Vectors of *Xylella fastidiosa* around the world: an overview

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Abstract

Long been considered restricted to the American continent, the bacterium *Xylella fastidiosa* has overcome the geographical barriers due to global trading, and is now present in several countries across Europe and Asia. The bacterium is transmitted by xylem-sap feeding insects likely without specificity. Therefore, once introduced into an environment with suitable climatic conditions, *X. fastidiosa* short range dispersal may rely on different vector taxa, being xylem-sap feeding apparently the only feature required for transmission. Sharpshooter leafhoppers (Hemiptera: Cicadellidae: Cicadellinae) represent the best-studied group of vectors of the bacterium. However, establishment of *X. fastidiosa* into new ecosystems lead possibly to new interactions with vector taxa others than sharpshooters, and to novel epidemiological scenarios. The critical analysis of similarities and differences among geographically distant outbreaks, each with its own vectors guilds and patterns of pathogen spread, might open new perspectives for a better understanding of vector-bacterium interaction, as well as for effective disease control. Therefore, the main aim of this review is to provide the readers with an overview on vectors of *X. fastidiosa* around the world, comprising the better-characterized North American, South American and Taiwan pathosystems, as well as the ongoing research in Europe. This organic collection would permit to reflect on differences and similarities among geographically and ecologically different bacterium outbreaks. Such critical analysis and comparison of vector role in diverse epidemiological contexts is essential for developing an effective bacterium control strategy.
Introduction

What is a vector? We would like to open this manuscript with a question that legitimately could raise up in the mind of the reader of a review on “vectors” of *Xylella fastidiosa*. Many parasites and pathogens responsible for some of the most important diseases in humans, agriculture and nature are routinely described as “vector-borne”. According to Purcell (1982), a vector is a specific organism that transmits a pathogen; a continuum of interactions, ranging from mutually beneficial to deleterious, may define the relationship between a plant pathogen and its vector. Alternatively, a vector could be defined as: i) a host within a multi-host transmission cycle; ii) the most mobile host in a transmission cycle of two or more hosts (Wilson et al. 2017). The key defining feature of vector transmission is that every pathogen generation (i.e. passing from one infected host to another infected host) involves contact with the vector (Gandon 2004); this continuous interaction possibly shape pathogen evolution. Many evolutionary and ecological models oversimplify much of the complexity of vectors: vectors are indeed often treated as mobile syringes rather than organisms in their own right, and their broader ecology and behavior are frequently ignored in transmission experimental schemes (Wilson et al. 2017; Del Cid et al. 2018). In contrast, presence, abundance, and behavior of insect vectors in relation to infected and healthy plants, are fundamental regulators of pathogen spread (Sylvester 1954; Irwin and Ruesink 1986; Mauck et al. 2018). Indeed, vector behaviour has profound ecological and evolutionary implications for the pathogens they transmit, as the latter rely nearly entirely on their vectors for passage to new hosts (Stafford et al. 2011). This is especially true for the bacterium *X. fastidiosa*, whose natural short-range spread depends exclusively on xylem-sap feeding insects (Frazier 1965), which are found in some groups of Auchenorrhyncha. All the members of Cercopoidea (commonly known as froghoppers or spittlebugs) and Cicadoidea (cicadas), as well as the leafhoppers (Membracoidea: Cicadellidae) of the subfamily Cicadellinae (also known as sharpshooters), are considered preferentially xylem-sap feeders (Novotny and Wilson 1997). Insects that feed preferentially on mesophyll or phloem, occasionally feed on xylem
(Pompon et al. 2011; Saguez et al. 2015), but are not able to transmit *X. fastidiosa* (Purcell, 1980). The bacterium can be transmitted by grafting techniques and stem cuttings, which are commonly used for propagation of fruit trees; other modes of spread independent of vectors, e.g. by pruning shears (Krell et al. 2007), are considered unlikely (EFSA 2015). *X. fastidiosa* is a gram-negative xylem-limited gammaproteobacterium (Xanthomonadales: Xanthomonadaceae), whose host list embraces 563 plant species belonging to 82 families (EFSA 2018). While the bacterium behaves as a harmless endophyte in the majority of its host plants (Purcell and Saunders 1999; Baccari and Lindow 2011), it causes disease symptoms (mostly leaf scorch and dieback) on economically important crops (Purcell 1997). The symptoms are thought to be the outcome of bacterial growth and clogging up of xylem vessels (Hopkins 1989). Sicard et al. (2018) suggests the bacterium is associated to a large number of plant species as commensalist, but a limited number of clades and bacterial genotypes are responsible for, and specific to, a small number of plant diseases. *X. fastidiosa* is unique as a vector-borne bacterium, since it is persistent and propagative but not circulative within its insect vector (Hill and Purcell 1995). The transmission is neither transstadial (Purcell and Finlay 1979) nor transovarial (Freitag 1951). After acquisition, the bacterium is retained on the cuticular lining of the insect foregut, mostly in the part of the pre-cibarium proximal to the cibarium (Almeida and Purcell 2006). Presence of *X. fastidiosa* cells inside the pre-cibarium has been correlated with successful inoculation (Almeida and Purcell 2006). Bacterial cells binding and successive foregut colonization is not a trivial process: it has been proposed that most of the *X. fastidiosa* cells ingested by the vector are swallowed without being retained, as a result of the strong turbulence originated within the foregut during sap ingestion (Dugravot et al. 2008; Retchless et al. 2014). Once inside the foregut, *X. fastidiosa* has a generation time of 7-8 hours, with a multiplication rate that remains constant up to four days, followed by a slow down due to limited space for colonization (Killiny and Almeida 2009). However, bacterial multiplication and extensive colonization of the foregut appears to be not necessary for transmission, since sharpshooters can inoculate healthy plants shortly (1-2 h) after
the onset of acquisition on infected plants (Purcell and Finlay 1979). Vectors of *X. fastidiosa*, long been treated merely as pathogen carriers, should on the contrary be re-considered as hosts, whether primary or alternative, of an organism “living in two worlds” (Chatterjee et al. 2008). Indeed the bacterium, through a recently identified chitinase, exploits vector cuticular chitin as food source for multiplication (Killiny et al. 2010; Labroussaa et al. 2017). Effects of this exploitation on vector behavior and performances deserve further investigation. The mechanism underlying *X. fastidiosa* inoculation to the host plants is one of the essential question mark of this fascinating pathosystem (Almeida 2016a). As demonstrated by Houston et al. (1947), infection of the host plant occurs only when the vector is given access to the xylem vessels. Backus (2016) proposed that *X. fastidiosa* is inoculated through a mechanism of salivation-egestion; although many indirect evidences support this theory, a conclusive proof is still missing (Almeida 2016a).

Long-range dispersal of the bacterium mainly relies on trading of contaminated plant materials (EFSA, 2018); once introduced in a new environment with suitable abiotic conditions, the bacterium requires the presence of efficient vectors for its short-range spread (Fereres 2015). Available data demonstrate that insect vectors are capable of transmitting different bacterial strains without specificity (Almeida and Nunney 2015; Esteves et al. in press). Therefore, independently from the genotype being introduced, any environment with suitable climatic conditions should be considered at risk if competent vectors are present. Moreover, climate change could broaden the suitable geographic range, making possible the establishment of the bacterium in areas previously unsuitable (Godefroid et al. 2018). *X. fastidiosa* remained until recently restricted to American continent (Almeida and Nunney 2015); Brazilian and USA outbreaks, where sharpshooters play the key role as vectors in epidemiology, are the best characterized so far. However, in the last decades, *X. fastidiosa* has been reported in several countries outside America: India (Jindal and Sharma 1987), Turkey (Guldur et al. 2005), Taiwan (Su et al. 2013), Iran (Amanifar et al. 2014) and several European countries (Berisha et al. 1998; Saponari et al. 2013; Denance et al. 2017; Olmo et al. 2017; EFSA 2018) (Fig. 1). Evidences collected so far (Saponari et al. 2014; EFSA 2015;
Cornara et al. 2017a; Cornara et al. 2017b; Cruaud et al. 2018; EFSA 2018) suggest that, at least in Europe, vectors other than sharpshooters, i.e. spittlebugs, cercopids, and cicadas, might play the key role in bacterium epidemiology. Research on previously disregarded vector taxa, and comparison with the long studied sharpshooters-\textit{X. fastidiosa} relationship, might open new possibilities in order to deeply understand the overall vector-bacterium interaction, and develop sustainable and effective disease control strategies.

Therefore, the main aim of this review is to provide the readers with an overview on vectors of \textit{X. fastidiosa} around the world, comprising both the better-characterized North American, South American and Taiwan pathosystems, and the more recent ongoing research in Europe. This organic collection would also permit to reflect on differences and similarities among geographically and ecologically different bacterium outbreaks. Such critical analysis and comparison of vector role in diverse epidemiological contexts is essential for developing an effective bacterium control strategy.
Europe

In Europe, Berisha et al. (1998) first reported the detection of *X. fastidiosa* on grapevine in Kosova, although the finding was never further confirmed. In 2012, the bacterium was detected in France, on coffee plants confined in a containment facility (Jacques et al. 2015), but no further spread has been reported. The first reported bacterium establishment in Europe took place in Apulia, South Italy (Saponari et al. 2013). In 2010, olive trees (*Olea europaea*) growing on the west coast of Salento Peninsula (Apulia, Italy), began to decline because of a hitherto unknown disease consequently named “Olive Quick Decline Syndrome” (OQDS) (Martelli et al. 2016). Following Saponari et al. (2013) detection, on 21th October 2013, Apulian Phytosanitary Service notified European Commission (EC) that the quarantine bacterium *X. fastidiosa* had been detected in olive trees in Gallipoli (Lecce) (Almeida 2016 b). Results from genome sequencing have shown that the bacterium has been likely introduced from Costa Rica (Giampetruzzi et al. 2017). Southern Italian strain corresponds to genotype ST53, an introgression of *X. fastidiosa* subspecies *pauca* genome into the genome of subsp. *fastidiosa*, which had been firstly reported by Nunney et al. (2014). Apulian finding prompted a large-scale survey all around Europe, that led to successive bacterium detection in Corsica, Balearic Islands, mainland France, mainland Spain, and Germany (Denance et al. 2017; Olmo et al. 2017; EFSA 2018) (Fig. 2). In this review we will try to organically collect and discuss observations carried out on proved/potential vectors within the European outbreaks currently spotted and described. *X. fastidiosa* is considered as “transient-under eradication” in all the European outbreaks detected so far, except for Southern Apulia, Corsica, and Balearic Islands, where the current status is “present with a restricted distribution”. The outbreak in Germany is currently considered eradicated (EFSA 2018). However, wherever in Europe *X. fastidiosa* is present or introduced, indigenous xylem-sap feeders are present and may act as vectors (EFSA 2018). Only few species of sharpshooters are present throughout the European countries, with a limited distribution (Wilson et al. 2009). Hence spittlebugs and cicadas, previously disregarded in outbreaks other than the European ones, seem likely to
play the key role in *X. fastidiosa* epidemiology in Europe. A list of candidate vectors present across the European detected bacterium outbreaks is provided in S. 1 (supplementary material); cicadas species have been excluded since their vector competence is still uncertain (EFSA 2015).

To date, bacterial epidemiology has been described only for the Southern Italian outbreak so far, and only focusing on olive orchards. No transmission studies have been carried out in other European countries, and only data on molecular detection of the bacterium in candidate vectors are available (EFSA 2018). By the way, all the data converge toward the hypothesis that the meadow spittlebug *Philaenus spumarius* L., 1758 (Hemiptera: Aphrophoridae) could be one of the most important bacterial vectors in all the epidemics described so far (EFSA 2018). The meadow spittlebug, an insect extremely polyphagous and widespread all over the continent (Cornara et al. 2018), is responsible for the spread of the bacterium inside cultivated olive orchards of South Italy, with olives serving either as reservoir or as recipient plant of the bacterium (Cornara et al. 2017a). Nymphs, characterized by reduced mobility and usually common on herbaceous plants belonging to Asteraceae, Fabaceae, Apiaceae and Geraniaceae families, likely play no role in bacterial epidemiology (Dongiovanni et al. 2018a; Morente et al. 2018a). Surveys conducted in South Italy, Portugal, Spain and Greece (Cornara et al. 2017a; Bodino et al. 2018; Dongiovanni et al. 2018b; Milonas et al. 2018; Morente et al. 2018a; Reis et al 2018) highlighted a similar trend of *P. spumarius* population in olive orchards: after emergence on ground cover, the adults move to olive plants. Pasture mowing or a general decrease in succulence of herbaceous hosts could underlie the dispersal toward olive canopies (Goidanich 1954; Pavan 2006; Cornara et al. 2017a). Spittlebug adults tend to aggregate on green succulent tissues (Wiegert 1964; Mangan and Wutz 1983). The aggregation, maintained within certain levels to avoid competition, ensures a bottom up effect, for example overcoming physical barriers to feed on xylem (Wise et al. 2006; Sanderlin and Melanson 2010; Cornara et al. 2018). Aggregation of several possibly infective individuals on the same tissue may increase the probability of systemic infection and reduce the incubation time (Daugherty et al. 2009; Krugner et al. 2012).
Furthermore, within-field vector aggregation could underlie the aggregated pattern of bacterial infections observed in olive orchards (Montes-Borrego et al. 2017). During summer, spittlebug population density within the olive orchard dramatically decreases, likely as a result of insect dispersal and search for over-summering hosts, such as Quercus sp., Lentiscus sp., Myrtus sp., Juniperus sp., Lavandula sp., among others (Cornara et al. 2017a; Bodino et al. 2018; Dongiovanni et al. 2018a; Milonas et al. 2018; Morente et al. 2018a; Reis et al. 2018). This dispersal could be epidemiologically relevant, determining a spillover of X. fastidiosa from cultivated olive groves to wild areas: infective insects moving outside the cultivated orchard could transmit the bacterium to unmanaged ecosystems, creating new and hardly detectable bacterium reservoirs. Spittlebugs active dispersal seems to be primarily limited by their short-range flight (Cornara et al. 2018). P. spumarius has been reported to move more than 30 m with a single flight and up to 100 m within 24 h (Weaver & King 1954; Cornara et al. 2018). Recently, dispersal capabilities of P. spumarius were studied through a Mark-Release-Recapture experiment carried out during summer and autumn in olive groves and meadow agroecosystems in Apulia (South Italy) and Piedmont (North Italy), respectively (Plazio et al. 2017). During this study, the authors reported a mean dispersal of 60-70 meters from the release point either on olive plants or meadow within approximately 15 days. In contrast with these observations, recent preliminary studies conducted with flight mill highlighted that P. spumarius could have the innate potential to fly longer distances (ranging from 100 to ca. 1000 meters with a single flight) (Lago, unpublished data). Passive movements of spittlebug through the wind, and through “hitchhiking” with vehicles, are also possible and may allow the dispersal of infected insects over long distances (Wiegert 1964; Halkka et al. 1971; Cornara et al. 2018). Successively, at the end of summer, the spittlebug tends to move back to the cultivated orchards for oviposition, with individuals been collected also on olive suckers. Infective individuals re-entering the cultivated orchards, attracted by the green succulent suckers, could infect/re-infect olive plants, with a higher transmission efficiency compared to younger adults (Bodino et al. 2018). Further xylem-sap feeding species, other than the meadow spittlebug,
were collected from olive canopies in Southern Italy and Spain: cicadas, mainly *Cicada orni* L., 1758 (Hemiptera: Cicadidae), and *Neophilaenus campestris* Fallen, 1805 (Hemiptera: Aphrophoridae) (Cornara et al. 2017a; Morente et al. 2018a). Regarding *C. orni*, in a recent unpublished natural infectivity test, three out of 160 cicadas tested positive to *X. fastidiosa* by qPCR, while no transmission to olive recipient plants occurred (Cornara et al. 2018). Nevertheless, even in case *C. orni* natural infectivity with *X. fastidiosa* and transmission competence were confirmed, the cicada’s role could be limited to secondary infection within a yet infected orchard. Indeed, the normal flight activity of almost all cicadas is limited to short flights in case of disturbances (Nickel and Hildebrandt 2003; Simões and Quartau 2007). *N. campestris* has been recently proven to be a competent vector of *X. fastidiosa* to olive, together with the South Italian endemism *P. italosignus* Drosopoulos & Remane, 2000 (Hemiptera: Aprophoridae) (EFSA 2018). *N. campestris*’ role in bacterial epidemiology in olive orchards appears unlikely (EFSA 2018). Indeed, species belonging to the genus *Neophilaenus* are usually associated to Poaceae in dry grasslands (Nickel and Remane 2002). *N. campestris* tends to prefer monocots such as *Avena* sp. and *Bromus* sp. Very few individuals can be occasionally collected on olive canopies, in correspondence with spittlebug dispersal toward over-summering hosts, mainly conifers as *Pinus halepensis* (Mazzoni et al. 2005; Lopes et al. 2014; Morente et al. 2018a). Despite its minor or no importance in bacterial transmission to olive, *N. campestris* could be relevant for maintenance of bacterial inoculum in wild areas bordering cultivated orchards during dispersal and oversummering. Therefore, future research should focus on wild areas surrounding cultivated orchards, seeking for bacterial reservoirs, and characterizing vectors ecology and dynamic in such areas. *P. spumarius* competence in transmitting the bacterium to plants other than olive has been demonstrated under controlled conditions (Cornara et al. 2017b). Nevertheless, without field observations on pathogen epidemiology, neither bacterial detection within vector nor transmission tests under controlled conditions could prove or disprove insect role in bacterial spread (EFSA 2018). As mentioned above, almost no epidemiological data are available for outbreaks others than the Southern
Italian one. Regarding mainland France, only faunistic studies were produced so far (EFSA 2018). On the contrary, a large range of potential vectors have been identified in Corsica, although only P. spumarius individuals were found infected with X. fastidiosa as determined by PCR. According to Cruaud et al. (2018), the key plant in X. fastidiosa epidemiology across the island is Cistus monspeliensis, which is also reported by the authors as the main host plant for either nymphs or adults of P. spumarius. Nevertheless, considering the meadow spittlebug polyphagy, the epidemiological frame described so far for Corsica appears scattered and incomplete, and deserve further investigation. Considering Balearic Islands outbreaks, several bacterial genotypes threatening different economically important crops such as olive, grapevine, fig and almond, have been spotted (Olmo et al. 2017). Among the xylem feeders sampled and tested for X. fastidiosa from the first detection (2016) to date, i.e. P. spumarius, N. campestris, and N. lineatus L., 1758 (Hemiptera: Aphrophoridae), none has proven to be infected with the bacterium. Balearic Islands outbreak differs in many ways from the two outbreaks detected in mainland Spain, i.e. Alicante (Valle de Guadalest, East coast) and Madrid (Villarejo de Salvanes, central Spain), where only one bacterial strain is apparently present (subspecies multiplex, strain ST6) (EFSA 2018). In Alicante, where almond is apparently the only economically important crop harboring X. fastidiosa, the bacterium has been detected in P. spumarius (27% of the individuals tested) and N. campestris (1.2%), which were sampled across infected almond orchards (EFSA 2018). The nymphs of both spittlebug species have been observed starting from April on ground cover within cultivated almond orchards; adults were found on almond canopies starting from mid-May (Morente et al. 2018b). As previously remarked, no transmission studies have been conducted so far, thus no conclusion about epidemiology can be drawn. Nevertheless, given the high transmission efficiency of X. fastidiosa to almond by P. spumarius (Purcell 1980), it can be hypothesized that the meadow spittlebug in almond orchards of Alicante could play a role similar to the one in olive orchards of Southern Italy. In Madrid, X. fastidiosa has been detected on olive trees cv. Picual; the outbreak is currently supposed to be eradicated (EFSA 2018). Morente et al. (2018a) found P.
*spumarius* and *N. campestris* to be associated with olive canopies in Madrid province, although at far lower extent than population densities observed in South Italy. Currently no data, neither molecular nor transmission tests, are available for this outbreak. The main differences between the Madrid and the Southern Italian outbreaks are apparently three: i) the different climatic conditions, with winter temperatures in South Italy milder than central Spain; ii) the possible low pathogenicity to olive of the strain detected in Madrid compared to the ST53 established in Italy (see Krugner et al. 2014); iii) the lower vector population density found in Madrid olive orchards compared to the one reported by Cornara et al. (2017a) for South Italy. These three factors could account for the current limited spreading of *X. fastidiosa* across Madrid province. Regarding Germany, strain ST1 (subspecies *fastidiosa*) was found in 2016 in the region of Saxony (Pausa, Center-East), at one location in isolated plants of *Nerium oleander*, *Rosmarinus officinalis*, *Streptocarpus* hybrids and *Erysimum* hybrids kept in a greenhouse (EFSA 2018). Although the outbreak is considered nowadays eradicated, the detection of the Pierce’s disease strain has been perceived as a serious threat to German viticulture. Therefore, surveys in German vineyards aimed at characterizing potential vectors of *X. fastidiosa* to grape were suddenly started after the first bacterial detection, and are currently ongoing (Markheiser et al. 2018). Apparently, the fauna of xylem-feeders associated to German vineyards (at least in the area where *X. fastidiosa* was detected) appears to be more variegated than that reported for other crops in Spain, Italy or France. Beside the predominant spittlebug species *P. spumarius*, other xylem-feeders were found in surveyed vineyards, namely *N. campestris*, *N. lineatus*, *Aphrophora alni* Fallen, 1805 (Hemiptera: Aphrophoridae), *Evacanthus interruptus* L., 1758 (Hemiptera: Cicadellidae: Evacanthinae), *E. acuminatus* Fabricius, 1794 and *Cicadella viridis* Latreille, 1802 (Hemiptera: Cicadellidae: Cicadellinae), as well as the froghopper *Cercopis vulnerata*, Leach 1815 (Hemiptera: Cercopidae) (Markheiser et al. 2017). Except for *Evacanthus* spp., all these species were collected on grapevine plants; an estimation of population abundance is ongoing (Markheiser et al. unpublished). *P. spumarius* has been demonstrated to be an efficient vector of *X. fastidiosa* to grapevine
Regarding the other six species found to be associated to grapevine, no data are available in literature on their vector competence. *Neophilaenus* spp. role in bacterium transmission to grape seems unlikely, given that the spittlebugs are generally associated with Poaceae (Braasch 1960). Nevertheless, *N. campestris* was collected together with *P. spumarius* on sprouting grapevines in Southern Italy (Cornara, pers. obs.). Considering *C. viridis*, Balachowsky (1941) observed that nymphs of this species migrate from trees, on which they hatch, to grass fields where they feed on the basal part of the plant, e.g. on *Polygonum fagopyrum*, *Phragmites* sp., *Cyperus* sp., *Arundo* sp. and *Juncus* sp. (Whalley 1958; Tay 1972). On the contrary, females lay eggs on different host plants, among which grapevine (Goidanich 1938; Betram and Mannheins 1939; Balachowsky 1941; Schindler 1960; Dirimanov and Kharizanor 1964; Tay 1972; Nickel and Remane 2002; Mazzoni 2005). Therefore, theoretically *C. viridis* could spread the bacterium to a large range of cultivated and wild host species during dispersal for oviposition, including grapevine. *A. alni* is assumed to feed on several broad-leaved trees and shrubs, especially in wild areas, including *Alnus* sp., *Elaeagnus* sp., *Myrica gale*, *Acer* sp., *Castanea sativa*, *Quercus* sp., fruit trees (*Prunus avium* and *P. dulcis*), and grapevine (Thompson 1999; Mazzoni 2005; Kunz et al. 2011; Markheiser et al. 2018). Therefore, at least at a theoretical level, *A. alni* could be relevant in *X. fastidiosa* transmission to economically important crops, including grape, and transmission studies with this candidate vector are urgently required. Another xylem-feeder, namely *Graphocephala fennahi* Young, 1977 (Hemiptera: Cicadellidae), characterized by a more restricted distribution compared to the other species previously described, was also collected on grapevine, although only occasionally (Markheiser et al. 2017). Hamilton (1983) reported the sharpshooter to feed exclusively on leaves and buds of *Rhododendron* sp. in the Nearctic region, whereas in Europe records of the insect refer to a broad spectrum of plant species. Adults were observed on *Acer platanoides*, *Platanus* sp. *Tilia* sp., *Ilex aquifolium*, *Hedera helix*, *Robina pseudoacacia*, *Rumex acetosa*, *Azalea* sp., *Pyris japonica* and
Forsythia sp. (Moacos 1953; Olthoff 1986; Sergel 1987). Overall, considering these reports, *G. fennahi*’s role in *X. fastidiosa* spread within German vineyards seems unlikely.
North America

Most of the background on X. fastidiosa transmission by vectors come from studies carried out in North America, mainly focusing on the pathosystem of the Pierce’s disease (PD) of grapevine in California (Rapicavoli et al. 2018). Many reviews thoroughly describe North American main vector species of the fastidious bacterium, together with their biology, bionomic, role in bacterium epidemiology and control strategies (Purcell and Frazier 1985, Redak et al. 2004; Almeida et al. 2005a; Janse and Obradovic 2010; among others). Therefore, here we provide just a brief summary about the current state of knowledge about vectors of X. fastidiosa in North America, in order to permit the comparison among the other geographical areas that is the main focus of the review. As remarked above, the main vectors of X. fastidiosa to different crops in North America are sharpshooters (Hewitt et al. 1942; Frazier and Freitag 1946; Houston et al. 1947; Delong and Severin 1949). Because of the low vector specificity and high diversity of Cicadellinae species in tropical and temperate regions of the Americas, some crops affected by X. fastidiosa are visited by numerous hopper species that can act as vectors (Redak et al. 2004). These numbers probably depend more on how many species have been tested than on how many species are capable of transmitting X. fastidiosa (Almeida et al. 2005a). Except for the report by Sanderlin and Melanson (2010) of Pecan Leaf Scorch in southeastern USA, spittlebugs involvement in bacterial epidemiology is considered marginal, and they might just play a role in inoculum maintenance (Almeida et al. 2005a). However, Purcell’s investigations on Almond leaf scorch (ALS) led to conflictive results about possible role of P. spumarius in ALS spread, with low spittlebug abundance in surveyed orchards compensated by very high bacterium transmission efficiency (Purcell 1980). The most important vectors of X. fastidiosa to different economically important crops in North America are: Cuerna costalis Fabricious, 1803 (Hemiptera: Cicadellidae), Draeculacephala minerva (known as green sharpshooter) Ball, 1927 (Hemiptera: Cicadellidae), Graphocephala atropunctata (known as blue-green sharpshooter, BGSS) Signoret, 1854 (Hemiptera: Cicadellidae), G. versuta Say, 1830, Homalodisca insolita Walker,
1858 (Hemiptera: Cicadellidae), H. vitripennis (known as glassy-winged sharpshooters, GWSS) Germar,
1821, Oncometopia nigricans Walker, 1851 (Hemiptera: Cicadellidae), O. orbona Fabricius 1798, and
Xyphon (formerly Carneocephala) fulgida (known as red-headed sharpshooter) Nottingham, 1932
(Hemiptera: Cicadellidae) (Janse and Obradovic 2010). A list of host plants and distributions of insect
vectors involved in the transmission of X. fastidiosa in Southern United States is reported by Overall and
Rebek (2017).

Among the vectors associated with PD, H. vitripennis is nowadays considered the most important because
of its high mobility, extreme polyphagy and wide distribution on various crops that are susceptible to X.
fastidiosa (Redak et al. 2004), even though its relatively inefficient transmission rate (Almeida and Purcell
2003). Nevertheless, the relatively low bacterium transmission efficiency is compensated by a very high
population density, built by the insects inside cultivated orchards, which reach levels up to 1-2 million
individuals/ha (Phillips 1998; Coviella et al. 2006). H. vitripennis is the only confirmed invasive vector
of X. fastidiosa (Almeida and Nunney 2015), native to the Southeast of the United States and North
Mexico (Young 1958; Turner and Pollard 1959). Furthermore, the species is thought to be relevant for
spreading of other X. fastidiosa-mediated diseases such as Oleander Leaf Scorch (OLS), Almond Leaf
Scorch (ALS), Phony Peach Disease (PPD) and Plum Leaf Scald (PLS) (Hernandez-Martinez et al. 2007;
2009). The species has a very broad host range, with more than 70 host plant species belonging to 35
families, including avocado, citrus, macadamia, and many woody ornamentals, e.g. Fraxinus sp.,
Lagerstroemia sp. and Rhus sp. (Redak et al. 2004; Almeida et al. 2005a).

G. atropunctata is also an important PD vector, although somewhat restricted to coastal areas of
California, where vineyards are bordered by riparian woods, which serve as overwintering habitats for
this sharpshooter (Purcell 1975). The BGSS is important for primary spread of X. fastidiosa from wild
vegetation bordering the vineyard to grapevine plants during early spring; secondary vine-to-vine spread
mediated by this vector, if occurring, does not lead to chronic infections (Purcell and Hopkins 2002; Redak
et al. 2004). Indeed, BGSS tends to settle and feed on the apical part of new succulent grapevine shoots; therefore, infections that take place after inoculation by BGSS later than May are much less likely to move down to woody tissues and to persist after winter pruning (Purcell 1975; Feil and Purcell 2001; Daugherty et al. 2010). On the contrary, GWSS tendency to feed on woody tissues, and capability to inoculate even dormant grapevines, potentially lead to chronic infections of *X. fastidiosa* even after summer or fall inoculations, thus exponentially increasing the importance of bacterium secondary vine-to-vine spread (Almeida and Purcell 2003; Almeida et al. 2005b). Moreover, *H. vitripennis’* active movements among several habitats and host plants allow rapid spread of *X. fastidiosa* over a wide area, whereas movements of *G. atropunctata* are more limited to riparian vegetation and neighbouring vineyards (Blua et al. 2001; Redak et al. 2004). Alfalfa (*Medicago sativa*), planted near to almond and grape, may play a role in the epidemiology of PD and ALS disease, since it may act as either bacterium or vectors reservoir, both BGSS and GWSS (Sisterson et al. 2010).

*D. minerva* and *X. fulgida* are more closely associated with PD epidemics in vineyards neighbouring irrigated pastures and alfalfa fields in the Central Valley of California (Hewitt et al. 1942; Winkler et al. 1949). Observations that the worst outbreaks of PD were invariably in vineyards or portions of vineyards near permanent pastures, alfalfa fields, or permanent irrigation ditches led early investigators to concentrate on these habitats as possible sources of insect vectors. Neither *D. minerva* nor *X. fulgida*, however, were ever found frequently on grape. Grapevine apparently was only an occasional or "accidental" host plant that, nonetheless, could be infected after exposure to infective individuals (Frazier 1943; Delong and Severin 1949; Winkler et al. 1949). Early studies by Weimar (1933; 1937) concluded that the frequency of irrigation exerted a "marked effect" in increasing the incidence and severity of the disease. The author suggested that frequent irrigation produces luxuriant stands of grass weeds, probably including *Echinochloa crusgalli* and *Cynodon dactylon*, triggering the built up of abundant populations of both the insect species.
In central Florida, *O. nigricans* is thought to be a more important vector of PD than *H. vitripennis* because it develops larger populations on grapevines in early spring (Adlerz and Hopkins 1979). Contrary to epidemiology observed in California, spread of PD in Florida depends primarily on secondary spread vine-to-vine (Adlerz and Hopkins 1979). Climatic factors seem to underlie the observed difference: Florida has warm night and long growing seasons that support uninterrupted multiplication by *X. fastidiosa*, thus even late inoculation might lead to chronic infections; in California, cool nights below 15°C could interrupt bacterial growth, shorter growing season, grapevine dormancy and limit the establishment of chronic infections to early spring inoculations (Feil and Purcell 2001; Hopkins and Purcell 2002).
South America

Plum leaf scald (PLS) was the first disease caused by *X. fastidiosa* reported in South America, initially in Argentina (Fernandez-Valiela and Bakarcic 1954; Kitajima et al. 1975) and decades later in Paraguay and Southern Brazil (French and Kitajima 1978; Kitajima et al. 1981). PLS is considered one of the most limiting factors for plum production in Southern states of Brazil (Eidam et al. 2012). Despite the severity of PLS disease, *X. fastidiosa* gained notoriety as a plant pathogen in South America only when it was shown to be the causal agent of a disease of sweet orange trees named Citrus Variegated Chlorosis (CVC) (the same disease was called “Pecosita” in Argentina) (Rossetti et al. 1990; Brlansky et al. 1991; Chang et al. 1993). CVC rapidly spread to all citrus growing regions of Brazil in the 1990’s and reached average incidences of up to 43% in Sao Paulo State, the major citrus growing region (Bové and Ayres 2007). All sweet orange varieties were found to be susceptible to CVC; on the contrary, most mandarins are tolerant, whereas limes and lemons are resistant (Laranjeira et al. 2005). During a search for alternative hosts of CVC in northern São Paulo state, coffee plants were also found infected with *X. fastidiosa*, showing a typical branch atrophy characterized by internode shortening, reduction in fruit and leaf size, premature senescence and fall of leaves at the basal portion of the stems (Paradella Filho et al. 1997). The Koch’s postulates were fulfilled showing that the bacterium is the causal agent of this disease, which was named as Coffee leaf scorch (CLS) (Lima et al. 1998). Further surveys showed that the bacterium is widespread in coffee plantations of several regions of Brazil (Rocha et al. 2010). Recently, *X. fastidiosa* was found in association with leaf scorching symptoms in olive trees in Argentina (Haelterman et al. 2015) and Southeastern Brazil (Coletta-Filho et al. 2016), causing a disease similar to OQDS in Italy. In Brazil, the disease is widely distributed in orchards of the states of Minas Gerais and São Paulo (Safady et al. in press). All strains of *X. fastidiosa* infecting citrus, coffee and olives in South America belong to subsp. *pauca*, whereas most plum-infecting strains belong to subsp. *multiplex* and a few of them to *pauca* (Almeida et al. 2008; Haelterman et al. 2015; Coletta-Filho et al. 2017).
After *X. fastidiosa* was confirmed as the causal agent of CVC (Chang et al. 1993), various surveys of Auchenorrhyncha species associated with affected crops were conducted in Brazil and Argentina in order to describe the community of xylem-sap feeders and identify potential vectors of the pathogen. Most xylem-sap feeders trapped in the surveyed crops were sharpshooters, followed by cercopids (Paiva et al. 1996; Yamamoto and Gravena 2000; Hickel et al. 2001; Ott et al. 2006; Coelho et al. 2008; Giustolin et al. 2009; Miranda et al. 2009; Ringenberg et al. 2010 and 2014; Schneider et al. 2016). The few cercopid species were grass feeders more commonly found on the ground vegetation. A high diversity of genera and species of sharpshooters was reported in citrus, coffee, grape and plum orchards, but marked variations in species composition was found between ground vegetation and crop canopy, among different crops or for a same crop in different regions. In the major citrus growing region of Brazil (São Paulo State), sampling with suction traps showed that some sharpshooter species are trapped mostly on the citrus canopy, such as *Acrogonia citrina* Marucci and Cavicchioli, 2002 (Hemiptera: Cicadellidae) (previously identified as *A. terminalis*), *Dilbopterus costalimai* Young, 1977 (Hemiptera: Cicadellidae) and *O. facialis* Signoret, 1854 (Hemiptera: Cicadellidae) (Paiva et al. 1996). Conversely, other sharpshooters e.g. *Ferrariana trivittata* Signoret, 1854 (Hemiptera: Cicadellidae), *Hortensia similis* Walker, 1851 (Hemiptera: Cicadellidae), *Plesiommata corniculata* Young, 1977 (Hemiptera: Cicadellidae), and *Sonesimia grossa* Signoret, 1854 (Hemiptera: Cicadellidae) are much more frequent on the ground vegetation than on the citrus canopy (Paiva et al 1996; Yamamoto and Gravena 2000). In Northeastern Brazil, different sharpshooter species predominate in citrus and grape orchards (Miranda et al. 2009; Ringenberg et al. 2014) compared to Argentina (Dellapé et al. 2016) and southern and southeastern Brazil (Yamamoto and Gravena 2000; Ott et al. 2006; Ringenberg et al. 2010). The reported variations in species composition and prevalence in communities of sharpshooters indicate that surveys for candidate vector species should be done in every region or crop system affected by *X. fastidiosa* (Lopes and Krugner 2016).
Despite the high number of xylem-sap feeders that are potential vectors of X. fastidiosa in South America, few species are considered key vectors of this pathogen in the affected crops (Lopes and Krugner 2016). The relevance of a particular species as a vector depends not only on its competence to transmit the pathogen, but also on ecological and behavioral attributes that will maximize its role in the natural spread of the related diseases (Purcell 1985; Almeida et al. 2005). In transmission assays, 15 species of sharpshooters have been confirmed as vectors of X. fastidiosa in citrus (Roberto et al. 1996; Yamamoto et al. 2002 and 2007; Dellapé et al. 2016; Lopes and Krugner 2016) and four in coffee (Marucci et al. 2008), with transmission efficiencies ranging from 1 to 30%. For CVC, citrus is the main (if not the only) source of inoculum for primary and secondary spread of CVC (Laranjeira et al. 1998). Although some weeds common in the ground vegetation of citrus orchards were found to be infected with X. fastidiosa, there is still no transmission or epidemiological evidences that they serve as important inoculum sources for CVC (Lopes et al. 2003). Therefore, sharpshooter species that predominate on citrus, such as A. citrina, D. costalimai and O. facialis (Coelho et al. 2008; Giustolin et al 2009), are considered key vectors of X. fastidiosa in São Paulo State (Redak et al. 2004; Almeida et al. 2005a). These three species lay eggs and develop as nymphs up to the adult stage on citrus (Almeida and Lopes 1999; Paiva et al. 2001; Milanez et al. 2001), and their immatures are often found on young branches of citrus trees in the state of Sao Paulo (Gravena et al. 1998). In addition, field-collected insects of these species transmitted X. fastidiosa to healthy citrus seedlings, showing their natural infectivity with the bacterium (Lopes and Krugner 2016).

Another sharpshooter species, Bucephalogonia xanthophis Berg, 1879 (Hemiptera: Cicadellidae), is particularly important as the most frequent one in young citrus orchards (0-2 years old) (Yamamoto et al. 2001), and one of the most efficient vectors of CVC strains of X. fastidiosa in laboratory assays, together with Macugonalia leucomelas Walker, 1851 (Hemiptera: Cicadellidae) (Lopes and Krugner 2016; Esteves et al. in press). Epidemiological studies indicate higher risks of infection of X. fastidiosa during spring and summer, when young citrus flushes and population peaks of sharpshooter vectors are more
frequent in the orchards (Roberto and Yamamoto 1998; Laranjeira et al. 2003; Coelho et al. 2008). The landscape composition is another important risk factor, with higher rates of CVC spread in orchards surrounded by older infected groves (Laranjeira et al. 1998), and higher vector species diversity and population on forest edges, where breeding hosts of various sharpshooters species are likely present (Coelho et al. 2008; Giustolin et al. 2009).

For other diseases caused by \textit{X. fastidiosa} in South America, there is little information on vectors and bacterium epidemiology. For CLS and PLS, disease spatial analyses showed a random distribution of infected plants at early stages of epidemics and a switch to aggregated pattern at higher incidences, indicating that secondary spread occurs (Rocha et al. 2010; Ferreira et al. 2016). Interestingly, aggregation occurred mostly within rows, indicating preferential spread to adjacent trees in the same row for both diseases. In the case of PLS, disease started mostly at the borders of the orchards, suggesting entrance of vectors from adjacent vegetation (Ferreira et al. 2016), but the primary sources of inoculum and vector species involved have not yet been determined. Interestingly, some plum genotypes show moderate to high levels of field resistance to PLS (Dalbó et al. 2018). For olive leaf scorch in Brazil, vector species and \textit{X. fastidiosa} strains associated with the disease are still under investigation, and no epidemiological data are available.
Taiwan

Pierce’s disease of grapevine was first reported in Taiwan in 2002 (Su et al. 2013); this case is considered the first *X. fastidiosa* outbreak in the Asian continent. Sequences analysis of 16S rRNA and the 16S-23S intergenic transcribed region (ITS) indicates that Taiwanese strains of *X. fastidiosa* are closely-related to the PD strains isolated in the US (Su et al. 2013). In addition to PD, in 1980s, a *X. fastidiosa*-elicited disease named pear leaf scorch (PLS) occurred in the areas where pear cv. Hengshan is grown in Taiwan (Leu and Su 1993). The causal agent of PLS has been proposed to be classified as a new species belonging to the genus *Xylella*, i.e. *X. taiwanensis* (Su et al. 2016).

According to field surveys, no confirmed vectors of PD in the US are present in vineyards and surrounding areas in Taiwan (Su et al. 2011). *X. fastidiosa*-infected grapevines are often close to *X. fastidiosa*-infected weeds that suggests PD in Taiwan is transmitted by native vector species (Su et al. 2011).

Five xylem feeder species, collected in the surrounding shrubs and weeds near PD occurring vineyards, were found infected with *X. fastidiosa*, as determined by PCR: *Kolla paulula* Walker, 1858 (Hemiptera: Cicadellidae), *Bothrogonia ferruginea* Fabricius, 1787 (Hemiptera: Cicadellidae:), *Xyphon* sp., (Hemiptera: Cicadellidae: Cicadellinae), *Anatkina horishana* Matsumura, 1912 (Hemiptera: Cicadellidae), and *Poophilus costalis* Walker, 1851 (Hemiptera: Aphrophoridae) (Su et al. 2011; Lin and Chang 2012). Two sharpshooter species, *K. paulula* and *B. ferruginea*, were demonstrated to be capable of transmitting *X. fastidiosa* to grapevine (Lin and Chang 2012, Chang et al. 2014, Tuan et al. 2016). The two sharpshooters showed a bacterial acquisition rate from infected grapevines ranging from 42 to 83%; their inoculation rates, comprised between 6.7 and 28.5%, greatly varies depending on vector species, source plant cultivars, and recipient plant cultivars (Chang et al. 2014; Tuan et al. 2016). Tuan et al. (2016) observed that *K. paulula* and *B. ferruginea* transmission efficiency of *X. fastidiosa* to grapevine is lower than the values reported for *G. atropunctata* and *H. coagulata* (Hill and Purcell 1995; Almeida and Purcell...
2003). No transmission experiments with *Xyphon* sp. and *A. horishana* have been carried out. Regarding the froghopper *P. costalis*, only 1% of the specimens collected during surveys in PD occurring vineyards in Taiwan tested positive for *X. fastidiosa* by PCR; however, the small size of the transmission experiments conducted so far does not allow to draw conclusions on the role of *P. costalis* in *X. fastidiosa* epidemiology (Lin and Chang 2012). Similarly, two specimens of *K. paulula* collected during surveys in PLS occurring peach orchards in Taiwan tested positive for *X. taiwanensis* by PCR that suggests it is a potential insect vector for PLS (Shih et al. 2013).

*K. paulula* is a common insect species inhabiting in shrubs and weeds near vineyards in Taiwan. The host plants of *K. paulula* are *Vitis* spp., *Mikania micrantha*, *Bidens pilosa* var. *radiata*, *Ageratum houstonianum*, and *Commelina diffusa* (Su et al. 2011). The population size of *K. paulula* is affected by host plants, temperature, rainfall, and typhoon (Shih et al. 2013). Because the generation time of *K. paulula* is around 1.5 months (Tuan et al. 2016), monthly mowing is suggested for the insect vector control at PD high risk areas (Shih et al. 2013).
The expansion of the geographic range where *X. fastidiosa* is present, and its introduction and establishment in Europe, represents both a problem and an opportunity. Looking at the problem, European outbreaks can be considered an emergency capable of leaving an undeletable trace in the history of phytopathology, as it was for potato famine in Ireland, blight of American chestnut in USA, and grapevine phylloxera in France (Almeida, 2016b). Actually, it is impossible to precisely estimate the economic loss associated with pathogen spread; considering olive affected by OQDS in Southern Italy, Sardaro et al. (2015) estimated in 111-119 euros the cost per infected plant, to which about 64 euros/plant should be added when considering the expense associated with the loss of landscape benefits. Moreover, the authors calculated an increase in management costs of about 31% in relation to mandatory control practices imposed by European Commission. Nevertheless, especially considering the case of OQDS in Southern Italy, *X. fastidiosa* introduction is far beyond any economic consideration; two other aspects should be considered when analyzing its impact. The first is the damage to Salento landscape and to the historical heritage represented by its centenary olive trees. As highlighted by Almeida (2016b), "olive tree is tightly linked to Salento people; it is their heritage, an indivisible part of who they are". The second is the social turmoil in response to compulsory removal of infected olive trees requested by European Commission to halt bacterial spread. Social turmoil triggered a general mistrust of science and scientists working on the epidemic, which attracted foreign press and became an interesting research field for anthropologists (Colella et al. 2016). Looking at the other side of the coin, invasions of new areas where *X. fastidiosa* could create new biotic associations, represent a unique opportunity for understanding how to ease the threat the bacterium poses to agriculture and landscape. As remarked by Almeida (2016a), research on *X. fastidiosa* has been discontinuous, and can be divided in three periods, each driven by a unique set of factors. European outbreaks might represent the fourth period, thus an opportunity to increase our knowledge on epidemics driven by the fastidious bacterium. *X. fastidiosa* transmission efficiency is
impacted by various factors: vector species, pathogen genotype, host plant species during acquisition and
inoculation, bacterial population within the plant and in different tissues in the same plant, vector host
range and within-host tissue preference, disease symptoms, temperature, vector and host plant biology
and ecology, seasonality, and crop management practices (reviewed in Sicard et al. 2018). Each bacterium
epidemic is characterized by its own, peculiar, combination of such factors. For example, while in PD in
Napa Valley *X. fastidiosa* spread from wild vegetation toward the vineyard is the key feature of bacterial
epidemiology, secondary spread where affected crop is the main bacterial source is the characteristic
shared by CVC in Brazil and OQDS in Italy. As a consequence, strategies applied to contain PD cannot
be effective against CVC and OQDS. Overall, the background on vectors and bacterial epidemiology
generated in well-characterized bacterial pathosystems, such as those in the Americas, is an essential
source for developing effective disease control strategies. However, *X. fastidiosa* epidemics in the
Americas showed how new bacterial outbreaks should be managed on a case-by-case basis, looking at all
the aspects of the multifaceted bacterium-vector-host interaction. Furthermore, vector-*X. fastidiosa*
interaction and the mechanisms leading to bacterium acquisition and inoculation remain the most poorly
understood aspects of the entire transmission process (Labroussaa et al. 2017). Almost all the background
on such aspects come from studies carried out with sharpshooters, and in the context of PD of grapevine
in California. However, research on new epidemics such as those that are being reported in Europe, where
the bacterium is transmitted by previously disregarded vector taxa, might fill our knowledge gap and open
new perspectives for a sustainable *X. fastidiosa* control.

Eventually, differences and similarities in *X. fastidiosa* transmission by vectors among geographically
distant bacterium outbreaks might shed the light on poorly known aspects of the complex vector-
bacterium-host plant interactions. All these data will contribute to deepening our knowledge about
diseases mediated by *X. fastidiosa*, prevent further spread of the fastidious bacterium, and ease its impact
on agriculture and landscape.
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Author Contribution

- DC and AF: coordination
- DC, AM, MM, NB: Europe and North America
- JRSL: South America
- TCW: Taiwan
- DC, AM, MM, NB, TCW, JRSL and AF reviewed and edited the manuscript.
- AF and JRSL secured funding.
- All authors read and approved the manuscript.
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Fig. 1 Global distribution of *X. fastidiosa*. Colored in red the countries where *X. fastidiosa* has been reported.
**Fig. 2** Outbreaks of *X. fastidiosa* around Europe. *= natural infectivity determined by molecular methods; **= competent vectors of *X. fastidiosa* as determined by transmission tests under controlled conditions; ***= epidemiologically relevant vector.
S.1 Candidate vectors of *X. fastidiosa* present across the detected bacterial outbreaks: distribution and host plants. Cicadas’ species have been excluded since their vector competence has still to be determined.