards for WPM to be used in international trade and was intended "*to reduce significantly the risk of introduction and spread of most quarantine pests that may be associated with that material"* (IPPC 2009). Nevertheless, several factors can theoretically impact the effectiveness of ISPM 15: i) possibility of colonization after treatment, ii) insect tolerance to treatment, iii) fraudulent use of the ISPM 15 mark; and iv) unintentional noncompliance, which may occur when operators attempt to treat WPM according to ISPM 15, yet the minimum required doses of fumigant or heat are not achieved (Haack et al. 2010; Haack et al. 2014). Still, ALB and CLB are highly unlikely to colonise sawn timber as in WPM, and survival of appropriately applied ISPM 15-compliant treatment is also very unlikely (e.g., Myers and Bailey 2011). So, in most cases, ISPM 15 failure can probably be attributed to fraudulent use of the ISPM 15 mark and unintentional noncompliance (factors iii and iv).

Regarding introductions in association with live plants, a new EU regulation was adopted in October 2016 and implemented since December 2019 (regulation (EU) 2016/2031), on protective measures against pests of plants (repealing Council Directive 2000/29/EC), which completely bans the import of high-risk plants and selected plant products from countries outside of the EU (EU 2016). This regulation is expected to reduce the number of introductions/interceptions of *Anoplophora* spp., particularly of CLB.

Emergency measures to prevent the introduction into and the spread within the EU of ALB and CLB are defined in Commission Implementing Decisions 2015/893/EU and 012/138/EU, respectively (EU 2012, 2015). These include mandatory annual surveys to be conducted by each member state.

In the last decade, changes to protocols for inspection at ports of entry have also been adopted: the standard "Methodologies for Sampling of Consignments" (ISPM 31) was adopted in 2008. This standard outlines different types of sampling methods that NPPOs may use to verify compliance of consignments with phytosanitary requirements and the sample sizes required for general phytosanitary inspection (IPPC 2008). It complements ISPM 23 "Guidelines for Inspection", adopted in 2005, where the general procedures for inspection of consignments are described (IPPC 2005).

2.1. Interceptions

In Europe, ALB and CLB were intercepted 140 and 95 times, respectively, from 1980 until 2019. Considering the periods from 1998 to 2008 and from 2009 to 2019, the number of CLB interceptions decreased, with 48 *vs* 30 cases, whereas the number of ALB interceptions almost doubled (48 *vs* 90 cases) (Fig. 1).

A sharp difference was observed between time periods for both species regarding the site of interception, i.e., whether the interceptions occurred at "entry" or "post-entry" such as nurseries, warehouses, private residences, etc. For ALB, during 1998-2008, 97% of interceptions occurred "post-entry", whereas during 2009-2019 these proportions reversed, with 94% of interceptions reported during "entry" inspections. This increase in interceptions during border inspections is possibly a result of changes in legislation, namely the implementation of ISPM 31 in 2008. For CLB, the percentage of interceptions at "entry" also increased during 2009-2019, albeit more moderately (19% *vs* 57%).

For the period from 2009-2019, information on the origin of the infested material arriving at EPPO region was available in 88% of the cases (98% for ALB and 60% for CLB), mostly obtained during border inspections. For ALB, all infested consignments arrived from China while for CLB, in addition to China (83%), infested material originating from Japan was intercepted twice (11%) and an infested bonsai of unknown origin was shipped from the Netherlands. ALB interceptions were associated with wood packaging material (WPM) in 96% of cases (mostly linked to stone and tile products) and once to an object with wooden parts (1%). On the other hand, CLB was found in WPM only once. In 20% of cases, CLB was found in bonsais and in 70% it was found in other trees for planting. In two cases, each of ALB and CLB, only adults were found and the associated material could not be identified.

Excluding border inspections, 87% of ALB detections outside of their native range occurred after establishment (54/62). In the remaining 13%, which corresponded to "post-entry" interceptions, only adults and/or infested WPM were found. Contrasting this with CLB, the corresponding value is much lower, with only 44% (20/45) of detections relating to established populations. These values reflect the different introduction pathways of each species: CLB is usually introduced in imported live plants whereas ALB is introduced in association with wood packaging materials (e.g. Eyre and Haack 2017). Live plants are subject to more intense inspection or incidental observation, either at nurseries or by the final consumer. Of the 25 post-entry interceptions of CLB approximately half (48%) occurred in nurseries, 40% at private residences, and three cases were detected in public parks and street trees.

Despite the adoption of ISPM 15 in 2002 which set strict standards for heat treatment and fumigation of WPM to be used in international trade (IPPC 2009), the number of reported interceptions with wood packaging in Europe has increased. Although this may be related to changes in inspection practices resulting from the implementation of ISPM 31, it still emphasises that ISPM 15 does not provide a guarantee that WPM is entirely pest-free, and that further improvements may be needed, especially to ensure prescribed treatments are indeed carried out (Haack et al. 2014).

In North America, a sharp decrease was observed in the number of interceptions of both ALB and CLB from 2009 to 2019 (18 ALB, zero CLB, Table 1), when compared to the period from 1998 to 2008 (72 ALB, 5 CLB, Haack et al. 2010).

In Europe, since 1998, three countries alone account for 70% *Anoplophora* spp. interceptions: The United Kingdom, the Netherlands and Germany. These three countries also ranked highest in international trade with East Asian countries during this period (WITS 2021), which may partially explain these results. In the United Kingdom, the number of interceptions of both species decreased in the last decade, by 88% for ALB and by 50% for CLB. By contrast, in Germany both increased (ALB by 108% and CLB by 40%). In the Netherlands, the number of ALB interceptions increased by 267% whereas CLB interceptions decreased by 55%. In Austria and Switzerland, while there were no ALB interceptions in the period 1998-2008, in the last decade, 18 and 17 cases were reported, respectively (Table 1). The different interception frequencies reported for each EU importing country are likely to reflect differences in inspection practices and differences in the reliance on ISPM 15 having solved the problem. Eyre and colleagues (2018) observed that the highest detection rates were achieved in Austria and France, whereas in Spain and Poland, despite the inspection of more than 500 consignments, no harmful organisms were detected. The authors suggested that harmonizing the inspection procedures to the most effective methodology may lead to an approximate sevenfold increase in the number of interceptions of invasive pests across all member states (Eyre et al. 2018). A study on relationships between interceptions and establishments of Cerambycidae (including ALB and CLB) found that there is a significant positive relationship overall between these parameters (Brockerhoff et al. 2014), which highlights the potential usefulness of recording interception data from inspections of relevant imports.

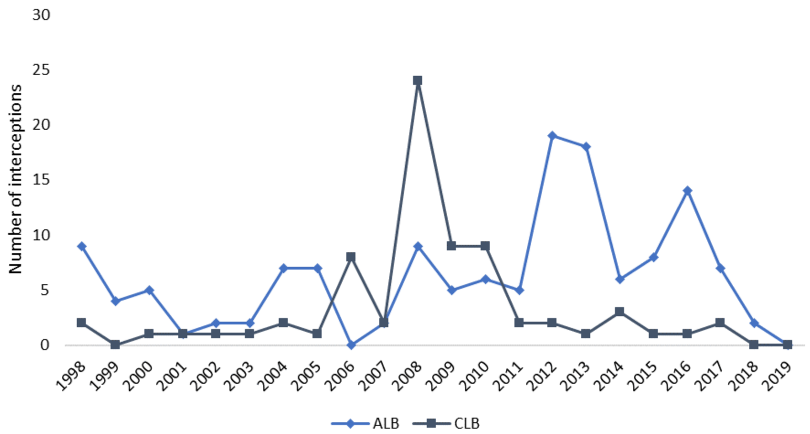

Figure 1 Temporal trend of the number of interceptions of *Anoplophora* spp. in Europe from 1998 to 2019.

Table 1 Interception data for *Anoplophora* spp. from 2009 to 2019

Year	2009		2010		2011		2012		2013		2014		2015		2016		2017		2018		2019		Total	
	A	C	A	C	A	C	A	C	A	C	A	C	A	C	A	C	A	C	A	C	A	C	A	C
Region/country																								
North America			5		1		6		3		2										1		18	
USA			5		1		6		3		2										NA	NA	17	
Canada																					1		1	
Europe	5	9	6	9	5		19	2	18	1	6	4	8	1	14	1	7	2	2				90	30
Austria									4		1		3		5		4		1				18	
Belgium					1			1															1	1
Czech Republic									2														2	
Cyprus		1																						1
Denmark						1*																		1
Estonia													1		1				1				3	
Finland													2				1						3	
France		2									1				1								2	2
Germany		1/2*	4	1	3		10	1	7		1	1*	1		1			1					27	7
Netherlands	3	3	1	4			3		1		1			1	2	1							11	9
Slovakia									1*														1	
Sweden	2																						2	
Switzerland					1*		6		3	1*	2	1*	1		3		1						17	2
Turkey												1*						1*						2
United Kingdom			1*	4*		1*						1*			1		1						3	5
Total	5	9	11	9	6	2	25	1	21	1	8	4	8	1	14	1	7	2	2	0	1	0	108	30

A=ALB, C=CLB. Numbers indicate interceptions at ports of entry or transitional facilities ("entry" interceptions). "Post-entry" interceptions are indicated by "*". Specimens identified as *Anoplophora* spp. from wood packaging material were designated ALB and those from live plants were designated CLB.

3. Establishments

3.1. Spatial and temporal patterns of establishments

<u>At the continental scale</u>

Since the first detection of an established population in New York in 1996 until the end of 2020, 56 ALB and 20 CLB established populations were reported worldwide. From 2009 to 2020, 37 ALB and 10 CLB establishments were detected in North America and Europe (Fig. 2). More recently, an established population has also been reported from Hyogo Prefecture in Japan (Akita et al. 2021). Until now, CLB breeding populations outside their native range were detected only in Europe. For CLB, the number of new detected establishments was identical to the previous period (1997- 2008). However, a sharp difference was observed in the number of ALB establishments, which have more than doubled from 2009 to 2020. Furthermore, out of the 37 ALB establishments detected in the last 12 years, 62% were detected between 2012 and 2016.

A summary table with all the identified establishments of ALB and CLB by detection date and geographical location is shown in Supplement S1. For ALB, a brief description of the last decade of establishments by region and country is presented in Supplement S2. The detailed invasion history of CLB in Europe has recently been reviewed by Hérard and Maspero (2019) and is thus not covered in detail in the present work.

For ALB, the number of new establishments detected in Europe has increased more than fourfold in the period 2009-2020 relative to the period from 1997 to 2008. Out of the 37 ALB establishments detected in the last period, 84% were in Europe (Fig. 3, 4 and 5). The increase in the geographical distribution of ALB establishments in Europe mainly reflects the high number of establishments detected in Germany (9) and Italy (8). In contrast, in North America, until 2020 only six new establishments were detected since 2009 (three in Ohio, one in Boston, one in South Carolina and one in Ontario), which is approximately half of the number reported from 1997 to 2008. New CLB establishments were detected in Italy, Turkey, Croatia, France and the Netherlands (Fig. 4). Despite the high number of establishments detected in Italy, no interceptions have ever been reported there (see above).

By the end of 2020, the total demarcated area in Europe affected by ALB was about 630 km^2. This area corresponds to a 10-fold increase compared with the area affected by 2008 (62 km^2). This expansion reflects the large increase in the number of active establishments. By comparison, the total affected area changed little in North America, with an increase from 580 km^2 in 2008 to 770 km^2 by 2020. Still, despite the number of total ALB establishments detected in Europe being higher than those in North America, the current demarcated areas are similar in the two regions. The demarcated areas in Europe are mainly concentrated in three countries, Italy, Germany and France (Supplement S1).

For CLB, although the number of detected establishments was identical from 1997-2008 to 2009-2019 (10 establishments, Fig. 4), the total demarcated areas of all active establishments (including establishments detected before 2009), almost quadrupled in Europe (150 km^2 in 2008 *vs* 590 km^2 in 2020). The demarcated areas by country expanded mostly in Italy (from 140 to 510 km^2), Croatia (from 0 to 55 km^2) and France (from 3.1 to 8.9 km^2) (Supplement S1).

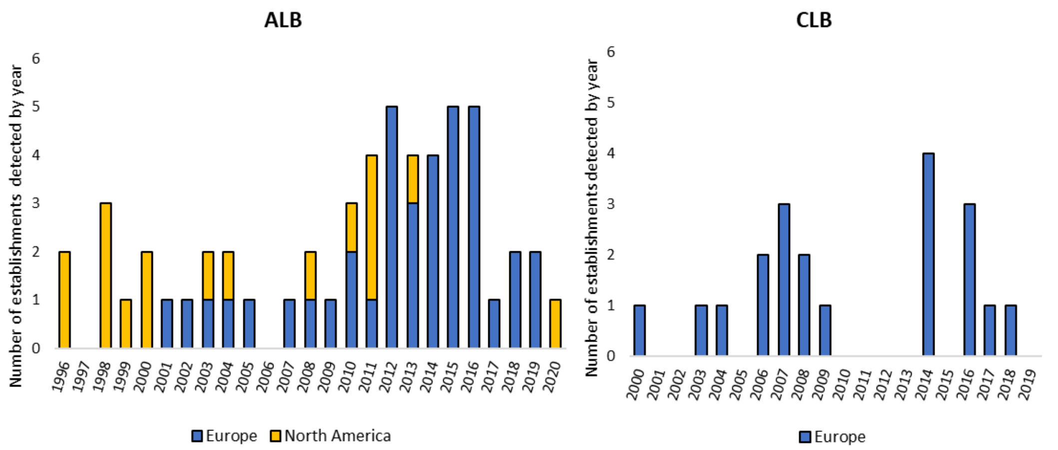

Figure 2 Number of *Anoplophora* spp. establishments detected by year, from 1996 to 2020.

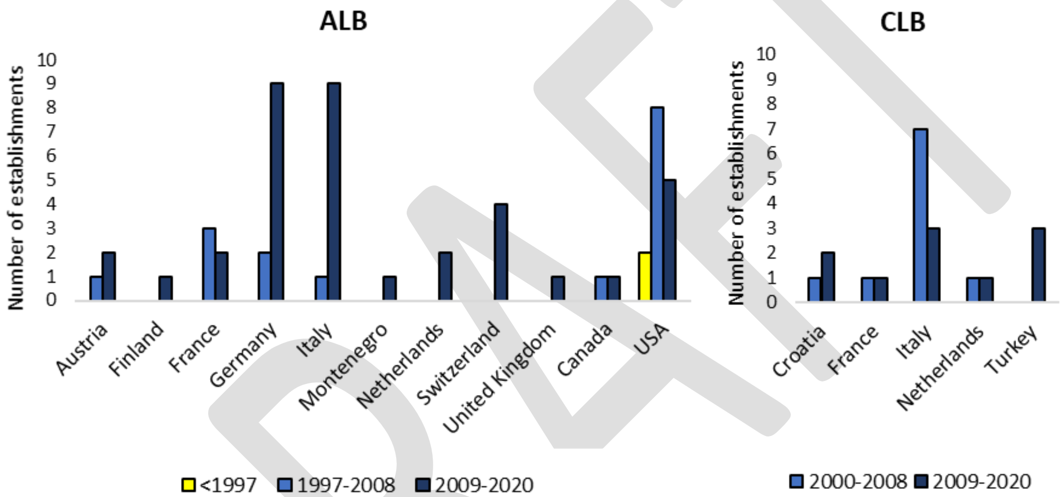

Figure 3 Number *Anoplophora* spp. establishments detected by time period and country.

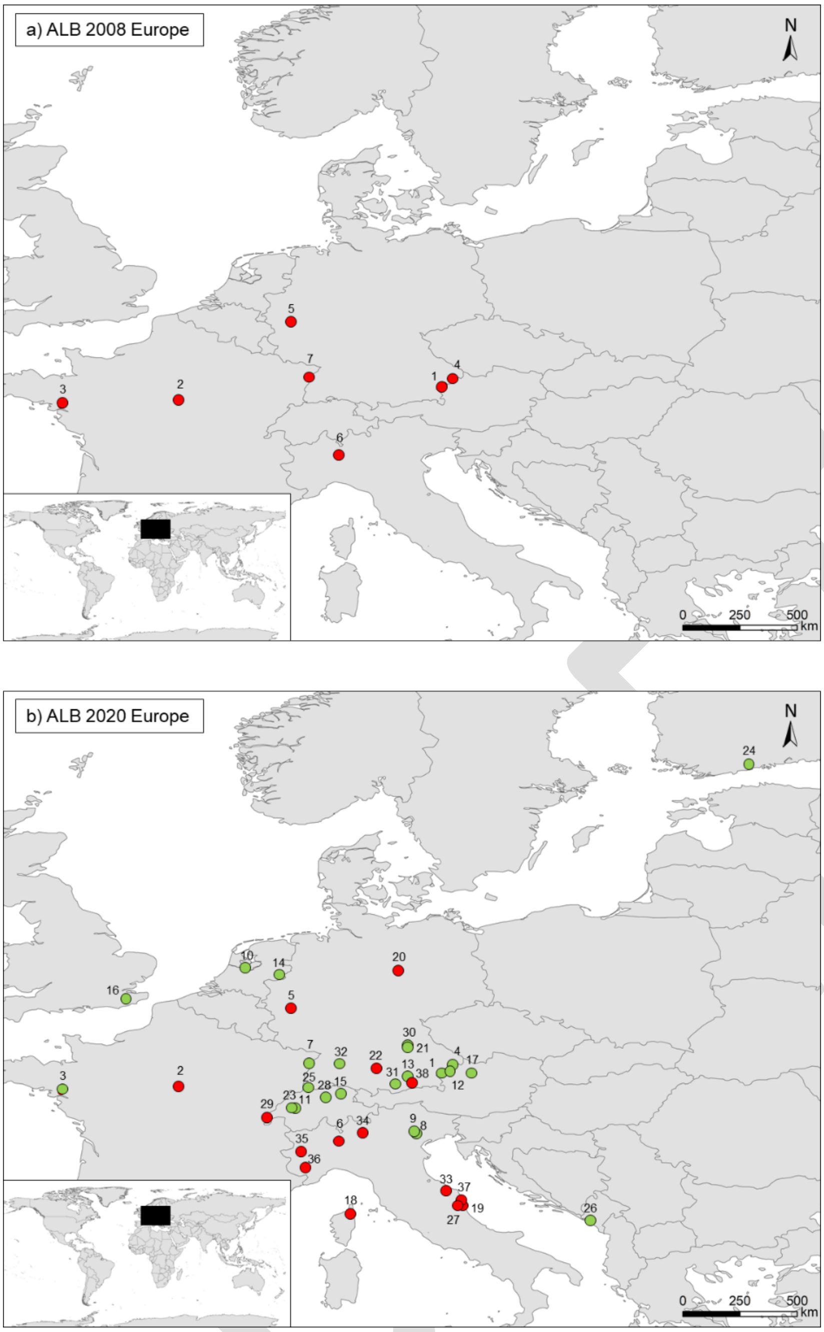

Figure 4 Geographical distribution of established populations of ALB in Europe by year of detection. a) Status of establishments up to 2008, b) status of establishments from 2009 to 2020. Red dots represent active establishments, green dots eradicated establishments (as of April 2021): 2001: Braunau, Austria (1); 2002: Gien, France (2); 2003: Sainte-Anne-sur-Brivet, France (3); 2004: Neukirchen, Germany (4); 2005: Bornheim, Germany (5); 2007: Corbetta, Italy (6); 2008: Strasbourg, France (7); 2009: Cornuda, Italy (8); 2010: Maser, Italy (9), Almere, Netherlands (10); 2011: Brünisried, Switzerland (11); 2012: Geinberg, Austria (12), Feldkirchen, Germany (13),Winterswijk, Netherlands (14), Winterthur, Switzerland (15), Paddock Wood, UK (16); 2013: Gallspach, Austria (17), Furiani, France (18), Grottazzolina, Italy (19); 2014: Magdeburg, Germany (20), Neubiberg, Germany (21), Ziemetshausen, Germany (22), Marly, Switzerland (23); 2015: Vantaa, Finland (24), Grenzach-Whylen, Germany (25), Budva, Montenegro (26), Porto San Giorgio,Italy (27), Berikon, Switzerland (28) ; 2016: Divonne-les-Bains, France (29), Kelheim, Germany (30), Murnau, Germany (31), Hildrizhausen, Germany (32), Ostra and Senigalia, Italy (33); 2017: Trescore Balneario, Italy (34); 2018: Vaie, Italy (35), Cuneo, Italy (36); 2019: Civitanova, Italy (37), Miesbach, Germany (38).

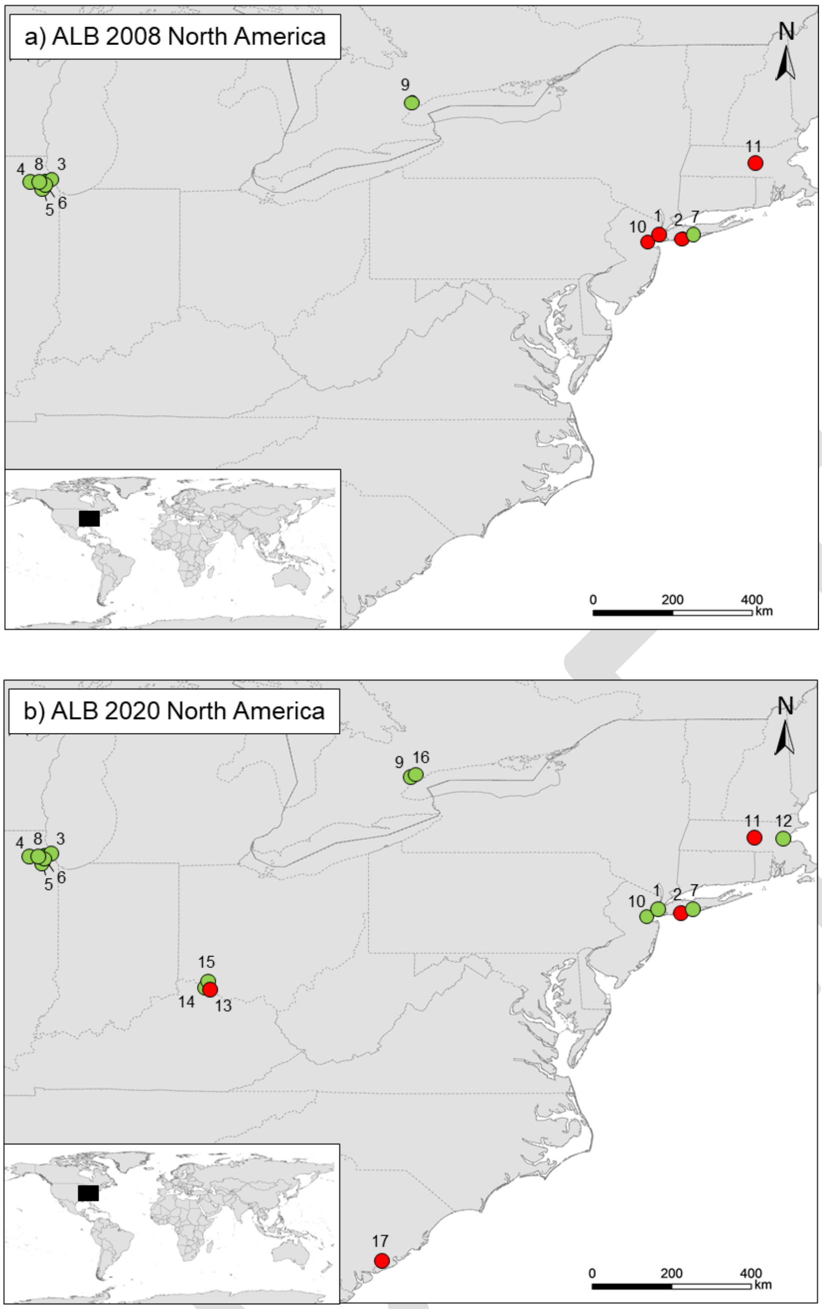

Figure 5 Geographical distribution of established populations of ALB in North America, by year of detection. a) Status of establishments up to 2008, b) status of establishments from 2009 to 2020. Red dots represent active establishments, green dots eradicated establishments (as of April 2021) 1996: Brooklyn, New York, USA (1), Long Island, New York, USA (2); 1998: Chicago, Illinois, USA (3), Addison, Illinois, USA (4), Summit, Illinois, USA (5); 1999: Park Ridge, Illinois, USA (6); 2000: Islip, New York, USA (7), Chicago O´Hare, Illinois, USA (8); 2003: Vaughan, Ontario, Canada (9); 2004: Carteret and Linden (2006), New Jersey and Prall and Staten Island (2007), New York, USA (10); 2008: Worcester, Massachusetts, USA (11); 2010: Boston, Massachusetts, USA (12); 2011: Tate Township, Ohio, USA (13), Monroe Township, Ohio, USA (14), Batavia/Stonelick Townships, Ohio, USA (15); 2013: Mississauga, Ontario, Canada (16); 2020: Hollywood, South Carolina, USA (17).

<u>At the local scale</u>

All established populations of *Anoplophora* spp. were initially detected in urban/peri-urban environments (Fig. 6). For both species, infested trees and live beetles were initially detected in private gardens in approximately half of the establishments (52% for ALB and 50% for CLB). Detections in public parks and street trees were also common, whereas detection in peri-urban forests was rare and occurred only once in one ALB and one CLB establishment, during official surveys.

In its native range in South Korea, ALB has been reported to be a riparian species adapted to the long edges of these habitats (Williams et al. 2004a). If this is the case, it might explain its adaptability to hedgerows (along roads, gardens, and parks) typical of urban habitats (Williams et al. 2004a; Faccoli et al. 2016). This is in accordance with the infestation pattern in Cornuda (Italy), where, although part of the quarantine area fell within a natural hardwood forest, infested trees have only been found along its edges (Faccoli et al. 2016). Similarly, in Chicago (USA) hundreds of Acer spp. were found infested along the edge of a 50-ha woodlot but not in the interior, suggesting a strong edge effect during the invasion (Sawyer et al. 2011). The infestation of hardwood stands in a large outbreak observed in Massachusetts (USA) has been pointed out as an exception (Dodds and Orwig 2011). However, the small size of the infested stands in Massachusetts, surrounded by city outskirts and streets, makes them comparable to urban parks and small rural stands (Faccoli et al. 2016).

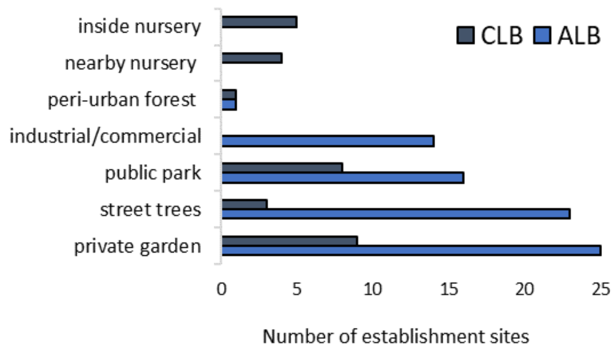

Figure 6 Sites of initial detection(s) of Anoplophora spp. establishments. This information was available for 49/55 and 18/20 of ALB and CLB establishments, respectively.

Differences between the two species can be seen which are related to their pathways. For ALB, industrial/commercial sites (areas that are likely to receive imports in WPM or live plants from potential source regions) are commonly affected and detections at such sites occurred in 30% of establishments. For CLB, 50% of detections involved sightings of insects or infested trees at plant nurseries (28%) or near plant nurseries (22%).

Considering how detections occurred initially, 73% of ALB establishments (33/45) were detected by passive surveillance and 24% were detected during official surveys. For CLB, 76% (13/17) of cases were reported during official surveys and the remaining 24% were the result of either passive surveillance (one case) or detected during scientific research activities (3 cases). Passive surveillance corresponded mostly to citizens who reported symptoms or sightings of adult insects to phytosanitary authorities, operators of nurseries and city parks and landowners. For most establishments, the first trees infested were maples (*Acer* spp.), corresponding to 90% and 95% of ALB and CLB cases, respectively (Fig. 7). However, while ALB was found infesting mostly local trees of *A. platanoides* and *A. pseudoplatanus*, CLB was mostly found infesting *A. palmatum* and *A. negundo*. For ALB, *Salix* sp., *Ulmus* sp. and *Aesculus hippocastanum* were also commonly found infested. For CLB, in addition to maples, the most common infested tree genera were *Carpinus*, *Corylus*, *Betula* and *Platanus* (Fig. 7). The host trees affected at each site are expected to be influenced by the host species available. Nevertheless, affected hosts may also reflect the origin of the local populations: in South Korea, for example, ALB riparian forest populations appear to display a different host usage when compared to urban populations, and the latter have been shown to result from recent invasions from China (Lee et al. 2020).

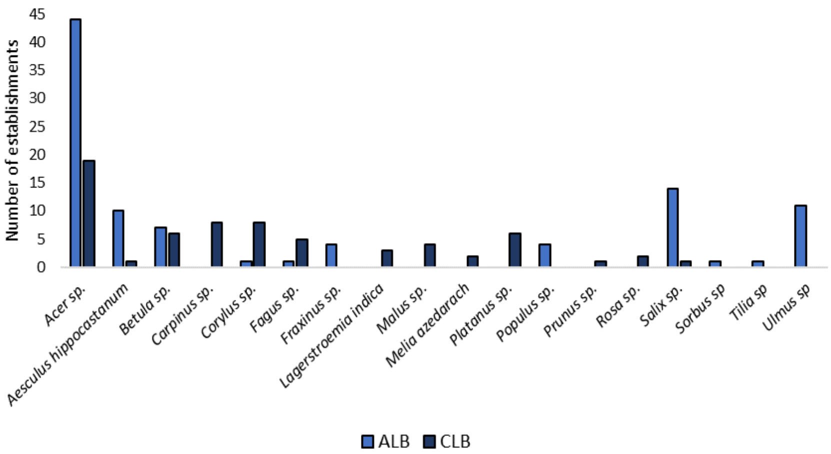

Figure 7 Tree species or genera in which establishments of ALB and CLB were detected either during passive surveillance or official or scientific surveys. This information was available for 49/55 and 20/20 of ALB and CLB establishments, respectively.

3.2. Pathways of introduction: reconstruction of invasion routes

<u>ALB</u>

The first studies on the intraspecific genetic diversity have focused mainly on the native Asian regions (An et al. 2004; Carter et al. 2009a). They reported that, although the Asian populations clustered roughly into two major groups, the population structure has been influenced by movement of beetles and consequent genetic admixture (Carter et al. 2009a). Javal et al. (2019a,b) highlighted signs of an ancestral structure in NE Asia, and a strong differentiation among most of the populations following a north-south gradient. These studies also considered human-mediated population translocations at large scale, especially those linked to afforestation projects initiated by the Chinese government since the 1960s in northern and eastern China (Li 2004; Haack et al. 2010).

Studies of North American establishments revealed a reduced genetic diversity within populations in either the USA or Canada due to genetic bottlenecks (Carter et al. 2009b, 2010). Separate introduction events were responsible for most North American populations, the founders of which likely originated from populations invasive within China (Carter et al. 2010; Javal et al. (2019a,b). In addition, some subsequent human-mediated regional spread occurred in the USA (e.g. New York City, Carter et al. 2010) and in Canada (Turgeon et al. 2015).

In Europe, mitochondrial DNA and microsatellite marker studies revealed a complex worldwide invasion scenario involving recurrent introductions coupled with a bridgehead event. The genetic structure observed suggests that European establishments originated mostly from multiple independent introductions from the native area in Asia (Fig. 8). The resulting genetic differentiation among European establishments may indicate limited gene flow between populations once established, mostly due to the poor dispersal behaviour of this species. A fine-scale study in Switzerland (Tsykun et al. 2019) showed that only one or a maximum of two genetic clusters were found within a given tree, suggesting that most ALB individuals remain in proximity to the tree from which they emerged when suitable host trees are available (Smith et al. 2001 and 2004; Javal et al. 2019a,b). Low levels of genetic diversity, high levels of inbreeding, small numbers of founders and large differences in the severity of bottlenecks encountered by introduced populations have shaped the genetic structure of invasive populations (Javal et al. 2019a,b). Natural dispersal and/or human-mediated transportation (e.g. hitch-hiking) at a small spatial scale were observed in some regions as in Corsica and in Switzerland (Javal et al. 2019a,b; Tsykun et al. 2019). Bridgehead events may have contributed to the worldwide spread of ALB (Javal et al. 2019). This appears to be the case for the French population in Gien that may have resulted from a bridgehead population from North America (Javal et al. 2019a,b) rather than Asia as suggested in previous publications (Cocquempot et al. 2003).

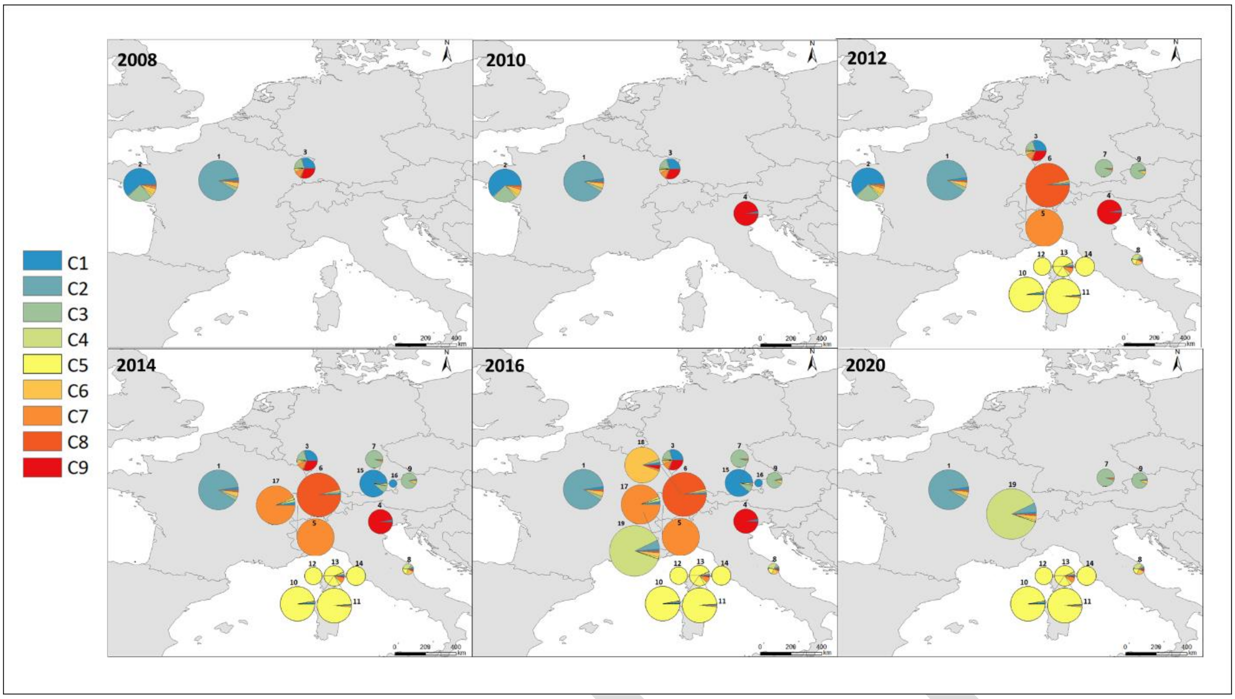

Figure 8 Distribution of some European ALB populations and their defined genetic clusters inferred by structure analysis. The numbers correspond to the sampled locations used in Javal et al. (2019a): 1 Gien, France; 2 Sainte-Anne-sur-Brivet, France; 3 Strasbourg, France; 4 Cornuda, Italy; 5 Brünisried, Switzerland; 6 Winterthur, Switzerland; 7 Feldkirchen, Germany; 8 Rapagnano, Italy; 9 Gallspach, Austria; 10 Arenau, Corsica; 11 Colast, Corsica; 12 Conouv, Corsica; 13 MCarlo, Corsica; 14 Costad, Corsica; 15 Neubiberg, Germany; 16 Ebersberg, Germany; 17 Marly, Switzerland; 18 Berikon, Switzerland; 19 Divonne les Bains, France. Each colour corresponds to a haplotype cluster.

CLB

The genetic structure and invasion pathways of CLB have not been studied as intensively as for ALB. Strangi et al. (2017) conducted a mitochondrial DNA analysis on native populations from East Asia and three Italian establishments. In Italy, a total of five haplotypes were identified in Lazio, Lombardy and Tuscany. Three of these haplotypes were only found in Tuscany, and these were closely related to haplotypes found in Chinese populations. The remaining two haplotypes, found in Lazio and Lombardy, corresponded to populations from North and Central Japan (Strangi et al. 2017). These results suggest that the Italian establishments originated from at least two separate events. CLB is known to show phenotypic polymorphism that allow for the distinction of two forms: *A. chinensis chinensis* and *A. chinensis malasiaca* (Ohbayashi et al. 2009). In the Lazio and Lombardy establishments, where the origin was traced back to Japan, specimens were identified as *A. chinensis malasiaca*, whereas in Tuscany, where the population origin was traced back to China, specimens were shown to be *A. chinensis chinensis*. In the recent establishment detected in Royan, the *A. chinensis chinensis* subspecies has been detected, and further studies are currently underway to uncover the origin of the specimens recovered at this location (ANSES 2019).

These recent studies have started to unravel the complexity of ALB´s and CLB´s invasion histories: multiple introductions have occurred, originating from several regions of Asia (China, Korea, Japan) and in some cases these appear to have included bridgeheads effects. Furthermore, studies have also shown that even genetic populations of extremely low genetic diversity can multiply to outbreak proportions in urban areas (Carter et al. 2009b).

4. Eradications

4.1. Methods of eradication

In the European Union, CLB and ALB infestations that affect a Member State are subject to specific management procedures defined by the European Commission (EC 2012 and 2015 respectively) and transcribed in national and regional decrees with the aim to eradicate all active infestations. Each country where an infestation is detected usually develops an eradication programme that incorporates activities focused on detecting infested trees, removing pest populations and limiting pest movement and spread, i.e. every eradication programme includes monitoring, control and containment components (see section 6 for their description). The first step is to delineate a demarcated area and forbid movement outside the demarcated area of infested or potentially infested wood material and host trees (EPPO 2013a,b). Whenever a new establishment is detected, an initial, intensive delimiting survey must be conducted to determine the extent of the infested area. Demarcated areas are then established including the infested area and a surrounding buffer zone of typically 2 km radius. Depending on the extent of the infestation and the site-specific characteristics, such as the local distribution of host plants, this buffer zone may be reduced to a radius of 1 km. The prescribed survey methodology is similar across all EU member states. Once trees are found to be infested by ALB/CLB, they are recorded and submitted to specific protocols aimed to eliminate insect populations, based on different types of measures including tree destruction, chemical and physical treatments (EPPO 2013a,b).

In North America, annual surveys to actively search for new infestations are, to our knowledge, not mandatory. However, once an infestation is detected, similar protocols apply: establishment of regulated areas consisting of a core area (0.8 km radius) and a buffer zone (1.6 km beyond the boundary of the core area). USDA APHIS (2020b) further outlines that the buffer zone should expand to a minimum of 4 km from areas of high ALB density (defined as presence of a cluster of trees with many exit holes or one or more trees with >100 exit holes). In North America, where only ALB establishments have been detected to date, the eradication procedures have been similar to those applied in Europe (Haack et al. 2010; USDA-APHIS 2014; Fournier and Turgeon, 2017). In the USA specific ALB response guidelines were published providing the technical and general information needed to implement any phase of an ALB eradication programme and the Federal Quarantine authority for ALB according to the US Federal Regulations 7 CFR 301.51 for eradication programs (USDA-APHIS 2014, 2020b).

4.2. Spatial and temporal pattern of successful eradications

<u>ALB</u>

Globally, as of December 2020, approximately half of all detected ALB establishments have been eradicated successfully (53%, since the first successful eradication of the establishment of Addison, Illinois, USA, in 2004) (Fig. 9). However, eradication success rates varied considerably among countries and continents. In Europe, all ALB establishments in Austria, the Netherlands, Switzerland and the UK have been declared eradicated. Austria, which had the highest affected area in 2008, succeeded to eradicate its largest establishment, with only a small area of active cases remaining in 2020, which was finally declared eradicated in January 2021 (Supplement S1). By contrast, in Italy, which ranks first in the number of active establishments, 80% of detected ALB establishments remain active.

A high rate of successful eradications was also achieved in North America. In the United States, where the highest number of ALB establishments (15) has been reported to date, 67% of eradication attempts have been successful so far. A few successful eradications have been achieved before 2008, in Jersey City and Illinois. The total area for which successful eradication of ALB was achieved in North America during the period from 2008 to 2020 was about double that in Europe (Fig. 10). A decrease in the area affected was achieved in both the USA and Canada.

<u>CLB</u>

Eradication of CLB establishments appear to be more challenging, as only 30% of detected establishments have been declared eradicated (until December 2020) (Fig. 9). Only six out of 20 established populations outside its native range have been eradicated successfully since 2008. Furthermore, eradication of most CLB establishment sites in Lombardy has recently been declared as unachievable. Currently, of the eight active establishments in Italy, only two are still under eradication. With the exception of the small establishment in Sirmione, which is still under eradication, a policy of containment is thus now in place at all other sites in Lombardy (SFRL 2020).

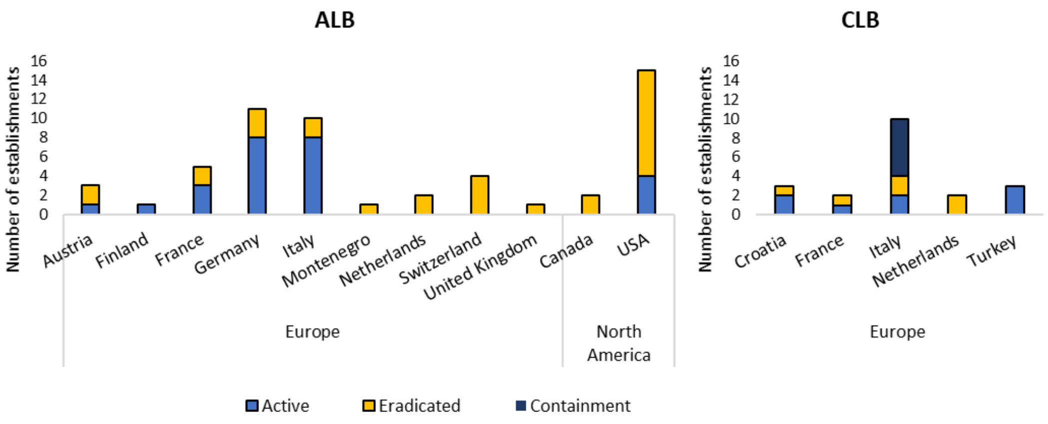

Figure 9 *Anoplophora* spp. eradication attempts by country and their respective status, as of December 2020 (active or eradicated).

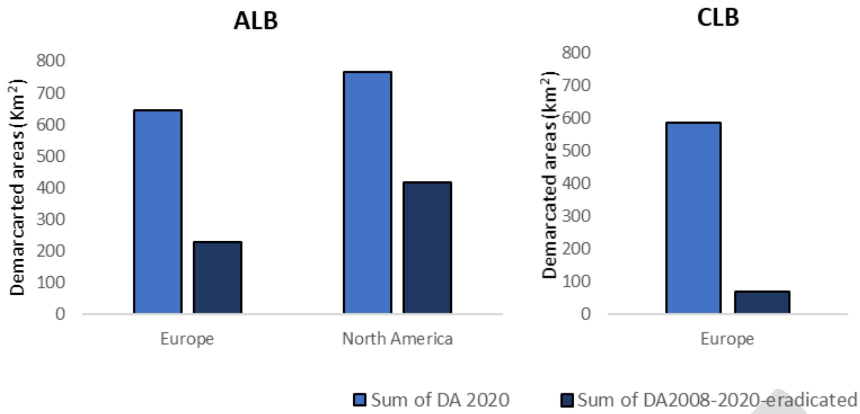

Figure 10 *Anoplophora* spp. demarcated areas (DA) by world region, Europe and North America: active in 2020 and eradicated in the period 2008-2020.

5. Spread

5.1. Methods to monitor and predict the spread

Information on how the invasive population will likely spread across the landscape is fundamental to delineate cost-effective monitoring and control strategies. Currently, certain distances from a discovered infestation of *Anoplophora* spp. are used in eradication programmes to define the boundaries of delimiting survey areas mandatory by law (EU 2012, 2015; USDA 2019). However, those boundaries need to be adjusted according to the available scientific knowledge on the beetles' dispersal ability. A number of dispersal studies have been published for ALB (e.g. Bancroft and Smith 2005; Li et al. 2010; Sawyer et al. 2011; Turgeon et al. 2015) whereas for CLB the information is scarce (Adachi 1990; Cavagna et al. 2013). Due to their morphological resemblances one may assume the dispersal ability of the two species to be similar.

When analysing different studies, we distinguish those based on insect dispersal ability and observations of population spread. Potential dispersal ability does not always match the observed spread due to landscape features and aspects of insect behaviour. Insect dispersal ability was studied by mark-release studies, flight mills and modelling whereas population spread is accessed by analysis of historical infestation cases, genetic analysis, and different kinds of models (see below).

5.2. Patterns of spread at local scale

For ALB, mark-release-recapture studies conducted in China reported mean dispersal distances during one season of 100 m to 270 m, with a 98% probability of beetle recapture within 560 m to 920 m and a maximum dispersal potential of 2,600 m (Wen et al. 1998; Smith et al. 2001, 2004; Williams et al. 2004b; Bancroft and Smith 2005; Li et al. 2010). Studies conducted with computerized flight mills have shown that some beetles can fly considerably longer distances, up to 14 km (Lopez et al. 2017; Javal et al 2018), although only 5% of individuals travelled more than 8 km within a 24-h period (Lopez et al.

2017). These extreme specimens may lead to infestations outside of quarantine zones (Javal et al. 2018b). However, it is important to note that the beetles' ability to fly long distances in flight mills does not necessarily translate into long distance flights in the field. There is some evidence that suggests ALB is reluctant to fly far even though they are physically able to do so in a flight mill situation.

By examining historical infestation cases, spread rates were seen to be highly variable both between infested sites and from one period to another within a given infested area. For example, Sawyer et al. (2011) observed in urban areas at Carteret (NJ; USA) and Chicago (IL, USA) that ALB spread slowly, concentrated within a few hundred metres during the first 5-6 years. Yet, in another location, in Linden (NJ, USA), the infestation spread much faster, about 3.2 km within five years. In a study conducted in southern England, it was estimated that ALB remained restricted to a small area for approximately 10 years near a heavily infested sycamore tree (Straw et al. 2016). Similar patterns of infestation, with the beetles remaining at or close to the natal tree have been observed in the early phases of infestation at other sites (Haack et al. 2010; Sawyer et al. 2011; Turgeon et al. 2015). The discrepancies between sites may in part be attributable to differences in the time until an established population was discovered, while landscape heterogeneity may also play a role. Some land cover types may offer lower resistance to beetle movement and low availability of suitable host trees, favouring longer dispersal flights (Keena 2018). ALB adults are assumed to move by walking in the vicinity of the natal tree and disperse by flying only when conditions become less favourable. Still, in North America long-range dispersers of up to ~1,400 m, were reported, even before the originally infested host trees were fully exploited (Hull-Sanders et al. 2017).

Climatic conditions may also play a role in the dispersal of ALB. The apparently lower rate of population increase and spread of ALB in southern England (Straw et al. 2016), when compared to Cornuda in Italy (Favaro et al. 2015) or Jersey City and Linden in the US (Sawyer et al. 2011), has been attributed to lower summer temperatures resulting in longer insect developmental times (Straw et al. 2016; Trotter and Keena 2016). In northern Italy, ALB dispersal was shown to be influenced by the distance of suitable hosts from the nearest infested trees ($p < 0.01$ for distances above 510 to 1,040 m, which varied among years) and the number of infested trees around uninfested ones (Favaro et al. 2015). In that study, although the probability of dispersing farther than 1,900 m from a previously attacked tree was very low ($p < 0.001$), one dispersal occurrence was registered at 2,224 m. The dispersal pattern was shown to be density-dependent, in accordance with previous mark-release studies.

Several modelling approaches have been developed to describe ALB dispersion patterns. Trotter and Hull-Sanders (2015) and Trotter et al. (2019) used graph theory to determine the topological connections between infested trees, which was then used to calculate dispersal patterns across the landscape in Massachusetts. Two scenarios were used in this study: one in which beetles only left the natal tree when it was overcrowded (strict scenario) and one under which all infested trees could act as sources of dispersing beetles (relaxed scenario). The longest dispersal distance, within a 99th percentile, was over 2.3 km for the strict scenario, and 1.3 km under the relaxed scenario. Fragnière et al. (2018) used data from establishments in Switzerland to develop a density-dependent model that relies on field observations of beetles and infested trees to provide a risk index (RI) of the presence of ALB in a given location. The output for Marly, for example, resulted in RI > 0.001 up to about 600 m of the centre of the highly infested area and RI > 0.0001 up to about 820 m. Elmes et al. (2019) modelled dispersal pathways using circuit theory. Their results showed that ALB tends to use non-habitat land-cover types to connect suitable habitat patches and that for this species, circuit theory was a better predictor of dispersal spatial patterns than least-cost dispersal models. The non-habitat land-cover type that displayed the lowest resistance was sealed surfaces (such as roads) followed by bare soil, grassland, trees, buildings, and water, in increasing resistance order. Recently, Huang et al. (2020) used a geographically weighted regression model to analyse the spatial differentiation of environmental drivers on the occurrence of ALB in China. Temperature, wind speed, precipitation and population density were shown to affect ALB occurrence in China, yet a high spatial heterogeneity was reported on the influence of these factors.

Studies on CLB dispersal are scarce compared with the information available for ALB. Its spread capacity is reported to be low (EFSA et al. 2019a). Similar to ALB, most adults are assumed to disperse by walking and remain in the vicinity of their natal tree unless conditions are unfavourable, although some adults were shown to be able to travel distances of 2 km (Adachi 1990). In Lombardy, Italy, the maximum distances between infestations in urban and agricultural areas were calculated to be about 500 m and 663 m, respectively (Cavagna et al. 2013). However, 97.0% and 99.2% of new cases were found within 200 m and 400 m, respectively. EFSA et al. (2019a) estimated the maximum distance of natural spread in one year to be approximately 194 m (with a 95% uncertainty range of 42–904 m), for a population with a 2-year life cycle (EFSA et al. 2019a).

As mentioned above, human-mediated dispersal related to commerce and transport of infested plants, wood and other materials is the major route for spread of both species at the continental scale. However, even at shorter distances, human-mediated dispersal is an important component that needs to be considered as a cause of satellite infestations, as has been shown, for example, in Switzerland, the USA and Canada (Turgeon et al 2015; Tsykun et al. 2019).

6. Control and Containment - current and future perspectives

6.1. Monitoring methods

In Europe, a survey is carried out in each demarcated area at least once per year to detect and monitor infested trees (EC 2012, 2015). The methods used have been quite similar among countries and mainly based on visual surveys. Advancements in alternative monitoring methods are described below.

Visual surveys

Despite the advances in new detection methods in the last decade, visual surveys remain the standard procedure for *Anoplophora* spp. monitoring (EFSA et al. 2019a,b). These surveys are generally based on examination of potential host trees looking for signs of infestation (i.e., exit holes, larval frass on the ground, oviposition pits and adult feeding, plant and branch dieback). CLB infestation signs are searched on the lower part of the trunk (usually the basal 50 cm, but infestations up to two meters high have been documented, Doris Hölling, Pers. Commun.), the root collar zone, and roots exposed above ground, while searches for ALB symptoms are focussed on the upper part of the trunk and the main branches (EFSA et al. 2019a,b). ALB surveys are usually conducted by observers on the ground equipped with binoculars to detect known signs and symptoms of attack. Turgeon et al. (2010) demonstrated that the efficacy of ground inspections is higher when the density of oviposition is higher, when signs are located lower on the tree, and when they are positioned on the main trunk. Furthermore, the authors observed that most infested trees were detected within the first 2 min of survey, and that using a team of inspectors to survey each tree would be more time effective than the use of a single inspector per tree (Turgeon et al. 2010). The type of environment on which the trees are located also affects detectability: infested street trees are more easily detected than those located in parks or woodland, therefore affecting the time required for tree inspection at different sites (Yemshanov et al. 2019). In addition to surveys carried out inside the demarcated area, specific surveys are usually conducted also randomly outside the demarcated area at high-risk sites such as commercial and industrial areas that receive imports from potential source regions, particularly those receiving wood packaging material or live plants (EFSA et al. 2019a,b).

Semiochemicals

For ALB, pheromone-based trapping systems have been developed (Nehme et al. 2014). Males of ALB are known to emit a sex pheromone composed of equal parts of 4-(n-heptyloxy)butan-1-ol and 4-(n-heptyloxy)butanal (Zhang et al. 2002; Nehme et al. 2009). Intercept panel traps baited with a combination of the pheromone and a mixture of selected host plant volatiles, namely linalool, linalool oxide, cis-3-hexen-1-ol and trans-caryophyllene, proved attractive to females (primarily virgin females) in field trials (Nehme et al. 2010, 2014). CLB males were shown to emit the same two functionalized dialkylethers as ALB males. In field bioassays both sexes were attracted to 4-(n-heptyloxy)butan-1-ol, suggesting that this compound is an important component of the CLB sex pheromone (Hansen et al. 2015). However, the effectiveness of these male pheromone-based trapping systems for monitoring *Anoplophora* spp. is thought to be limited (EFSA et al. 2019a,b), not only because the lures used primarily attract only virgin females but it is also likely that at close range mate finding includes additional visual and chemical cues, including those coded in specific host phytochemicals (particularly sesquiterpenes) which require further research (Nehme et al. 2014; Hoover et al. 2014; Xu and Teale 2021).

New possibilities may arise from the identification of female-produced pheromones. For ALB, female-produced aggregation (Wickman et al. 2012; Xu et al. 2020a,b), contact (Zhang et al. 2003) and trail pheromones (Hoover et al. 2014) have been reported. Wickham et al. (2012) identified an ALB female-produced aggregation pheromone composed of a blend of heptanal, nonanal and hexadecanal, which proved attractive when combined with host volatiles. Xu et al. (2020a) showed that α-longipinene is a major component in extracts of virgin ALB female genitalia and that in olfactometer bioassays, both sexes were attracted to this sesquiterpene. Although α-longipinene is also released by males and host twigs, the authors suggest that the ratios released by these different sources may encode information pertaining to multiple purposes such as aggregation, mate and host location, and that identification of the naturally produced enantiomer in ALB and its hosts is also needed (Xu et al. 2020b).

For CLB, the sesquiterpenes b-elemene, b-caryophyllene, a-humulene, and a-farnesene, released both by the beetles and by the host plant, *Citrus unshiu*, after beetle feeding or after mechanical wounding, proved attractive to males and are thought to act both as kairomones and sex pheromones (Yasui et al. 2007, 2008; Yasui 2009). A female-produced contact sex pheromone of CLB has also been described (Fukaya et al. 2000; Akino 2001; Yasui et al. 2003, 2007).

Sniffer dogs

Recently, “sniffer dogs” have been trained and used in several European countries to identify infested trees through the specific odours released by ALB/CLB larvae and their frass. The use of sniffer dogs specifically trained for the detection of *Anoplophora* spp. was pioneered in 2009 by the Austrian Federal Forest Office (Bundesforschungszentrum für Wald (BFW)) in Vienna (Hoyer–Tomiczek and Sauseng 2013). These detection dogs proved effective at detecting all developmental stages of ALB/CLB in wood packaging materials, imported plants and standing trees in areas where establishment had occurred (Hoyer–Tomiczek and Sauseng 2013). In field experiments, trained dogs displayed high levels of sensitivity in the order of 75–88% (correct positives out of all positives) and specificity of 85–96% (correct negatives out of all negatives) (Hoyer–Tomiczek et al. 2016). This method is already being used in addition to visual surveillance in several areas in Europe and good results have been obtained in Austria, France, Italy, Switzerland and Germany (Hoyer–Tomiczek et al. 2016; EFSA et al. 2019a,b). New dog training teams have now been established in Austria and Switzerland (EFSA et al. 2019a,b). In the US, canine detector units were also evaluated with success in Worcester, Massachusetts (Errico 2012). The downside of this method is that in order to maintain a high-performance level, these dogs must continuously be stimulated with *Anoplophora* material such as frass and live or dead larvae that are still relatively fresh, and they can only be used for limited periods per day so that a large number of trained dogs is necessary to inspect all relevant imports and potentially infested sites (Hoyer–Tomiczek et al. 2016; EFSA et al. 2019a,b).

Other detection methods

Bioacoustic detection methods use portable detectors attached to trees to record the sounds and vibrations produced by larvae (Mankin et al. 2008; Sutin et al. 2019). The potential use of acoustic methods for *Anoplophora* spp. detection has been acknowledged by the international EPPO standards. However, so far, the use of acoustic sensors in the field is difficult and the sensitivity and measuring accuracy of these devices are strongly influenced by the nature of the sensor-substrate interface. These factors limit these methods practical applications (Zorović and Čokl 2015; Hérard and Maspero 2019). More recently, laser vibrometry has been developed for this purpose. With this method, a laser beam is used to detect the vibrations produced by larvae. Recording is carried out directly from the vibrating surface avoiding the need to mount detectors on the tested materials (Zorović and Čokl 2015). Although only laboratory tests have been conducted to date, the methods displayed high sensitivity and a high signal to noise ratio (Zorović and Čokl 2015; Hérard and Maspero 2019). However, a major drawback is that eggs, pupae, and diapausing insects cannot be detected by these methods.

Citizens' involvement in monitoring and surveillance have been proposed and carried on in a few countries, namely in Austria (EC 2010), France (EPPO RS 2017/005), Italy (Jucker et al. 2007), Germany (StMELF 2020) and Switzerland (EFSF 2020).

6.2. Control and Containment

Tree destruction and physical treatments

Eradication programmes include the removal (felling) and destruction (chipping or burning) of infested trees and possibly their replacement with non-host tree species. Whereas many countries fell and destroy only infested trees, other countries apply preventive tree destruction of all host plants, even if healthy, within in a certain radius around infested trees. This radius usually ranges between 20 m and 100 m (EPPO 2013a,b) (Supplement S3). Under current EU legislation preventive tree destruction of high-risk hosts trees is now mandatory (EC 2012, 2015). Other differences among countries in the management of the CLB infestations concern the treatment of stumps, which could be uprooted and destroyed, covered with metal nets to avoid adult emergence, or treated with herbicide to prevent regrowth (Supplement S3) (EPPO 2013a). These measures are effective in reducing ALB/CLB populations and can contribute to eradication, although they are very laborious, expensive, and time-consuming.

Chemical methods

In the past, trunk or soil injections with imidacloprid, a neonicotinoid systemic insecticide, were applied in the USA and Japan to each potential host tree growing within an 800 m radius from infested trees to reduce ALB population density and prevent infestation spread (Hu et al. 2009; Haack et al. 2010). Chemical treatments of healthy trees were combined with removal of infested trees, which proved to be effective. In China, ALB populations were controlled by spraying pyrethroids (cypermethrin) in the tree canopies or coating trunks of host trees to kill adults. Another strategy was inserting wooden sticks containing aluminium phosphide (generating phosphine) into larval galleries to kill ALB larvae, or injecting trunks with organophosphate insecticides such as methamidophos (Wang et al. 2005; Hu et al. 2009). Most systemic insecticides were found to persist at lethal levels for several months after injection, but they require new treatments year after year, and their uniform distribution within trees is still uncertain. A potential alternative might be the use of emamectin benzoate trunk injections. In a study recently conducted in an infested willow forest in Beijing, China, this compound proved effective at reducing ALB larval populations by 89% in the first spring after application and by >99% during the second year. Only in the third year after application did re-infestation occur (Wang et al. 2020). Nevertheless, insecticides are costly and their use is labour intensive, making chemical control economically and environmentally expensive (Hu et al. 2009).

In Europe, the use of chemical treatments has been rare (Supplement S3): it has long been acknowledged that insecticides may cause significant negative externalities including biodiversity loss, ground and surface water contamination (including off-field habitat contamination), impacts on non-target organisms including biocontrol agents, pollinators and earthworms, bio-amplification of toxic substances within the food web with potential effects on human and animal health and development of resistance (Pimentel 2005; Pelosi et al. 2021). The severity of these impacts will depend on the specificity and toxicity levels of the substances used. Therefore, in case eradication fails, additional management options such as biological control are required.

Genetic and cultural methods

Research on the identification of tree species or clones resistant to ALB and CLB has not been successful in the last decade. However, the increased use of non-host trees would be suitable for reducing new ALB and CLB infestations. Under current EU legislation the planting of high-risk species in the infested areas is prohibited (EC 2012, 2015).

Biological control

Many studies have been carried out on natural enemies that could be used as potential biocontrol agents of ALB, including pathogens (bacteria, fungi, and nematodes), parasitoids and predators (reviewed by Brabbs et al. 2015). Virulent strains of *Beauveria brongniartii* (Sacc.) (Hypocreales: Cordycipitaceae), *Beauveria. asiatica* Rehner and Humber, and *Metarhizium brunneum* Petch (formerly *M. anisopliae* (Metschnikoff) (Hypocreales: Clavicipitaceae) are under development for control of ALB (Goble et al. 2014, 2016; Meng et al. 2015; Clifton et al. 2020a). *Beauveria brongniartii* has already been developed into a commercial product in Japan, and *M. brunneum* is available for commercial use in the US, both inducing high mortality rates (Brabbs et al. 2015, Clifton et al., 2020a,b). *Beauveria brongniartii* (Hypocreales: Cordycipitaceae) and *M. brunneum* have also been shown to infect CLB (Brabbs et al. 2015). Exposure to *M. brunneum* fungal infection synergize with neonicotinoid insecticides (Imidacloprid) used for tree protection resulted in accelerated host death (Fisher et al. 2017). However, the fungal virulence of *M. brunneum* is limited by unsuitable environmental conditions and its effectiveness is affected by adult age (Fisher and Hajek 2014, 2016).

Entomopathogenic nematodes belonging to the genera *Steinernema* and *Heterorhabditis* were also tested against ALB (Fallon et al. 2004; Pan 2005). Strains of *Steinernema carpocapsae* and *S. feltiae* have proven to be capable of infecting both *Anoplophora* species and they have potential for use as biopesticides as an alternative to chemical treatments. Of the different application methods tested, the most effective included using sponges or gauze to block or cover larval tunnels for CLB (90%-91% mortality rate) and directly spraying into tunnels for ALB (86%). Simple trunk applications were also effective when tested against CLB, albeit more moderately (60 to 77%) (Brabbs et al. 2015).

Two woodpecker species native to Eurasia, *Dendrocopos major* Beicki and *Picus canus* Gmelin, are the major predators of ALB in China (Brabbs et al. 2015) and they have been shown to be effective at controlling ALB in Chinese forests where nesting has been encouraged (Pan 2005, Golec et al. 2018). Nevertheless, the low levels of mortality attained (less than 16%) are unlikely to provide population control on their own. No detailed information on insect predators of ALB is available.

The main ALB parasitoids in Asia are larval ectoparasitoids in the genera *Dastarcus* (Coleoptera: Bothrideridae) and *Scleroderma* (Hymenoptera: Bethylidae) (Golec et al. 2018; Wang et al. 2021a). Nevertheless, more than 20 parasitoid species associated with ALB have been reported in China and Korea (Wang et al. 2021a). *Dastarcus helophoroides* (= *D. longulus*) is an important natural enemy of ALB, CLB and other long-horned beetles in China, Japan, and Korea (Golec et al. 2018). However, *Dastarcus* and *Scleroderma* species native to Asia that attack ALB and CLB have broad host ranges, and their release as biological control agents is unlikely to be approved in Europe or North America (Meng et al. 2015; Gould et al. 2018). In a recent survey using sentinel logs with ALB larvae, *Oxysychus* sp. (Hymenoptera: Pteromalidae) and *Bracon planitibiae* Yang, Cao et Gould (Hymenoptera: Braconidae) were the most abundant parasitoids species recovered (Li et al 2020). Further studies are underway to assess their potential as biological control agents against ALB.

Regarding parasitoids of non-Asian origin, Lupi et al. (2017) tested the reproductive performance of *Sclerodermus brevicornis* (Kieffer), a bethylid wasp native to Europe, reared on ALB and CLB larvae. Based on their results, the authors suggest that *S. brevicornis* has the potential to be efficiently mass-reared and actively deployed in the biological control of these two longhorn beetles (Lupi et al. 2017). Also in Europe, eight species of idiobiont ectoparasitoids were discovered attacking both CLB and ALB, all of which were already known from other cerambycid hosts (Hérard et al. 2013; Maspero, 2015). The two species most frequently found were *Spathius erythrocephalus* Wesmael (Hymenoptera: Braconidae) and *Trigonoderus princeps* Westwood (Hymenoptera: Pteromalidae) (Hérard et al. 2013; Brabbs et al., 2015). Their mass release was so far not considered due to their wide host range (Hérard et al. 2013). In North America, several groups of native braconid parasitoids were found to be capable of attacking ALB larvae in laboratory trials (Duan et al. 2016). *Ontsira mellipes* Ashmead was shown to be the most promising species: it can be reared continuously with short generation times and produces a high female-biased progeny with rapidly maturing eggs (Duan et al. 2016; Golec et al. 2016; Wang and Aparicio 2020; Wang et al. 2020). In a study conducted to assess the potential host range and preferences of *O. mellipes*, this braconid successfully attacked ALB and CLB as well as three of six tested longhorned beetles native to North America (Wang et al. 2019). Field trials to assess the potential of *O. mellipes* to effectively reduce ALB populations are being carried out in Worcester, Massachusetts (USDA-APHIS 2021).

An egg parasitoid native to Asia that attacks CLB, *Aprostocetus fukutai* (Hymenoptera: Eulophidae), was detected in Northern Italy in 2002 and initially described as a new species, *Aprostocetus anoplophorae* (Delvare et al. 2004; Hérard et al., 2017). The parasitoid is thought to have accidently been introduced in Italy from Japan with bonsais containing parasitized CLB eggs (Brabbs et al. 2015, Hérard et al., 2017). So far, *Aprostocetus fukutai* is regarded as the most promising biological control against CLB because i) it attains high rates of parasitism in the field of up to 72% of CLB eggs (Hérard et al. 2005a, 2013), ii) it is CLB specific and not able to parasitize ALB or the Italian native cerambycid *Saperda carcharias* L. (Coleoptera: Cerambycidae) (Herard et al. 2005 a,b), iii) it does not show specificity in terms of the host plant (Hérard et al. 2005a), iv) it is socially gregarious which facilitates the rearing procedures (Maspero 2015), and v) the host and its parasitoid have a high degree of developmental synchronicity (Hérard et al. 2013; Maspero 2015). Furthermore, the parasitoid persists even at the very low host densities that resulted from the extensive eradication efforts conducted in Northern Italy (Hérard et al., 2017; Wang et al. 2021b). For ALB, no egg parasitoids have been identified (Golec et al. 2018; Wang et al. 2021a). Under such circumstances, it has been suggested that biological control programmes should resort to the use of natural enemies native to regions where ALB has been introduced via novel associations and augmentative releases (e.g. Wang et al. 2019; Wang et al. 2021a)

7. Conclusion and future outlooks

Major efforts have been put into achieving successful eradication of establishments of ALB and CLB. International collaborative activities translated into legislative changes to harmonize detection and eradication as well as prevention methods towards a common goal. We conclude that these efforts have resulted in considerable success as more than 45% of eradication programmes were successful (and some are still ongoing). Several countries were able to completely eradicate all ALB and/or CLB populations, and other managed to reduce the area affected. Still, these efforts are hampered by the ongoing arrival of new beetles, both from their native regions in Asia and in some cases apparently also from other invaded regions via the bridgehead effect.

Several biological traits of ALB and CLB may have favoured eradication success, such as long-life cycles, relatively low fecundity, low spread rate and their tendency to remain in the vicinity of the natal trees unless conditions are unfavourable (Haack et al. 2010). Detectability has been identified by Tobin et al. (2014) as another factor relevant for the success of eradication programmes. Thus, the fact that ALB develops mostly in the upper part of trees and CLB in the lower trunk and roots, may translate into a higher relative detectability of ALB, which in some cases might facilitate early detection and consequently its eradication success.

Eradication campaigns have hitherto been expensive. For example, just for Lombardy in Italy, the costs of CLB eradication campaigns between 2008 and 2013 totalled almost 20 million Euros (Cavagna 2014, in Hérard and Maspero 2019). Nevertheless, although the costs of these eradication programmes can be extremely high, the benefits still outweigh inaction in most cases. For ALB, the costs of eradication campaigns undertaken between 1996 and 2013 in the USA were estimated to have exceeded US$537 million (Eyre and Haack 2017). However, estimations of potential economic loss in compensatory value, resulting from a widespread ALB outbreak could exceed US$670 billion (over one trillion US dollars, if adjusted to 2021 values) and a potential loss of approximately 35% of urban tree cover across the United States (Nowak et al. 2001). For the small ALB outbreak in Cornuda, Italy, Faccoli and Gatto (2016) estimated that during the first year of the eradication program, the ornamental value of the saved trees was six times higher than the eradication costs. Pedlar et al. (2020) estimated that the annual costs of inaction in an ALB outbreak in Eastern Canada could exceed CDN$12 billion (considering street tree-related costs, standing timber value and maple food products), which contrasts with an annual control expenditure of approximately 5% of this value (CDN$0.5 billion).

The methods used for eradication have not seen many changes during the last decade, and host removal is still the method most commonly used, with or without preventive felling. In North America, the use of preventive chemical treatment may have yielded good results in containing the spread of established populations and facilitating their eradication, yet the externalities arising from large-scale use of most insecticides may outweigh the benefits of their use. On the other hand, detection methods have evolved significantly during the last decade, even if visual surveys remain the "gold standard". In Fig. 11, a summary of the known steps of invasions by the two longhorned beetles and the available management strategies is presented.

Despite the advances of the last decade, prevention and management of ALB and CLB is still challenging but not impossible. Research avenues that could be pursued further to improve prevention, eradication and management include technical solutions such as sensors in containers to detect infestations based on acoustic signals or VOCs signals, improving trapping methods based on the use of semiochemicals, new models to predict spread particularly in urban areas, diversification of tree species in urban and peri-urban areas, and citizen science programmes to improve detection and responses.

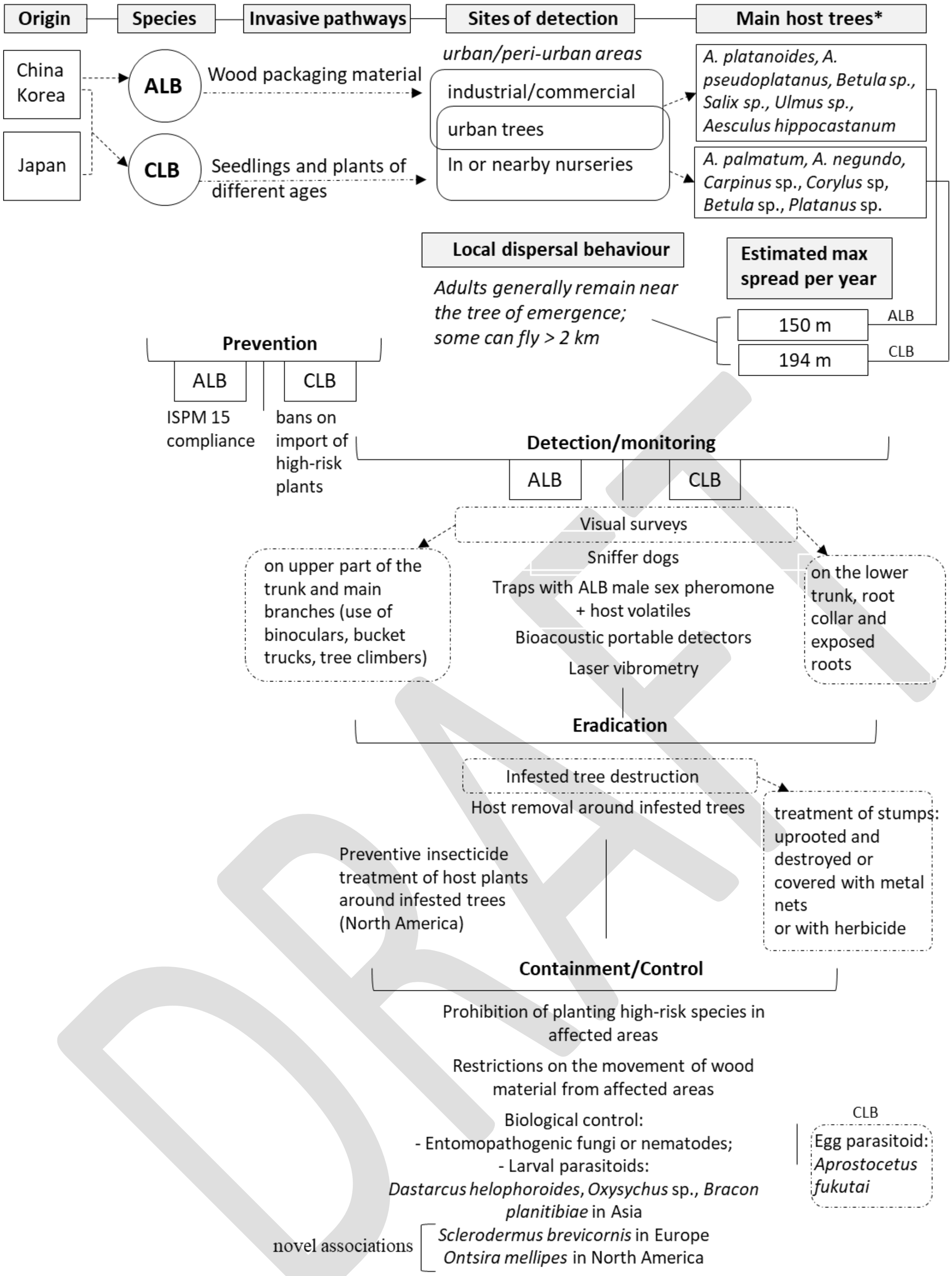

Figure 11 Summary of the steps of invasion and management strategies of Anoplophora spp.
* in invaded range.

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