Pathways for introduction and dispersal of invasive *Aedes* mosquito species in Europe: a review

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First published online: 17th December 2020

Abstract: In the last decades, *Aedes* invasive mosquito species (AIMs) have arrived in Europe from overseas, introduced via different pathways. Several species such as *Aedes albopictus*, *Ae. japonicus* and *Ae. koreicus* were introduced, built populations, and expanded their distribution into new regions. The introduction and establishment of AIMs in Europe is a risk to public health, due to the ability of these mosquitoes to transmit diverse pathogens of vector-borne diseases. The objective of this manuscript is to review knowledge of pathways associated with the introduction and dispersal of AIMs in Europe. The identification of pathways for introduction of AIMs is critical to decide on surveillance strategies needed to reduce the risk and control future introductions. Four main routes are identified and discussed: the passive transport of AIMs via (1) the trade of used tyres, (2) the trade of Lucky bamboo plant cuttings, (3) vehicles (traffic by road, airplanes, and sea), as well as (4) the active natural dispersal of AIMs. We conclude that the trade of used tyres remains the main pathway for long distance transportation and introduction of AIMs into and within Europe. Furthermore, passive transport by road in ground vehicles (e.g. car, truck) represents the major driving force for dispersion from already established populations. ***Journal of the European Mosquito Control Association*** **38: 1 – 10, 2020**

Keywords: *Aedes*, Europe, vector-borne diseases, invasive mosquitoes, dispersal, pathway, surveillance

Introduction

In the last decades, *Aedes* exotic mosquito species with invasive potential (AIMs) have been found introduced in Europe due to trade and transport. Species such as *Aedes albopictus* (Skuse, 1895), *Aedes japonicus* (Theobald, 1901), *Aedes koreicus* (Edwards, 1917), *Aedes aegypti* (Linnaeus, 1762), *Aedes atropalpus* (Coquillett, 1902), *Aedes triseriatus* (Say, 1823) and *Aedes flavopictus* Yamada, 1921 have arrived from overseas (Medlock et al. 2015, Ibáñez-Justicia et al. 2019b), introduced by different pathways. Once introduced, some species have established populations and spread across the continent. Following establishment and spread, efforts to control AIMs populations are complex and eradication is considered extremely difficult if not impossible (Paupy et al. 2009, Baldacchino et al. 2015). The introduction and possible establishment of AIMs in Europe is a risk for public health, due to the ability of these mosquitoes to transmit several pathogens of vector-borne diseases (VBDs). This has been demonstrated for *Ae. albopictus* with outbreaks of dengue and chikungunya in France (Gould et al. 2010, La Ruche et al. 2010, Calba et al. 2017), dengue in Croatia and Spain (Gjenero-Margan et al. 2010, ECDC 2019), chikungunya in Italy (Rezza et al. 2007, Venturi et al. 2017), and Zika in France (Giron et al. 2019). Similarly, populations of *Aedes aegypti* (L.) have been implicated in a dengue outbreak on Madeira island (Portugal) (Sousa et al. 2012). It is generally agreed that these outbreaks were only possible because of the presence of established populations of AIMs, capable to transmit these VBD.

The identification of the pathways for the introduction of AIMs is key to design proper surveillance strategies to effectively detect and control introductions in non-infested areas (Ibáñez-Justicia et al. 2019a). In 2012, Medlock et al. published a review of AIMs in Europe including an overview of the importation routes of the exotic aedine mosquitoes established or intercepted in European countries (Medlock et al. 2012). Nowadays, in 2020, AIMs have expanded their distribution in Europe, including new countries, and they have been associated to new pathways for introduction and dispersal. The main objective of this review is to compile information on known and suspected pathways for introduction and dispersal of AIMs, and discuss their relative importance in Europe. Therefore we performed an exhaustive review identifying the known pathways, and evaluating their importance at the European level to provide a "check list" for AIMs surveillance in Europe. This "check list" will provide all identified pathways (e.g. used tyre trade, road transport, etc.) for each AIMs, and may be used by surveillance teams and decision makers at national and regional level within Europe to decide on surveillance strategies needed to early detect introduced AIMs. Risk based surveillance of AIMs is key for timely application of control measures in order to prevent establishment and spread of AIMs populations.

Materials & Methods

The literature review was performed using EndNote™ X9 by searching the bibliographic database PubMed. The search included (i) in the title all possible combinations of AIMs names found in Europe to date (i.e. *Ae. albopictus*, *Ae. aegypti*, *Ae. flavopictus*, *Ae. atropalpus*, *Ae. triseriatus*, *Ae. japonicus* and *Ae. koreicus*), and (ii) the terms "record", "introduction", "spread", "pathway", "dispersal", and "detection" in any field. Using EndNote™ X9 duplicates were removed from the database. All remaining articles were screened based on the title and abstract. Only articles including information on surveillance of AIMs in European regions were considered eligible for full text screening to extract the following information: species, pathway, country, region, year, establishment after instruction in the area, and spread after introduction. Additionally, the reference list of full text screened articles was searched for additional articles that were not included in the PubMed database.

Overview of pathways for introduction and dispersal in Europe

The bibliographic search, after removing duplicates, provided 980 publications including the search keywords. After screening of the title and abstract from the publications, the following pathways were identified in Europe (Table 1): trade of used tyres, trade of Lucky bamboo (*Dracaena* sp.) plant cuttings, passive transportation by aircraft, ground traffic and maritime sea traffic, and natural dispersal.

Trade of used tyres

The global trade and transport of used tyres is considered as the greatest risk for importation and dispersal of AIMs. In Europe, the first discoveries of *Ae. albopictus* in Italy in 1990 (Dalla Pozza and Majori 1992) and its dispersal within Albania in 1979 and beyond (Adhami and Reiter 1998) were associated to the trade of used tyres. Trade of used tyres has also been incriminated in the introduction of *Ae. albopictus* in countries such as France, Belgium, Croatia, the Netherlands, and recently in Portugal (Schaffner and Karch 2000, Petrić et al. 2001, Scholte and Schaffner 2007, Scholte et al. 2010b, Osorio et al. 2018). Furthermore, the import of used tyres has been confirmed as the main source of introduction of *Ae. albopictus* in the Netherlands, with yearly detections at companies that import used tyres since 2010 (Ibáñez-Justicia et al. 2020a). Also, using this pathway, the North American species *Ae. triseriatus* (Say, 1823) was intercepted in France in 2004 when it was introduced with used tyres originating from Louisiana (USA) (S. Chouin & F. Schaffner, unpublished data *in* (Medlock et al. 2012)). Similarly, *Ae. japonicus* has been also detected in used tyre companies in France and Belgium (Schaffner et al. 2003, Versteirt et al. 2009) and in The Netherlands (Ibáñez-Justicia et al. 2020a). In Belgium, larvae of *Ae. japonicus* were collected in consecutive years from the used tyres, and also early in the season (March) indicating overwintering of the species at these locations. In Europe, *Ae. atropalpus* was found in Italy in 1996 (Romi et al. 1997), in France in 2003 and 2005 (S. Chouin and F. Schaffner, unpublished data *in* (Medlock et al. 2012)), and in The Netherlands in 2009 (Scholte et al. 2009) through import of used tyres. In 2010, *Ae. aegypti* was detected for the first time in the Netherlands at two used tyre companies (Scholte et al. 2010b). Back-tracing data of the companies suggests the introduction of the species by a shipment of used airplane tyres at the end of May 2010, originating from southern Florida, an area where the species is widely present (Scholte et al. 2010b).
Aedes flavopictus was the last AIMs found in Europe, and it was detected in a used tyre company in The Netherlands in 2019 (Ibáñez-Justicia et al. 2019b). This discovery is the first finding of this AIMs outside its area of origin (Japan), and the first association of this species with the import of used tyres.

*Trade of Lucky bamboo (*Dracaena *sp.) plant cuttings*

Dracaena sanderiana (Sparagalus: Dracaenaceae [Agavaceae]), an ornamental plant species known as 'Lucky bamboo', is popular in Europe. Plant cuttings are imported from southern China and Taiwan, usually by ship, and they are transported in Perspex® boxes containing a few centimetres of water or with gel protecting them from desiccation during transport. Long-distance spread of *Ae. albopictus* has been linked to the importation of this plant. The Netherlands is an important trading country for flowers and plants and the principal port of entry of Lucky bamboo plants in Europe. After the first findings of *Ae. albopictus* specimens in a Lucky bamboo nursery in the Netherlands in 2005 (Scholte et al. 2007), it was proposed that transporting the plants on gel rather than in water would reduce the presence of *Ae. albopictus* adults in Lucky bamboo shipments. However, 70% of the Dutch nurseries where adult *Ae. albopictus* were found in later inspections, claimed to have imported plants on gel only (Scholte et al. 2008). Furthermore, in 2013 in Belgium, a live *Ae. albopictus* larva was detected on a gel substrate being the first direct evidence of the importation of this species on gel-transported Lucky bamboo (Demeulemeester et al. 2014).

Using this pathway, the AIM *Ae. japonicus* was also identified associated with the import of Lucky bamboo in the Netherlands in 2013 (Ibáñez-Justicia et al. 2020a). This finding represents the first associated *Ae. japonicus* import with this plant in the world.

Passive transportation by aircraft

In Europe, AIMs have also been introduced via transport by airplanes. In 2016, adult *Ae. aegypti* mosquitoes were captured indoors and outdoors at the airport of Schiphol in the Netherlands (Ibáñez-Justicia et al. 2017), and in 2017 *Ae. aegypti* and *Ae. albopictus* were also found at the same airport (Ibáñez-Justicia et al. 2020b) confirming, for the first time, air transport of these mosquito vector species in Europe. Another AIM, *Ae. koreicus*, was found in 2015 inside the premises of the international airport of Genova (Ballardini et al. 2019). No clear relationship was established with accidental aircraft mediated transport, but the presence of an AIMs at the airport, nearby an important commercial port is worrisome for a potential further spread of this AIMs via aircrafts or boats in Italy and beyond.

Passive transportation by ground vehicles

In newly colonised areas, dispersal of AIMs has been also related to ground transport. In Europe, it has been hypothesised that *Ae. japonicus* individuals could have been transported by vehicles along the motorways between the German federal states (Zielke et al. 2015). This assumption is supported by the fact that the initial findings of *Ae. japonicus* in northern Germany were concentrated in cemeteries of towns close to a motorway running northwards from West Germany (Werner and Kampen 2013). Similarly, passive dispersal of adults of *Ae. albopictus* in private vehicles could partly explain the rapid spread of the species within European countries. Ground transport from areas heavily infested with *Ae. albopictus* has resulted in the spread of this species from Italy into new areas in Europe such as France, Switzerland, the Czech Republic, Croatia, Greece or Germany (Samanidou-Voyadjoglou et al. 2005, Klobucar et al. 2006, Scholte and Schaffner 2007, Sebesta et al. 2012, Kampen et al. 2013, Flacio et al. 2016), and has also been incriminated as the source in Spain (Aranda et al. 2006). In France (Roche et al. 2015) human transportation was considered a key factor for *Ae. albopictus* dispersal, and the model predicted that *Ae. albopictus* would extend its distribution in southern France, following mostly highways present in this area. This has also been a likely mode of transportation to the Czech Republic from southern Europe in 2016 and 2017 (Rudolf et al. 2018), to Slovenia in 2013 (Kalan et al. 2017), and to Slovakia in 2012 (Bockova et al. 2013). In the United Kingdom, eggs of *Ae. albopictus* were detected in one ovitrap placed in a lorry park at Folkestone service station (England), close to the Eurotunnel (Medlock et al. 2017).

Table 1: Overview of pathways for introduction and dispersal of invasive mosquito species reported in Europe.

Pathway	Species	Country (Region)	Year	References
Lucky bamboo	*Aedes albopictus*	The Netherlands	2005	(Scholte et al. 2008, Hofhuis et al. 2009)
		Belgium	2013	(Demeulemeester et al. 2014)
	Aedes japonicus	The Netherlands	2013	(Ibáñez-Justicia et al. 2020a)
Used tyres	*Aedes aegypti*	The Netherlands	2010	(Scholte et al. 2010b, Ibáñez-Justicia et al. 2020a)
	Aedes atropalpus	Italy (Veneto)	1996	(Romi et al. 1997)
		France	2003	(ECDC 2014b)
		The Netherlands	2010	(Scholte et al. 2010b)
	Aedes albopictus	Albania	1979	(Adhami and Reiter 1998)
		Italy	1991	(Dalla Pozza and Majori 1992)
		France	1999	(Schaffner and Karch 2000)
		Belgium	2000	(Schaffner et al. 2004)
		Montenegro	2001	(Petrić et al. 2001)
		Croatia	2005	(Scholte and Schaffner 2007)
		Spain (Lleida)	2008	(Generalitat de Catalunya 2008)
		The Netherlands	2010	(Scholte et al. 2010b)
		Turkey (Black Sea Region)	2016	(Akiner et al. 2016)
		Portugal	2018	(Osorio et al. 2018)
	Aedes japonicus	Belgium	2002	(Versteirt et al. 2009)
		The Netherlands	2013	(Ibáñez-Justicia 2019)
	Aedes triseriatus	France	2004	(ECDC 2014a)
	Aedes flavopictus	The Netherlands	2019	(Ibáñez-Justicia et al. 2019b)
Passive transport ground vehicles	*Aedes albopictus*	Czech republic	2012	(Sebesta et al. 2012, Rudolf et al. 2018)
		Germany	2013	(Kampen et al. 2013, Becker et al. 2017)
		Germany	2008	(Pluskota et al. 2008)
		Germany	2011	(Werner et al. 2012)
		Spain	2016	(Eritja et al. 2017)
		Switzerland	2003	(Flacio et al. 2016)
		Germany	2012	(Becker et al. 2013)
		England	2016	(Medlock et al. 2017)
		Montenegro	2001	(Scholte and Schaffner 2007)
		Slovakia	2012	(Bockova et al. 2013)
		Slovenia	2013	(Kalan et al. 2017)
Passive aircraft transport	*Aedes aegypti*	The Netherlands	2016	(Ibáñez-Justicia et al. 2017, Ibáñez-Justicia et al. 2020b)
	Aedes albopictus	The Netherlands	2017	(Ibáñez-Justicia et al. 2020b)
Passive Sea/Ferry traffic transport	*Aedes albopictus*	Italy (Sicilian islands)	2017	(Di Luca et al. 2017)
		Italy (Tyrrhenian sea islands)	2017	(Toma et al. 2017)
		Spain (Ibiza)	2014	(Barceló et al. 2015)
		Spain (Minorca)	2015	(Bengoa et al. 2016)
		Spain (Majorca)	2013	(Miquel et al. 2013)
		Greece	2003	(Samanidou-Voyadjoglou et al. 2005)
		Malta	2009	(Buhagiar 2009)
Natural dispersal	*Aedes japonicus*	Italy (Austrian border)	2015	(Seidel et al. 2016b)
		Austria	2011	(Seidel et al. 2016a)
		Croatia	2013	(Klobucar et al. 2018)
		Luxembourg	2018	(Schaffner and Ries 2019)
Unknown	*Aedes aegypti*	Canary Islands (Spain)	2017	(ECDC 2018)
		Turkey (Black Sea Region)	2016	(Akiner et al. 2016)
		Madeira	2005	(Seixas et al. 2019)
	Aedes albopictus	Spain (Catalonia)	2004	(Collantes et al. 2015)
		Spain (Valencia)	2007	(Roiz et al. 2007)
		Spain (Basque Country)	2014	(Delacour et al. 2015)
		Spain	2006	(Aranda et al. 2006)
		The Netherlands	2016	(NVWA 2016)
		The Netherlands	2017	(NVWA 2018)
	Aedes koreicus	Germany	2015	(Werner et al. 2016)
		Hungary	2016	(Kurucz et al. 2016)
		Belgium	2008	(Versteirt et al. 2012)
		Russia	2013	(Bezzhonova et al. 2014)
		Switzerland	2015	(Suter et al. 2015)

	Italy (Veneto)	2011	(Capelli et al. 2011)
	Italy (Veneto)	2012	(Montarsi et al. 2013)
Aedes japonicus	The Netherlands	2012	(Ibáñez-Justicia et al. 2014)
	Germany/Switzerland	2008	(Schaffner et al. 2009)
	Spain	2018	(Eritja et al. 2019)
	Slovenia	2013	(Kalan et al. 2014)

The authors conclude that the finding of eggs in one ovitrap is probably indicative of an individual female mosquito having entered the UK in a vehicle from continental Europe. However, the first evidence of the role of passive transportation of *Ae. albopictus* in private vehicles was obtained in an experimental study performed in Catalonia, Spain (Eritja et al. 2017). The study concluded that passive transportation in vehicles is a major driving force for *Ae. albopictus* dispersion in Europe.

Passive transportation by maritime sea traffic

Nowadays, the high number of containers and goods transported by ship, and the high number of direct ferries carrying vehicles with tourists from locations colonised by *Ae. albopictus* on the European mainland, are attributed as the main factors for introduction and dispersal of *Ae. albopictus* to Mediterranean islands and northern Africa. In this case, introduction can be facilitated by unintentional mass transportation of desiccation-resistant eggs, together with imported goods, and with the passive dispersal of adults of *Ae. albopictus* in private vehicles carried by the ferries. Using this pathway, *Ae. albopictus* has been reported to arrive and colonise Corsica (Scholte and Schaffner 2007), Greek islands (Samanidou-Voyadjoglou et al. 2005), Malta (Buhagiar 2009), Majorca (Miquel et al. 2013), Ibiza (Barceló et al. 2015), Minorca (Bengoa et al. 2016) and Thyrrhenian islands (Toma et al. 2017). Probable introduction into ports is also suspected for the establishment of *Ae. albopictus* on the Sicilian islands of Lampedusa, Linosa and Pantelleria, representing the Southernmost European limit of the species (Di Luca et al. 2017).

Natural dispersal

In our literature search, records of natural dispersal of the AIMs *Ae. japonicus* were found only in Europe. Since its detection in Western Germany in 2012 (Kampen et al. 2012), the annual geographic expansion of the population was monitored. Results showed an important increase of the colonised area to more than 8,000 km^2 in 2015 (Kampen et al. 2016), probably resulting from a combination of natural spread and human-aided transportation. The natural dispersal of *Ae. japonicus* is suggested as the pathway for the introductions in Austria from Germany (Seidel et al. 2016a), the introductions in Italy from Austria (Seidel et al. 2016b), and from Germany to Luxemburg (Schaffner and Ries 2019). The invasion in Slovenia showed similar patterns to that in West Germany (Kalan et al. 2017). Since the first detection of *Ae. japonicus* close to the Austrian border, the population spread across the border to Croatia, and by 2015 it was present almost throughout Slovenia (Kalan et al. 2017).

Discussion

The results of this literature review list the main pathways for introduction and dispersal of AIMs in Europe that are the passive transportation via (1) the trade of used tyres, (2) the trade of Lucky bamboo plant cuttings, (3) vehicles (by ground, sea, air), and (4) the active natural dispersal of the AIMs.

Based on the reviewed literature, the global and national transportation of used tyres represents one of the greatest risks for long distance importation of AIMs into and within Europe. As a consequence, this advocates for a specific surveillance scheme at these import location sites and the reinforcement of risk management of used tyres storage by requiring proper storage conditions. All except one AIMs, i.e. *Ae. aegypti*, *Ae. albopictus*, *Ae. atropalpus*, *Ae. flavopictus*, *Ae. japonicus*, *Ae. triseriatus* have been detected using this pathway (see Table 1). This fact stresses the importance of the used tyre pathway for introducing a large range of AIMs. Used tyres that accumulate rainwater while stored outdoors provide excellent larval habitats for a number of container-breeding mosquito species. Exposed to the elements, this water accumulates organic material and microbes that are used as larval nutrition (Yee 2008). In addition such artificial breeding sites offer high humidity, high temperatures, and a lack of natural enemies. Female AIMs lay their eggs in these tyres, and when tyres are transported, they serve as a 'vehicle' to accidentally transport eggs to new areas (Reiter and Sprenger 1987). These eggs are drought-resistant and therefore able to withstand prolonged periods without water when tyres are transported to other countries or continents. When the water level inside tyres rises due to rain (e.g., in a new area where that species did not previously occur) the eggs can hatch. Adult mosquitoes that originate from such breeding sites can subsequently invade other man-made or natural water containers near the site where the tyres were stored, and initiate new, viable mosquito populations. An evidence of the important role of the import of used tyres as source of introduction of AIMs in non-colonised areas are the yearly detections of *Ae. albopictus* at companies that import used tyres in the Netherlands (Ibáñez-Justicia et al. 2020a), and the first findings of *Ae. japonicus* in France and Belgium (Schaffner et al. 2003, Versteirt et al. 2009). The trade in used tyres has also been the principal hypothesis as introduction pathway for *Ae. albopictus* from endemic areas in Asia to the United States (Hawley et al. 1987). The transport of used tyres was also confirmed as the pathway for introduction of *Ae. japonicus* in New Zealand, when larvae were found in used tyres imported from Japan (Derraik 2004).

In 2001, *Ae. albopictus* was reported in California (USA) associated to import of *Dracaena sanderiana* plants (Linthicum et al. 2003, Madon et al. 2003) and linked to sea-trailer import of these plants from southern China. In Europe, depending on the demand in the market, different volumes of containers with Lucky bamboo plants from southern Asia are imported. To date, the role of Lucky bamboo for introducing AIMs has only been confirmed in The Netherlands and, more recently, in Belgium. The import to Belgium is partly explained by the expiration of the exemption on the biocide legislation in the Netherlands in June 2013. By then, all lucky bamboo shipments destined for a Lucky bamboo import company in Belgium arrived at the port of Antwerp instead of at the port of Rotterdam in the Netherlands (Deblauwe et al. 2015). In both countries, arriving plants are grown and acclimated in greenhouses before to be sent to all other EU countries. Since the plants are first in contact with water in The Netherlands or Belgium, possible eggs attached to the plant stems are most probably hatching in these greenhouses, lowering the risk of *Ae. albopictus* egg transport to other EU countries. The mosquitoes reported on the nurseries had probably developed from eggs that had been deposited near the water level, either on the plants or the Perspex® boxes, at the moment the plants were still in southern China. In The Netherlands, public health responses have been formulated with the aim of reducing the risks of importation such as covenants and Commodities Act Decrees for the import of Lucky bamboo (Staatsblad van het Koninkrijk der Nederlanden 2011, 2014).

The finding of *Ae. japonicus* in a Dutch greenhouse represents the first association of the species with the import of plants (Ibáñez-Justicia et al. 2020a). *Aedes japonicus*, similar to *Ae. albopictus*, is native to southern China (Tanaka et al. 1979) and has a similar oviposition behaviour by laying eggs in bamboo stumps (Sota et al. 1994). Although not confirmed in the field, the possible egg laying on Lucky bamboo cuttings maintained in water may explain the presence of *Ae. japonicus* in the imported plants shipments originating from southern China.

Although clear evidence is lacking, the import of plants other than Lucky bamboo has been suggested as a pathway for introduction of AIMs into Europe in two cases. *Aedes koreicus* was first detected in 2011 in the Province of Belluno, Italy, during a routine monitoring for *Ae. albopictus* (Capelli et al. 2011). In 2012 it was already found in 37 municipalities (Montarsi et al. 2013). According to the authors (F. Montarsi, pers. comm.), the route of entry has not been traced to date. One of the author's hypothesis is that *Ae. koreicus* could have been introduced with the trade of ornamental plants considering the small number of tyre traders, and the large amount of garden centres in the area of the first finding. Moreover, plant importers in the area trade with companies that import ornamental plants from Belgium where the first finding of this species was reported in Europe. The species is established in Belgium in an industrial areas which harbours several recycling companies, and it was suggested to be most probably introduced through international trade (Versteirt et al. 2012). In the Netherlands, the import of plants (other than Lucky bamboo) was also suggested as the pathway for *Ae. albopictus* introduction in 2017. An adult specimen of the species was caught in a trap inside the premises of one of the largest flower auctions in Europe (NVWA 2017). However, tracing the import data at the auction did not reveal the presence of Lucky bamboo plants during the trapping period (A. Ibáñez-Justicia, unpublished). Introduction of larvae or pupae in buckets, or adults within the thousands of fresh flowers that are imported daily from south European areas could not be ruled out in this case.

The active natural dispersal of AIMs, but in combination with possible human-aided transport, has only been suggested as the pathway for spread populations of *Ae. japonicus* to new areas in Western Europe (Seidel et al. 2016b, Seidel et al. 2016a, Klobucar et al. 2018, Schaffner and Ries 2019). Instead, the greatest concern in Europe is represented by the association of AIMs dispersal to passive ground transportation (e.g. cars, trucks). This threat is especially relevant for areas adjacent to established populations of the species, and well connected by roads.

Similarly, the maritime traffic transportation has played an important role to introduce *Ae. albopictus* from colonised coastal areas in Europe, to almost all the islands in the Mediterranean sea. Thus far, *Ae. albopictus* is the only AIMs that has been recently introduced and dispersed with maritime traffic transport, and most probably introduced in cars/trucks transported on ferries due to the hitchhiking behaviour of the species. In North Africa, the intense maritime traffic of travellers and goods from southern Europe were considered as the main routes of its introduction in the town of Ain Turk in West Algeria (Benallal et al. 2016).

Due to globalisation and increased air connectivity of major cities, air travel has been considered to play a major role in long-distance dispersal of vectors as well as VBD pathogens (Gezairy 2003, Tatem et al. 2006). In areas with high mosquito densities, there is a greater probability that mosquitoes can enter aircrafts at the airports following their human hosts (Gratz et al. 2000). These aircrafts can then transfer mosquitoes to another country rapidly, thus increasing the chance of mosquitoes surviving the trip and reaching a location where the mosquitoes are non-native (Tatem et al. 2006). Upon arrival, mosquitoes may colonise new areas. In Europe, mosquitoes have also been introduced from abroad with airplanes. In a French study (Giacomini et al. 1995) it was estimated that 8-20 *Anopheles* mosquitoes were imported into France on each flight from Africa. In 2008, the Netherlands reported live mosquitoes on a flight from Tanzania to Schiphol airport in Amsterdam, with several passengers complaining of being bitten on board (Scholte et al. 2010a). A follow-up study in Schiphol showed that exotic mosquitoes were transported on 10 of the 38 aircrafts inspected (Scholte et al. 2014). Repeated introductions of *Ae. aegypti* and *Ae. albopictus* specimens at the international airport of Schiphol in The Netherlands has shown that transportation of AIMs in aircrafts is possible in Europe (Ibáñez-Justicia et al. 2017, Ibáñez-Justicia et al. 2020b). The substantial number of mosquito species introduced via aircrafts into European countries indicates that accidental introductions are not unusual. In comparison with other pathways that can transport large numbers of mosquito eggs (e.g. used tyres), this can be considered a less likely means of establishment due to the low number of individuals potentially introduced inside the aircrafts (Lounibos 2002, Scholte et al. 2010a). However, due to the increase of air-travel and the possibility of repeated undetected introductions of AIMs individuals, this could increase the risk of establishment of AIMs species. The International Health Regulations (World Health Organisation 2008) makes mandatory the surveillance and control of vectors to avoid the export from airports. Furthermore, disinsection of aircraft cabins, containers and their storage compartments inside the aircrafts could contribute to preventing future introductions of AIMs (Gratz et al. 2000). However, as shown from the results, AIMs still arrive at European airports. It is strongly recommended that European regions harmonise the surveillance methodologies at these points of entry (ports and airports) to warn for the introduction of AIMs that have been implicated as vectors of disease.

The active migration of mosquitoes plays a minor role over long distances (Egizi et al. 2016). The flight of mosquitoes is influenced by factors such as oviposition site availability, climate (e.g., wind, humidity, temperature, rainfall), terrain, vegetation, housing characteristics and blood source (Forattini 1962, *in* Honorio et al. (2003)). Specially, AIMs have a relatively low capability for active dispersal over long distance. Females of *Ae. albopictus* are only capable of autonomous dispersal over short distances (Hawley 1988, Liew and Curtis 2004). For example, in Missouri, USA, non-blood fed *Ae. albopictus* females marked with fluorescent dyes dispersed up to 525 m (female) and 225 m (male) (Niebylski and Craig 1994). In a study in a dengue endemic area, the dispersal of *Ae. aegypti* and *Ae. albopictus* was measured over a distance of at least 800 m within a six day period (Honorio et al. 2003). Furthermore, results of an extensive literature survey showed that in comparison with other *Aedes* species (e.g. *Aedes vexans* 5,727 m), the average maximum flight distances of *Ae. albopictus* (676 m) and *Ae. aegypti* (333 m) are considered weak and very weak, respectively (Verdonschot and Besse-Lototskaya 2014). The autonomous dispersal capabilities of *Ae. japonicus* has been reported to be moderate in comparison with other species (Verdonschot and Besse-Lototskaya 2014) with an average maximum flight distance of 1,600 m. Furthermore, it has been proposed that *Ae. japonicus* adults may autonomously disperse along stream corridors, since this species often deposits eggs in rock pools along streams when they are available (Bevins 2007).

However, the detection of an established population in a municipality in The Netherlands at more than 100 and 150 km from the Belgium and German borders respectively was surprising (Ibáñez-Justicia et al. 2014). Natural dispersal of the species from neighbouring populations in Belgium or Germany was not considered likely due to the absence of the species during monitoring activities in surrounding municipalities contiguous to Lelystad (Ibáñez-Justicia et al. 2018). Similarly, *Ae. japonicus* was discovered in 2018 in north-western Spain, more than 1,000 km away from the French closest populations and without an evident link to a known pathway (Eritja et al. 2019). Beside The Netherlands and Spain, other examples of unidentified pathways of introduction are the discoveries of *Ae. japonicus* in Switzerland and Germany (Schaffner et al. 2009, Kampen et al. 2012), the uneven dispersal of *Ae. albopictus* in regions in Spain (Roiz et al. 2007, Collantes et al. 2015, Delacour et al. 2015), the finding of *Ae. aegypti* on the Canary Islands (Spain), Madeira and in the Caucasus (Akiner et al. 2016, ECDC 2018, Seixas et al. 2019), and the findings of *Ae. koreicus* in Belgium, Russia, Switzerland, Hungary, Italy and Germany (Versteirt et al. 2012, Bezzhonova et al. 2014, Suter et al. 2015, Kurucz et al. 2016, Werner et al. 2016, Ballardini et al. 2019). The import of stone fountains was only suggested as a possible route of introduction of *Ae. albopictus* from China to the French Riviera (ECDC 2012).

The introduction and dispersal of AIMs in Europe is a risk for public health in the mid and long term and the identification of their pathways of movement within regions is pivotal to decide on surveillance strategies. Since the review of Medlock et al. in 2012, we added to the list of pathways for introduction of AIMs in Europe the introductions with aircrafts (Scholte et al. 2014, Ibáñez-Justicia et al. 2017, Ibáñez-Justicia et al. 2020b). Furthermore, new evidences were collected to support the introduction and dispersal of AIMs in Europe with maritime sea traffic in European islands (Miquel et al. 2013, Barceló et al. 2015, Bengoa et al. 2016, Di Luca et al. 2017, Toma et al. 2017), with Lucky bamboo imported from Asia (Demeulemeester et al. 2014, Ibáñez-Justicia 2019), and with the movement of AIMs in ground vehicles (Becker et al. 2013, Kampen et al. 2013, Flacio et al. 2016, Becker et al. 2017, Eritja et al. 2017, Rudolf et al. 2018). This review collected evidences to support that the trade in used tyres is one of the greatest risks for long distance transportation of AIMs into and within Europe, and the passive transport of AIMs in ground vehicles as the major driving force for dispersion within Europe.

The importance of pathways for introduction and dispersal of AIMs has changed since several AIMs have nowadays established populations in large areas in Europe. Pathways for first introductions in new areas seem nowadays less associated to the "usual suspects" such as used tyres or Lucky bamboo, but more associated to other human activities (international or domestic travel/trade). In the European regions, based on the results provided in this review, it is recommended to implement a risk-based surveillance of AIMs, and according to existing guidelines (ECDC 2012), prioritising on the main pathways that could introduce or disperse new AIMs in non-colonised areas. Identification of potential pathways for introduction of AIMs, and evaluating the importance of the different pathways are critical for designing surveillance strategies to promptly detect and control introductions in non-infested areas.

Acknowledgements
I would like to thank Prof. Willem Takken, Dr. Sander Koenraadt and Dr. Ron van Lammeren for their valuable suggestions and for critically review the first draft of the manuscript.

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