



Xylella fastidiosa in Europe: From the Introduction to the Current Status

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Xylella fastidiosa is xylem-limited bacterium capable of infecting a wide range of host plants, resulting in Pierce's disease in grapevine, citrus variegated chlorosis, olive quick decline syndrome, peach phony disease, plum leaf scald, alfalfa dwarf, margin necrosis and leaf scorch affecting oleander, coffee, almond, pecan, mulberry, red maple, oak, and other types of cultivated and ornamental plants and forest trees. In the European Union, *X. fastidiosa* is listed as a quarantine organism. Since its first outbreak in the Apulia region of southern Italy in 2013 where it caused devastating disease on *Olea europaea* (called olive leaf scorch and quick decline), *X. fastidiosa* continued to spread and successfully established in some European countries (Corsica and PACA in France, Balearic Islands, Madrid and Comunitat Valenciana in Spain, and Porto in Portugal). The most recent data for Europe indicates that *X. fastidiosa* is present on 174 hosts, 25 of which were newly identified in 2021 (with further five hosts discovered in other parts of the world in the same year). From the six reported subspecies of *X. fastidiosa* worldwide, four have been recorded in European countries (*fastidiosa*, *multiplex*, *pauca*, and *sandyi*). Currently confirmed *X. fas-*

tidiosa vector species are *Philaenus spumarius*, *Neophilaenus campestris*, and *Philaenus italosignus*, whereby only *P. spumarius* (which has been identified as the key vector in Apulia, Italy) is also present in Americas. *X. fastidiosa* control is currently based on pathogen-free propagation plant material, eradication, territory demarcation, and vector control, as well as use of resistant plant cultivars and bactericidal treatments.

Keywords : leaf scorch, olive quick decline, Pierce's disease

Xylella fastidiosa Wells et al. is a gram-negative, slow-growing, fastidious bacterium of the *Xanthomonadaceae* family that colonizes the xylem vessels of its host plants and is transmitted by insect vectors that feed by sucking xylem sap (Uceda-Campos et al., 2022). It is extremely polyphagous and attacks a large number of taxonomically different host plant species on which it causes great economic damage. Although the symptoms caused by *X. fastidiosa* vary depending on the host plant, in general, because the bacteria block the transport of water and soluble minerals through the xylem, infected plants exhibit the leaf margin necrosis symptoms, along with the wilting and then drying of leaves, twigs and branches, as well as stunted growth and withering of certain plant parts. These processes often result in the death of diseased plants, thereby signifying the great economic importance of this bacterium.

X. fastidiosa causes a number of diseases of economic importance, namely Pierce's disease (PD) in grapevine, olive quick decline syndrome (OQDS), citrus variegated chlorosis (CVC) or citrus X disease, pony peach disease and plum leaves scald, as well as diseases such as margin necrosis and leaf scorch affecting oleander, coffee,

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almonds, pecans, as well as other types of cultivated and ornamental plants and forest trees (De Lima et al., 1998; Saponari et al., 2017; Trkulja et al., 2014; Uceda-Campos et al., 2022). In addition, the bacterium has been found to behave as a commensal endophyte in a range of its plant hosts (Almeida and Nunney, 2015; Sicard et al., 2018). Thus far, at least 595 plant species from 275 genera and 85 families have been found to be infected with *X. fastidiosa* or *X. taiwanensis* (Su et al., 2016; Waliullah et al., 2022).

In many countries across the globe, *X. fastidiosa* is regulated as a quarantine pest. If its presence has been established, this strategy prevents the introduction of its new subspecies, while in countries where this bacterium has not been established the aim is to prevent its introduction into their territory. It is important to point out that, in countries where this pathogen has not been identified so far, *X. fastidiosa* vectors from the American continent are typically added to the list of harmful organisms. This bacterium has been on the EPPO A2 list since 2017, while according to Commission Implementing Regulation (EU) 2019/2072, *X. fastidiosa* is included in the List of Union quarantine pests and their respective codes, Annex II, Part B: Pests known to occur in the Union territory.

The phytopathogenic bacterium *X. fastidiosa* is currently one of the greatest phytosanitary threats to agricultural production in Europe (Trkulja et al., 2019b), where the presence of this pathogen was first identified in Italy in 2013, causing catastrophic economic damage, primarily to olive groves, some of which were hundreds of years old. As a result of this event, the centuries-long tradition of growing olives in the south of Italy has been called into question. After its first appearance in Italy, *X. fastidiosa* spread in a short time to several European countries.

Geographical Distribution in Europe

The liberalization of world trade and the use of different modes of transport has created a significant international threat from the increased spread of numerous types of harmful quarantine organisms to the most remote parts of the world through the transport of live plants, plant parts and plant products (Chapman et al., 2017; Trkulja et al., 2012). The plant pathogenic bacterium *X. fastidiosa* is an important example of this process (Frem et al., 2020).

Bacterium *X. fastidiosa* is a well-known pathogen on the American continent, from where it spread to Europe. The bacterium is particularly widespread in the Mediterranean region, where it causes significant economic damage to numerous cultivated and spontaneously growing plants (Goddefroid et al., 2022). In Europe, it was officially confirmed

for the first time in 2013 in Italy on olives (Saponari et al., 2013). Not long after its first detection, *X. fastidiosa* was detected in 2015 in France (EFSA Panel on Plant Health, 2015) and Switzerland (EPPO, 2015), followed by Germany (EPPO, 2016), and Spain in 2016 (Olmo et al., 2017), as well as Portugal in 2019 (EPPO, 2019a).

Preceding these developments, the occurrence of *X. fastidiosa* in Europe was reported on grapevines in Kosovo (Berisha et al., 1996, 1998); however, due to the lack of further research and doubts about the origin of the material, these reports remain unconfirmed (EPPO, 1998). Moreover, in 2011, a positive reaction to the presence of *X. fastidiosa* was recorded on one apricot sample in France using a serological test based on immunofluorescence, but these findings were not corroborated by further serological and molecular testing (Manceau et al., 2012). However, in 2012, in a greenhouse near Tours, also in France, *X. fastidiosa* was isolated from coffee plants (*Coffea arabica* and *C. canephora*), but these plants were soon eradicated (EPPO, 2012). In addition, since 2012, various European countries have reported the interception of coffee plants infected with *X. fastidiosa* from Latin America (Mexico, Ecuador, Costa Rica, and Honduras) (Bergsma-Vlami et al., 2015; EPPO, 2019b; Jacques et al., 2016; Legendre et al., 2014).

In Italy, *X. fastidiosa* was first discovered in 2013, in one of the main olive (*Olea europaea* L.) production areas—the Salento peninsula in the Apulia region—where it caused OQDS, resulting in the widespread drying of olive trees in this area (Fig. 1), and thus causing enormous socioeconomic and ecological damage (De Pascali et al., 2022; Girelli et al., 2022; Martelli et al., 2016; Saponari et al., 2013, 2019; Strona et al., 2017). The extent of the damage was exacerbated by water scarcity (De Pascali et al., 2022). In 2018, *X. fastidiosa* was also discovered on the *Spartium junceum* plants in the municipality of Monte Argentario (Grosseto) in Tuscany (Marchi et al., 2018), and in November 2021, the presence of this bacterium was also confirmed in the Canino municipality in the Lazio region (European Food Safety Authority et al., 2022b). When assessing the risk of the further spread of *X. fastidiosa* in Italy, forecast models of species distribution applied to the Italian territory showed a high probability of its occurrence in the Apulia, Calabria, Basilicata, Sicily, and Sardinia regions, as well as the coastal areas of Campania, Lazio, and southern Tuscany (Bosso et al., 2016b).

In Spain, *X. fastidiosa* was first discovered in 2016 in Majorca (Balearic Islands) on cherry (*Prunus avium*) and *Polygala myrtifolia* (Olmo et al., 2017), after which occurrences of this bacterium were recorded on numerous analyzed plants throughout the Balearic Islands (Majorca,

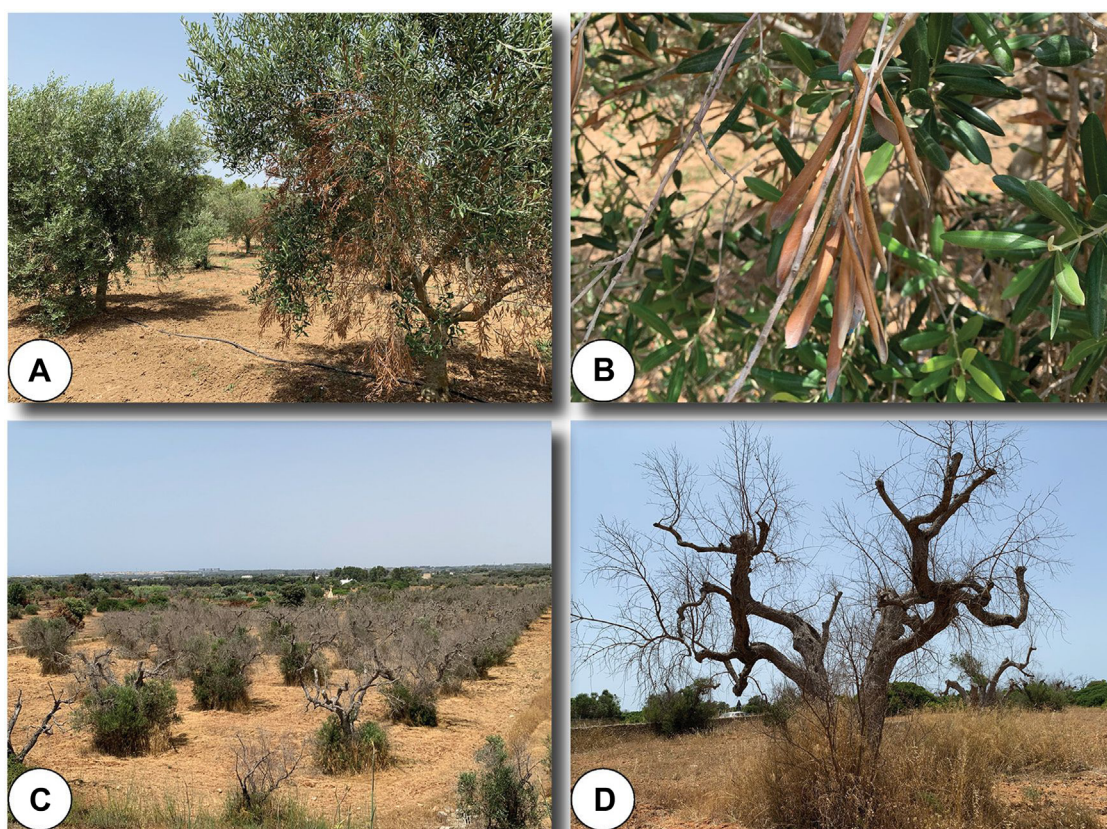


Fig. 1. Symptoms caused by *Xylella fastidiosa* on olive in Apulia-South Italy: (A) initial symptoms on young trees, (B) leaves scorch (detail), (C) quick decline on olives, (D) dead olive tree (photo by Trkulja).

Menorca and Ibiza) (EFSA Panel on Plant Health et al., 2018). In 2017, *X. fastidiosa* was also confirmed on grapevine in Mallorca (Moralejo et al., 2019), almonds in central Spain in the Alicante region (Giampetruzzi et al., 2019), as well as in Madrid in 2018 (European Food Safety Authority et al., 2021; Tihomirova-Hristova et al., 2019). In the same year, its presence was recorded on *P. myrtifolia* in the ornamental plant nursery located in Andalusia (Morelli et al., 2021).

In France, the first occurrence of the disease caused by *X. fastidiosa* was recorded in July 2015 on *P. myrtifolia* growing on the island of Corsica. At the beginning of November 2016, the total number of outbreaks in Corsica reached 289, with *X. fastidiosa* detected on 27 different plant species. In October 2015, the first outbreak of *X. fastidiosa* was also detected on *P. myrtifolia* along the southeastern Mediterranean coast of France. At the beginning of November 2016, 15 outbreaks were recorded in the French Riviera area of Provence and two new host plants (*Spartium junceum* and *Lavandula angustifolia*) were identified (Legendre et al., 2017). Moreover, *X. fastidiosa* was confirmed in 2019 in Provence (southwest), and then in Occitania

(south) in 2020 on lavender hybrid plants, as well as on Afghan lavender and Jerusalem sage (European Food Safety Authority et al., 2022b; Morelli et al., 2021).

In Portugal, *X. fastidiosa* was first detected at the end of 2018 on asymptomatic lavender plants (*Lavandula dentata*) in the Porto region (EPPO, 2019a), and then in the surroundings of Lisbon and in the Algarve region in 2021 (EPPO, 2022).

In Switzerland, *X. fastidiosa* was detected on imported coffee plants in 2015, after which measures were taken to eradicate infected plants and ban the import of potential host plants (EPPO, 2015). Testing and monitoring in the following years confirmed that the bacterium did not infect any other host around the area where *X. fastidiosa* was initially found (EPPO, 2018a).

In Germany, *X. fastidiosa* was first identified in Saxony (EPPO, 2016) on privately grown oleander plants (*Nerium oleander*) as well as on individual *Rosmarinus* sp., *Streptocarpus* sp. and *Erysimum* sp. specimens (Julius Kühn-Institut, 2018). Rapid eradication of infected plants, followed by an administrative ban on the import of host plants, prevented further occurrences of this bacterium (EPPO,

2018b).

Due to the increased phytosanitary risk from the introduction and further spread of *X. fastidiosa*, special monitoring programs focusing on this quarantine phytopathogenic bacterium are being implemented across Europe, but its presence in other European countries has not been established to date (Cara et al., 2017; Gottsberger et al., 2019; Holeva et al., 2017; Jakovljevic, 2019; Jančar et al., 2019; Kornev et al., 2019; Mastin and Parnell, 2017; Mastin et al., 2019; Spasov et al., 2017; Trkulja et al., 2016, 2017a, 2019a).

Based on the aforementioned findings, it is evident that this dangerous quarantine phytopathogenic bacterium has spread very quickly in several European countries, posing the risk to other parts of Europe, especially the Mediterranean where olives and grapes are mostly produced. According to a maximum entropy (MaxEnt) model aimed at determining the current and forecasting the future distribution of *X. fastidiosa* in the Mediterranean region under climate change conditions, the potential distribution area of this bacterium presently includes Italy, Corsica, Spain, Portugal, Albania, Montenegro, Greece and Turkey, as well as all North African and Middle Eastern countries (Bosso et al., 2016a).

Host Plants in Europe

Bacterium *X. fastidiosa* is a polyphagous pathogen that attacks a wide range of host plants, from weeds and ornamental plants and shrubs to economically very important fruit-growing, woody and forest plants (Girelli et al., 2022; Godefroid et al., 2022). Currently, the list of host plants maintained by EFSA includes 694 plant species from 299 genera and 88 botanical families that have been confirmed to be infected with *X. fastidiosa* regardless of the detection method used, with 412 plant species from 190 genera and 68 botanical families of infections confirmed by at least two different detection tests (European Food Safety Authority et al., 2022a). Moreover, 174 host plant species from 91 genera and 44 botanical families are currently identified in Europe (European Food Safety Authority et al., 2022a, 2022b), as shown in Table 1.

The number of plant species positive for *X. fastidiosa* increases every year because the list of host plants for this bacterium in Europe is regularly updated. Thus, as can be seen from Table 2, the number of host plants in Europe has consistently increased during the 2013-2021 period, and a similar upward trend was noted in the number of newly discovered host plants in the world as well as in Europe (EFSA Panel on Plant Health, 2015; EFSA Panel on Plant

Health et al., 2018; European Food Safety Authority, 2016, 2018, 2020; European Food Safety Authority et al., 2021, 2022a, 2022b).

For example, in 2020, 28 new host plant species in the world susceptible to *X. fastidiosa* were reported in France, Spain, Italy and Portugal, while further 25 in the same four countries were identified in 2021. In addition, 12 new genera of host plants naturally infected with *X. fastidiosa* that were newly identified in the world were recorded in France, Spain and Portugal in 2020, while in 2021, 13 new genera of host plants were identified in France, Portugal and Italy. Moreover, two host plant families (*Woodsiaceae* and *Dennstaedtiaceae*) that had not been previously discovered at the global level were also confirmed in Portugal in 2020, and further two (*Elaeagnaceae* and *Hypericaceae*) were recorded in 2021 (European Food Safety Authority et al., 2021, 2022a, 2022b).

In Europe, the most important and economically significant *X. fastidiosa* hosts are olive, stone fruit species, grapevine, citrus and forest trees (European Food Safety Authority et al., 2021; Frem et al., 2021). According to Markheiser et al. (2020), cherry and grapevine may be seriously threatened by the further spread of this pathogen in Europe. Among woody and forest species in Europe, natural infections have been recorded on plants from the genera *Acer* (*A. pseudoplatanus*), *Ficus* (*F. carica*), *Fraxinus* (*F. angustifolia*), *Juglans* (*J. regia*), *Olea* (*O. europaea*), *Prunus* (*P. avium*, *P. cerasifera*), and *Quercus* (*Q. ilex*, *Q. suber*) (Desprez-Loustau et al., 2021). Symptoms caused on the economically important plant species such as grapevine, citrus, peach, coffee, olive, plum, and sweet orange were described by Baldi and La Porta (2017).

In Italy, after the first discovery of *X. fastidiosa* in olives, and subsequently on the surrounding oleander and almond plants in the Apulia region, this bacterium was also confirmed on other plants, such as ornamental plants, endemic species of the Mediterranean flora, cherry, as well as milkweed, rosemary and acacia (Cavalieri et al., 2019; Cornara et al., 2017a; Saponari et al., 2019). Apart from olive, EFSA Panel on Plant Health et al. (2018) states that the species most commonly and most severely affected by this pathogen are *N. oleander*, *Acacia saligna*, and *P. myrtifolia*, which tend to exhibit more intense drying and withering symptoms, while *Rhamnus alaternus*, *Myoporum insulare* and *Westringia glabra* serve as hosts without developing marked disease symptoms. According to Saponari et al. (2019), infected *P. myrtifolia*, *Laurus nobilis*, *Myrtus communis*, *M. insulare*, and *Dodonaea viscosa purpurea* specimens were discovered on the Salento peninsula. Aimed to determining the possibility of vector transmission

Table 1. List of host plants on which *Xylella fastidiosa* has been confirmed in European countries

No.	Scientific names of plant	Family	IT	FR	ES	PT
1	<i>Acacia cultriformis</i> A. Cunn. ex G. Don.	<i>Fabaceae</i>		+		
2	<i>Acacia dealbata</i> Link	<i>Fabaceae</i>	+	+		
3	<i>Acacia longifolia</i> (Andrews) Willd.	<i>Fabaceae</i>				+
4	<i>Acacia melanoxylon</i> R. Br.	<i>Fabaceae</i>				+
5	<i>Acacia saligna</i> (Labill.) H.L. Wendl.	<i>Fabaceae</i>	+		+	
6	<i>Acacia</i> sp.	<i>Fabaceae</i>			+	
7	<i>Acer pseudoplatanus</i> L.	<i>Sapindaceae</i>		+		
8	<i>Acer</i> sp.	<i>Sapindaceae</i>			+	
9	<i>Adenocarpus lainzii</i> (Castrov.) Castrov.	<i>Fabaceae</i>				+
10	<i>Amaranthus retroflexus</i> L.	<i>Amaranthaceae</i>	+			
11	<i>Anthyllis hermanniae</i> L.	<i>Fabaceae</i>		+		
12	<i>Arbutus unedo</i> L.	<i>Ericaceae</i>		+		
13	<i>Argyranthemum frutescens</i> (L.) Sch. Bip.	<i>Asteraceae</i>		+		
14	<i>Artemisia absinthium</i> L.	<i>Asteraceae</i>		+		
15	<i>Artemisia arborescens</i> (Vaill.) L.	<i>Asteraceae</i>		+		+
16	<i>Artemisia</i> sp.	<i>Asteraceae</i>				+
17	<i>Asparagus acutifolius</i> L.	<i>Asparagaceae</i>	+	+	+	+
18	<i>Athyrium filix-femina</i> (L.) Roth	<i>Dryopteridaceae</i>				+
19	<i>Berberis thunbergii</i> DC.	<i>Berberidaceae</i>				+
20	<i>Calicotome spinosa</i> (L.) Link	<i>Fabaceae</i>	+	+	+	
21	<i>Calicotome villosa</i> (Poiret) Link	<i>Fabaceae</i>	+	+		
22	<i>Callistemon citrinus</i> (Curtis) Skeels	<i>Myrtaceae</i>		+		
23	<i>Calluna vulgaris</i> (L.) Hull	<i>Ericaceae</i>				+
24	<i>Calocephalus brownii</i> (Cass.) F. Muell.	<i>Asteraceae</i>		+		
25	<i>Catharanthus roseus</i> (Linn.) G. Don.	<i>Apocynaceae</i>	+			
26	<i>Catharanthus</i> sp.	<i>Apocynaceae</i>	+			
27	<i>Cercis siliquastrum</i> L.	<i>Fabaceae</i>	+	+		
28	<i>Chamaesyce canescens</i> (L.) Prokh.	<i>Euphorbiaceae</i>	+			
29	<i>Chenopodium album</i> L.	<i>Amaranthaceae</i>	+			
30	<i>Cistus albidus</i> L.	<i>Cistaceae</i>			+	
31	<i>Cistus creticus</i> L.	<i>Cistaceae</i>	+	+		
32	<i>Cistus inflatus</i> Pourr. ex Demoly	<i>Cistaceae</i>				+
33	<i>Cistus monspeliensis</i> L.	<i>Cistaceae</i>	+	+	+	
34	<i>Cistus salvifolius</i> L.	<i>Cistaceae</i>	+	+	+	+
35	<i>Cistus</i> sp.	<i>Cistaceae</i>	+	+		
36	<i>Cistus x incanus</i> L.	<i>Cistaceae</i>	+			
37	<i>Clematis cirrhosa</i> L.	<i>Ranunculaceae</i>			+	
38	<i>Clematis vitalba</i> L.	<i>Ranunculaceae</i>	+			
39	<i>Convolvulus cneorum</i> L.	<i>Convolvulaceae</i>		+		
40	<i>Coprosma repens</i> A. Rich.	<i>Rubiaceae</i>				+
41	<i>Coronilla</i> sp.	<i>Fabaceae</i>		+		
42	<i>Coronilla valentina</i> L.	<i>Fabaceae</i>		+		
43	<i>Coronilla valentina</i> subsp. <i>glauca</i> L.	<i>Fabaceae</i>		+		
44	<i>Cytisus scoparius</i> L.	<i>Fabaceae</i>	+	+		+

Table 1. Continued

No.	Scientific names of plant	Family	IT	FR	ES	PT
45	<i>Cytisus</i> sp.	<i>Fabaceae</i>		+		
46	<i>Cytisus spinosa</i> (L.) Link	<i>Fabaceae</i>		+		
47	<i>Cytisus villosus</i> Pourr.	<i>Fabaceae</i>		+		
48	<i>Dimorphotheca ecklonis</i> (DC.) Norl.	<i>Asteraceae</i>				+
49	<i>Dimorphotheca fruticosa</i> (L.) DC.	<i>Asteraceae</i>	+			
50	<i>Dodonaea viscosa</i> Jacq.	<i>Sapindaceae</i>	+			+
51	<i>Echium plantagineum</i> L.	<i>Boraginaceae</i>				+
52	<i>Elaeagnus angustifolia</i> L.	<i>Elaeagnaceae</i>	+			
53	<i>Elaeagnus x submacrophylla</i> Servett.	<i>Elaeagnaceae</i>				+
54	<i>Eremophila maculata</i> (Ker Gawl.) F. Muell.	<i>Myoporaceae</i>	+			
55	<i>Erica cinerea</i> L.	<i>Ericaceae</i>				+
56	<i>Erigeron bonariensis</i> L.	<i>Asteraceae</i>	+			
57	<i>Erigeron canadensis</i> L.	<i>Asteraceae</i>				+
58	<i>Erigeron karvinskianus</i> DC.	<i>Asteraceae</i>		+		
59	<i>Erigeron</i> sp.	<i>Asteraceae</i>	+			
60	<i>Erigeron sumatrensis</i> Retz.	<i>Asteraceae</i>	+			
61	<i>Eriocephalus africanus</i> L.	<i>Asteraceae</i>		+		
62	<i>Erodium moschatum</i> (L.) L'Héritier	<i>Geraniaceae</i>				+
63	<i>Euphorbia chamaesyce</i> L.	<i>Euphorbiaceae</i>	+			
64	<i>Euphorbia terracina</i> L.	<i>Euphorbiaceae</i>	+			
65	<i>Euryops chrysanthemoides</i> (DC.) B. Nord.	<i>Asteraceae</i>		+		+
66	<i>Euryops pectinatus</i> L.	<i>Asteraceae</i>		+		
67	<i>Ficus carica</i> L.	<i>Moraceae</i>	+		+	
68	<i>Frangula alnus</i> Mill.	<i>Rhamnaceae</i>				+
69	<i>Fraxinus angustifolia</i> Vahl	<i>Oleaceae</i>			+	
70	<i>Gazania rigens</i> (L.) Gaertn.	<i>Asteraceae</i>				+
71	<i>Genista corsica</i> (Loisel.) DC.	<i>Fabaceae</i>		+		
72	<i>Genista ephedroides</i> DC.	<i>Fabaceae</i>		+		
73	<i>Genista hirsuta</i> Vahl	<i>Fabaceae</i>			+	
74	<i>Genista lucida</i> Camb.	<i>Fabaceae</i>			+	
75	<i>Genista scorpius</i> (L.) DC.	<i>Fabaceae</i>			+	
76	<i>Genista</i> sp.	<i>Fabaceae</i>		+		
77	<i>Genista tridentata</i> L.	<i>Fabaceae</i>				+
78	<i>Genista valdes-bermejoi</i> Talavera & L. Sáez	<i>Fabaceae</i>			+	
79	<i>Genista x spachiana</i>	<i>Fabaceae</i>		+		
80	<i>Grevillea juniperina</i> R. Brown	<i>Proteaceae</i>	+			
81	<i>Hebe elliptica</i> (G. Forst.) Pennell	<i>Plantaginaceae</i>		+		
82	<i>Hebe</i> sp.	<i>Plantaginaceae</i>	+	+		+
83	<i>Helichrysum italicum</i> (Roth) G. Don	<i>Asteraceae</i>	+	+	+	
84	<i>Helichrysum</i> sp.	<i>Asteraceae</i>	+			
85	<i>Helichrysum stoechas</i> (L.) Moench	<i>Asteraceae</i>		+	+	
86	<i>Heliotropium europaeum</i> L.	<i>Boraginaceae</i>	+			
87	<i>Hibiscus syriacus</i> L.	<i>Malvaceae</i>				+
88	<i>Hypericum perforatum</i> L.	<i>Hypericaceae</i>				+

Table 1. Continued

No.	Scientific names of plant	Family	IT	FR	ES	PT
89	<i>Ilex aquifolium</i> L.	<i>Aquifoliaceae</i>				+
90	<i>Jacobaea maritima</i> (L.) Pelsler & Meijden	<i>Asteraceae</i>		+		
91	<i>Juglans regia</i> L.	<i>Juglandaceae</i>			+	
92	<i>Laurus nobilis</i> L.	<i>Lauraceae</i>	+		+	+
93	<i>Laurus</i> sp.	<i>Lauraceae</i>			+	
94	<i>Lavandula angustifolia</i> Miller	<i>Lamiaceae</i>	+	+	+	+
95	<i>Lavandula dentata</i> (L.) Miller	<i>Lamiaceae</i>	+	+	+	+
96	<i>Lavandula latifolia</i> Medik.	<i>Lamiaceae</i>			+	
97	<i>Lavandula</i> sp.	<i>Lamiaceae</i>	+	+		+
98	<i>Lavandula stoechas</i> L.	<i>Lamiaceae</i>	+	+		+
99	<i>Lavandula x heterophylla</i> Poir.	<i>Lamiaceae</i>		+		
100	<i>Lavandula x intermedia</i> Emeric ex Loiseleur	<i>Lamiaceae</i>		+		
101	<i>Lavatera cretica</i> L.	<i>Malvaceae</i>				+
102	<i>Lonicera implexa</i> Aiton	<i>Malvaceae</i>	+			
103	<i>Magnolia grandiflora</i> L.	<i>Magnoliaceae</i>				+
104	<i>Magnolia x soulangeana</i> Soul.-Bod.	<i>Magnoliaceae</i>				+
105	<i>Medicago arborea</i> L.	<i>Fabaceae</i>		+		
106	<i>Medicago sativa</i> L.	<i>Fabaceae</i>		+		+
107	<i>Metrosideros excelsa</i> Sol. ex Gaertn.	<i>Myrtaceae</i>		+		+
108	<i>Metrosideros</i> sp.	<i>Myrtaceae</i>				+
109	<i>Myoporum insulare</i> R. Brown	<i>Scrophulariaceae</i>	+			
110	<i>Myrtus communis</i> L.	<i>Myrtaceae</i>	+	+		+
111	<i>Nerium oleander</i> L.	<i>Apocynaceae</i>	+		+	+
112	<i>Olea europaea</i> L.	<i>Oleaceae</i>	+	+	+	+
113	<i>Olea europaea</i> subsp. <i>sylvestris</i> (Mill.) Rouy	<i>Oleaceae</i>			+	
114	<i>Osteospermum ecklonis</i> (DC.) Norl.	<i>Asteraceae</i>		+		
115	<i>Osteospermum fruticosum</i> L.	<i>Asteraceae</i>	+			
116	<i>Pelargonium fragrans</i> L.	<i>Geraniaceae</i>	+			
117	<i>Pelargonium graveolens</i> L'Héritier ex Aiton	<i>Geraniaceae</i>		+		+
118	<i>Pelargonium</i> sp.	<i>Geraniaceae</i>	+	+		
119	<i>Perovskia abrotanoides</i> Kar.	<i>Lamiaceae</i>		+		
120	<i>Phagnalon saxatile</i> (L.) Cass.	<i>Asteraceae</i>	+	+	+	
121	<i>Phagnalon</i> sp.	<i>Asteraceae</i>			+	
122	<i>Phillyrea angustifolia</i> L.	<i>Oleaceae</i>			+	
123	<i>Phillyrea latifolia</i> L.	<i>Oleaceae</i>	+			
124	<i>Phlomis fruticosa</i> L.	<i>Lamiaceae</i>		+		
125	<i>Phlomis italica</i> L.	<i>Lamiaceae</i>			+	
126	<i>Pistacia vera</i> L.	<i>Anacardiaceae</i>	+			
127	<i>Plantago lanceolata</i> L.	<i>Plantaginaceae</i>				+
128	<i>Polygala myrtifolia</i> L.	<i>Polygalaceae</i>	+	+	+	
129	<i>Polygala</i> sp.	<i>Polygalaceae</i>		+		
130	<i>Polygala x dalmaisiana</i> Dazzler	<i>Polygalaceae</i>		+		
131	<i>Polygala grandiflora</i> Walter	<i>Polygalaceae</i>		+		
132	<i>Prunus armeniaca</i> L.	<i>Rosaceae</i>			+	

Table 1. Continued

No.	Scientific names of plant	Family	IT	FR	ES	PT
133	<i>Prunus avium</i> (L.) L.	Rosaceae	+	+	+	
134	<i>Prunus cerasifera</i> Ehrh.	Rosaceae		+		
135	<i>Prunus domestica</i> L.	Rosaceae			+	
136	<i>Prunus dulcis</i> (Mill.) D. A. Webb.	Rosaceae	+	+	+	
137	<i>Prunus laurocerasus</i> L.	Rosaceae				+
138	<i>Prunus persica</i> (L.) Batsch	Rosaceae		+		+
139	<i>Pteridium aquilinum</i> (L.) Kuhn	Dennstaedtiaceae				+
140	<i>Quercus ilex</i> L.	Fagaceae		+		
141	<i>Quercus pubescens</i> Willd.	Fagaceae		+		
142	<i>Quercus robur</i> L.	Fagaceae				+
143	<i>Quercus rubra</i> L.	Fagaceae				+
144	<i>Quercus suber</i> L.	Fagaceae		+		+
145	<i>Retama monosperma</i> (L.) Boiss.	Fabaceae		+		
146	<i>Rhamnus alaternus</i> L.	Rhamnaceae	+		+	
147	<i>Rhamnus</i> sp.	Rhamnaceae		+		
148	<i>Rosa canina</i> L.	Rosaceae		+		
149	<i>Rosa</i> sp.	Rosaceae	+			+
150	<i>Rosmarinus</i> sp.	Lamiaceae		+		
151	<i>Rubus ulmifolius</i> Schott	Rosaceae				+
152	<i>Ruta chalepensis</i> L.	Rutaceae			+	
153	<i>Salvia officinalis</i> L.	Lamiaceae			+	+
154	<i>Salvia rosmarinus</i> Spenner	Lamiaceae	+	+	+	+
155	<i>Salvia</i> sp.	Lamiaceae	+			
156	<i>Sambucus nigra</i> L.	Adoxaceae				+
157	<i>Santolina chamaecyparissus</i> L.	Asteraceae		+	+	+
158	<i>Santolina magonica</i> (O. Bolòs et al.) Romo	Asteraceae			+	
159	<i>Scabiosa</i> sp.	Caprifoliaceae	+			
160	<i>Spartium junceum</i> L.	Fabaceae	+	+	+	
161	<i>Strelitzia reginae</i> Banks ex W. T. Aiton.	Strelitziaceae				+
162	<i>Teucrium capitatum</i> L.	Lamiaceae			+	
163	<i>Ulex europaeus</i> L.	Fabaceae				+
164	<i>Ulex minor</i> Roth	Fabaceae				+
165	<i>Ulex parviflorus</i> Pourr.	Fabaceae			+	
166	<i>Ulex</i> sp.	Fabaceae				+
167	<i>Viburnum tinus</i> L.	Adoxaceae		+		
168	<i>Vinca major</i> L.	Apocynaceae				+
169	<i>Vinca minor</i> L.	Apocynaceae	+			
170	<i>Vinca</i> sp.	Apocynaceae	+			+
171	<i>Vitex agnus castus</i> L.	Lamiaceae		+	+	
172	<i>Vitis vinifera</i> L.	Vitaceae			+	
173	<i>Westringia fruticosa</i> (Willd.) Druce	Lamiaceae	+	+		
174	<i>Westringia glabra</i> R. Brown	Lamiaceae	+			

+, present; IT, Italy; FR, France; ES, Spain; PT, Portugal.

Source: EFSA Panel on Plant Health, 2015; EFSA Panel on Plant Health et al., 2018; European Food Safety Authority, 2016, 2018, 2020; European Food Safety Authority et al., 2021, 2022a, 2022b.

Table 2. Number of *Xylella fastidiosa* hosts present in Europe during the 2013–2021 period

Description	Year						
	2013	2014	2015	2017/18	2019	2020	2021
Total number of host plants in Europe by year	1	8	–	83	114	144	174
Increasing the number of host plants in Europe compared to the previous year	0	7	–	74	31	30	30
The number of new host plants for the first discoveries in the world	–	–	44	69	37	43	30
The number of new host plants in Europe identified for the first time in the world	–	0	31	37	19	28	25

–, no data.

Source: EFSA Panel on Plant Health, 2015; EFSA Panel on Plant Health et al., 2018; European Food Safety Authority, 2016, 2018, 2020; European Food Safety Authority et al., 2021, 2022a, 2022b.

of the bacterium to different host plants, Cornara et al. (2017a) noted that the bacterium was confirmed in olive, oleander, grapevine, sweet orange (*Citrus sinensis*), stone fruit rootstock GF677 (*Prunus persica* × *Prunus dulcis* hybrid) and flowers (*Catharanthus roseus*). In Italy, 62 *X. fastidiosa* host plants are currently identified—including olive, *S. junceum*, *P. myrtifolia*, almond, rosemary, lavender, common myrtle and fig—which are typical for the Italian region (European Food Safety Authority et al., 2022b).

In France, after the first discovery of *X. fastidiosa* in Corsica on *P. myrtifolia* plants, the bacterium was also found in mainland regions. Analyses involving 45,000 samples of different plant species revealed presence of this bacterium in approximately 3% of plant material taken from 49 plant species, including mainly ornamental plants and shrubs, but also several forest species, such as *Acer pseudoplatanus*, *P. avium*, *Quercus suber*, and *Q. ilex* (Desprez-Loustau et al., 2021). In France, 72 *X. fastidiosa* host plants are currently identified—including *P. myrtifolia*, rosemary, lavender, as well as olive and almond—which are typical for this region, but also Afghan lavender and Jerusalem sage (European Food Safety Authority et al., 2022b).

In Spain, the pathogen was first detected on cherry (*P. avium*) and *P. myrtifolia* (Olmo et al., 2017). In the Balearic Islands, 18 host plant species have been identified, including *J. regia*, *P. avium* and some forest tree species such as *Fraxinus angustifolia* (Desprez-Loustau et al., 2021). In Spain, 46 *X. fastidiosa* host plants are currently identified—including olive, grapevine and almond—which are typical for this region, as well as rosemary, *Helichrysum italicum*, and several other spontaneous flora species (European Food Safety Authority et al., 2022a, 2022b; Moralejo et al., 2019).

In Portugal, 62 *X. fastidiosa* host plants are currently identified—including olive, lavender, asparagus, *Q. suber*, rosemary, *Artemisia arborescens*, *Coprosma repens*, *Vinca*

major, *M. communis*, and *Ulex minor*—which are typical for this region (European Food Safety Authority et al., 2022a, 2022b).

X. fastidiosa Subspecies Present in Europe

X. fastidiosa populations are highly heterogeneous, and based on DNA-DNA hybridization and 16S-23S rRNA internal transcribed spacer (ITS) sequencing, Schaad et al. (2004a) described and formally proposed three subspecies within this species, namely *X. fastidiosa* subsp. *piercei*, which was later modified to subsp. *fastidiosa* (Schaad et al., 2004b), *X. fastidiosa* subsp. *multiplex* and *X. fastidiosa* subsp. *pauca*. Three further subspecies within this species were subsequently described, resulting in the following six *X. fastidiosa* subspecies: (1) *X. fastidiosa* subsp. *fastidiosa*; (2) *X. fastidiosa* subsp. *multiplex*; (3) *X. fastidiosa* subsp. *pauca*; (4) *X. fastidiosa* subsp. *sandyi*; (5) *X. fastidiosa* subsp. *tashke*; and (6) *X. fastidiosa* subsp. *morus* (Almeida and Nunney, 2015; EFSA Panel on Plant Health et al., 2018). Currently, more than 80 sequenced whole genomes of all six *X. fastidiosa* subspecies are available in the National Center for Biotechnology Information (NCBI) database with genome sizes ranging from 2.4 to 2.7 Mb, with a G + C content of 51–52 mol%, with contig numbers ranging from 1 to over 400, ambiguous base counts ranging from 0 to over 300, and completeness generally exceeding 99% (Johnson et al., 2022).

Among all listed subspecies, the most economically harmful are *fastidiosa*, *pauca*, *multiplex* and *sandyi*, which have been confirmed in numerous countries around the world (Denancé et al., 2019; Sertedakis et al., 2022). In addition, different *X. fastidiosa* subspecies cause different disease symptoms on different host plants, with the *fastidiosa* subspecies causing PD in grapevine (*Vitis vinifera*), the *multiplex* subspecies causing almond leaf scorch and simi-

Table 3. List of *Xylella fastidiosa* subspecies present in European countries

No.	Subspecies	IT	FR	ES	PT
1	<i>X. fastidiosa</i> subsp. <i>fastidiosa</i>	+	+	+	+
2	<i>X. fastidiosa</i> subsp. <i>multiplex</i>	+	+	+	+
3	<i>X. fastidiosa</i> subsp. <i>pauca</i>	+	+	+	+
4	<i>X. fastidiosa</i> subsp. <i>sandyi</i>	–	+/-	–	–
5	<i>X. fastidiosa</i> subsp. <i>tashke</i>	–	–	–	–
6	<i>X. fastidiosa</i> subsp. <i>morus</i>	–	–	–	–

+, present; –, absent; +/-, established presence, which was no longer detected following the eradication of infected plants; IT, Italy; FR, France; ES, Spain; PT, Portugal.

Source: Cuntly et al., 2022; Denancé et al., 2017; EFSA Panel on Plant Health et al., 2018, 2019b; European Food Safety Authority et al., 2021, 2022a, 2022b; Giampetruzzi et al., 2016; Luvisi et al., 2017; Mang et al., 2016; Marcelletti and Scortichini, 2016a, 2016b; Moralejo et al., 2019; Olmo et al., 2017.

lar symptoms on other nut and woody plants, and subsp. *pauca* causing CVC (*Citrus* spp.), as well as coffee leaf scorch and OQDS, while subsp. *sandyi* is responsible for oleander leaf scorch (OLS) (Schaad et al., 2004a; Trkulja, 2014; Baldi and La Porta, 2017; Rapicavoli et al., 2018).

In several European countries (Italy, France, Spain and Portugal), the presence of *multiplex*, *pauca* and *fastidiosa* subspecies characterized by different sequence types was established (Denancé et al., 2017; EFSA Panel on Plant Health et al., 2019b; Giampetruzzi et al., 2016; Marcelletti and Scortichini, 2016a) reflecting the diversity of subspecies currently present in Europe (Table 3). Although the number of hosts that these subspecies infect in Europe varies, it is gradually increasing. According to European Food Safety Authority et al. (2022b), in nature, the greatest number of plants are infected by the *multiplex* subspecies, followed by *pauca* and *fastidiosa* (202, 56, and 53, respectively), while artificial inoculation by *fastidiosa* is most effective, followed by *pauca* and *multiplex* subspecies (with 74, 27, and 25 infected plants, respectively).

The name *X. fastidiosa* subsp. *fastidiosa* derives from the Latin term *fastidiosus*, meaning highly critical, and referring to the nutritional fastidiousness of the organism. Strains of this subspecies grow faster on PD2, PW, BCYE, and CS20 media, and are more resistant to penicillin and less resistant to carbenicillin than subsp. *multiplex* and *pauca*. This subspecies causes PD in grapevine (*Vitis vinifera*), almond (*Prunus amygdalus* L.), cherry (*Prunus avium*), alfalfa (*Medicago sativa*), coffee (*Coffea arabica* and *C. canephora*), oleander (*Nerium oleander*), maples (*Acer* spp.), and American black elderberry (*Sambucus canadensis*) (Marcelletti and Scortichini, 2016a). According

to the EFSA Panel on Plant Health et al. (2018) report, the *fastidiosa* subspecies is found on a larger number of perennial plants, shrubs and trees. In Europe, it was detected for the first time on *P. avium* and *P. myrtifolia* plants grown in Spain (Olmo et al., 2017), where it was later established on grapevine (*Vitis vinifera*) (Moralejo et al., 2019). This event was followed by its discovery in the Saxony region in central-western Germany, on a privately grown oleander that was infected with the *X. fastidiosa* subsp. *fastidiosa* ST1, after which this subspecies was soon discovered on *Rosmarinus* sp., *Streptocarpus* sp. and *Erysimum* sp. (Julius Kühn-Institut, 2018; Markheiser et al., 2020). The first record of *X. fastidiosa* subsp. *fastidiosa* in Europe on new hosts involved one naturally infected (*Ruta chalepensis*) and three artificially inoculated plant species from the genus *Vitis* (*Vitis × doaniana*, *Vitis treleasei*, and *V. vinifera* hybrid) in Spain (European Food Safety Authority et al., 2021).

X. fastidiosa subsp. *multiplex* derives its name from the adjective *multiplex*, meaning numerous, referring to the large number of host plants in which the bacterium causes disease, the most important of which are peach (*Prunus persica*), plum (*Prunus domestica*), almond (*P. dulcis*), elm (*Ulmus* spp.), pigeon grape (*Vitis aestivalis*), sycamore (*Platanus* spp.), and other forest trees. Strains of the *multiplex* subspecies grow much faster on PW medium than on PD2, BCYE or CS20, and are more sensitive to penicillin and more resistant to carbenicillin than the *fastidiosa* subspecies (Marcelletti and Scortichini, 2016a). The subspecies *multiplex* was established in Spain on *P. myrtifolia* (Olmo et al., 2017). In France, ST6 and ST7 were found in Corsica and Provence-Alpes-Côte d'Azur (PACA) regions on *P. myrtifolia*, *S. junceum* and in almost 70 other plant species (Cuntly et al., 2022; Denancé et al., 2017), ST6 in new region Occitanie (Aude area) from natural and urban settings and from a nursery (Cuntly et al., 2022) and recently discovered two new variants genetically related to the subsp. *multiplex* and assigned to ST88 found on *Polygala myrtifolia*, *Hebe* sp. *Osteospermum ecklonis*, *Lavandula x intermedia*, *Coronilla glauca*, *Euryops chrysanthemoides*, and ST89 on *Myoporum* sp., and *Viburnum tinus* in two areas of PACA region (Cuntly et al., 2022). In Italy, the *multiplex* subspecies was first discovered in Tuscany (Monte Argentario site) in *S. junceum*, *P. myrtifolia*, and *R. alaternus* plant samples (Marchi et al., 2018), whereas in Portugal, it first emerged on lavender (*L. dentata*) in 2019 (EPPO, 2019a). In 2021, this subspecies was identified in Spain, Italy, Portugal and France in 24 new plant species naturally infected in the EU (European Food Safety Authority et al., 2021). The following year, 19 new host plants were

identified in Portugal, Spain and France, and the *multiplex* subspecies was determined in 15 of these cases, while the exact subspecies was not specified for the remaining four host plants (European Food Safety Authority et al., 2022b).

X. fastidiosa subsp. *pauca* derives its name from the Latin term *pauca*, meaning few, reflecting its narrow host range. The *pauca* and *multiplex* subspecies grow more slowly on PD2, PW, BCYE, and CS20 media, and are more sensitive to penicillin and more resistant to carbenicillin than the *fastidiosa* subspecies (Marcelletti and Scortichini, 2016a). This subspecies causes disease to citrus (*Citrus* spp.) and coffee (*C. arabica*), and have been found associated with oleander, almond, cherry and with olive (*O. europaea*) trees showing extensive leaf scorching/wilting and twig die-back in Apulia (Southern Italy), Argentina and Brazil. The symptoms caused by this subspecies vary from host to host, but usually manifest as leaf margin burns, leaf nerve chlorosis, wilting and stunting (Marcelletti and Scortichini, 2016a). The *pauca* subspecies causes nerve chlorosis in citrus and develops on fewer hosts. In Italy, it was found in coffee as well as olive plants (EFSA Panel on Plant Health et al., 2018; Luvisi et al., 2017; Mang et al., 2016; Marcelletti and Scortichini, 2016b), representing the first confirmed record of this bacterium in Europe (De Pascali et al., 2022). This subspecies was introduced from Central America where it is an endemic pathogen (Girelli et al., 2022). Its identification on Italian olive grown in Apulia commonly known as “CoDiRO” or “ST53” raised concern for other plant species, *Citrus* spp. in particular, where this subspecies causes extensive damage. Although Italian strains failed to infect citrus (Elbeaino et al., 2014a; Guan et al., 2015), infections were noted in 30 other host plants surrounding olive groves in Apulia (Saponari et al., 2019). Millions of olive trees have perished due to the damage caused by this subspecies, with devastating socioeconomic consequences for the local communities (Godefroid et al., 2019). In France, ST53 of the *pauca* subspecies was found in Corsica on *P. myrtifolia* and *Q. ilex* plants (Denancé et al., 2017) and in a unique area in PACA region (Cunty et al., 2022). Its presence on two new hosts in Europe was also confirmed, one of which was naturally infected (*Ulex parviflorus*) in Spain while the other (basil, *Ocimum basilicum*) was artificially inoculated under experimental conditions (European Food Safety Authority et al., 2021).

X. fastidiosa subsp. *sandy* was described and formally proposed by Schuenzel et al. (2005) when the isolates that cause OLS were determined on the American continent. Subsequently, based on the findings yielded by multiple molecular analyses (multiplex polymerase chain reaction [PCR], incurred sample reanalysis, and random amplified

polymorphic DNA), Hernandez-Martinez et al. (2007) established that the strains isolated from *Hemerocallis* spp., *Jacaranda mimosifolia* and *Magnolia grandiflora* belong to the subspecies *sandyi*. In Europe, the presence of ST76 of this subspecies was determined on *P. myrtifolia* in Corsica, but since eradication measures were immediately undertaken, no further instances of this strain were detected (Denancé et al., 2017) (Table 3).

X. fastidiosa subsp. *tashke* was proposed by Randall et al. (2009) based on the sequence analysis of the 16S-23S ribosomal ITS region of isolates obtained from the plant *Chitalpa tashkentensis* and other sequences sourced from gene banks. Using these findings, the phylogenetic tree, and the previously described four subspecies, these authors grouped the isolates obtained from *C. tashkentensis* into a separate cluster as a new subspecies for which the authors proposed the name *X. fastidiosa* subsp. *tashke*. Thus far, its presence has not been established in Europe.

X. fastidiosa subsp. *morus* was isolated by Guan et al. (2014) from white mulberry (*Morus alba*) in 2011 in Beltsville, USA. In Europe, its presence has not been established thus far.

The climate of a large area of Europe (including Spain, France, the British Isles, Italy, the Adriatic coast, Greece, Turkey and some coastal areas of the Black Sea) appears to be very suitable for the potential distribution of the *multiplex* subspecies. According to Godefroid et al. (2019), the climate in Spain, France, Italy, Croatia, Greece, and Turkey, as well as the coastal regions of North Africa, seems very favorable for the potential distribution of the *fastidiosa* subspecies, whereas the climatic conditions prevailing in the coastal regions of the Mediterranean (with the exception of southern Portugal and the Spanish Atlantic coast) is conducive for the spread of the *pauca* subspecies. The same authors state that the climatic conditions in the northern and eastern regions of Europe (northeastern France, Belgium, the Netherlands, Germany, etc.) are less favorable for the spread and distribution of the pathogen *X. fastidiosa*.

X. fastidiosa Vectors in Europe

X. fastidiosa is a phytopathogenic bacterium that develops in the xylem of host plants. A large number of potential vectors of this bacterium are presently known, all of which are insects that feed on xylem sap. While the *X. fastidiosa* vectors in North and South America are relatively well known, since the first appearance of this quarantine bacterium in Italy in 2013, only a few vectors have been identified in Europe. Thus, expanding the current knowledge about

its vectors is essential for better understanding the cycle of disease development, as well as adopting adequate vector control measures with the aim of mitigating and preventing attacks and disease occurrence on new host plants and in new localities (EFSA Panel on Plant Health et al., 2019c; Elbeaino et al., 2014b; Trkulja et al., 2017b).

According to the EFSA Panel on Plant Health et al.'s (2019c) report, the vectors of this phytopathogenic bacterium are species belonging to the cicada families *Aphrophoridae*, *Cicadellidae*, and *Membracidae*, but only members of *Aphrophoridae* family serve as *X. fastidiosa* vectors in Europe. According to Di Serio et al. (2019), 99 potential European vectors feed on xylem sap, while Cornara et al. (2019) recognize 78 potential vectors from *Cercopoidea* and *Cicadoidea* families and *Cicadellidae*: subfamily *Cicadellinae*.

Three cicada species from the *Aphrophoridae* family—*Philaenus spumarius* L., *Neophilaenus campestris* Falén, and *Philaenus italosignus* Drosopoulos & Remane (Elbeaino et al., 2014b; European Food Safety Authority et al., 2019; López-Mercadal et al., 2021)—are the most important and fully competent vectors of *X. fastidiosa* that have been confirmed in Europe to date, with *P. spumarius* having particular significance for the spread of this pathogen across the continent (Avosani et al., 2022).

P. spumarius (meadow spittlebug) is one of the most numerous, widespread and important, and thus the most studied vectors of this bacterium in Europe (Cruaud et al., 2018; EFSA Panel on Plant Health et al., 2018; European Food Safety Authority et al., 2019; Godefroid et al., 2022; Morente et al., 2022), even though it is present worldwide, including Africa, Asia and North America. In Europe, the widespread distribution of this vector—from Lapland (Finland) to the Mediterranean (Cornara et al., 2018)—causes concern about the mass transmission and spread of *X. fastidiosa*, especially in the Mediterranean countries, where the plant species susceptible to its attacks (olive in particular) are mostly produced. Using molecular PCR tests, Cuntly et al. (2020) determined the enormous potential of bacterial transmission by this insect, which is not surprising given that *P. spumarius* is a highly polyphagous species and can survive on different hosts from several plant families. This assertion was confirmed by investigations in Italy (Liguria and Apulia) (Di Serio et al., 2019), where *P. spumarius* individuals developed and lived on the members of all tested plant families. However, *P. spumarius* specimens favored plants from the families *Fabaceae* and *Asteraceae*, while a significantly lower number was recorded on plants from the *Poaceae*, *Apiaceae* and *Rubiaceae* families (Di Serio et al., 2019). In Spain (Majorca), although

P. spumarius nymphs were observed on numerous hosts, they showed the greatest preference for plants from the *Asteraceae* and *Fabaceae* families (López-Mercadal et al., 2021). In the central and southern regions of Spain, as well as in the northwest of Portugal, *P. spumarius* was present in olive groves on herbaceous vegetation, mainly on plants from the *Asteraceae*, *Apiaceae* and *Geraniaceae* families (Morente et al., 2018). In Germany, *P. spumarius* is widespread, and is found on ornamental, autochthonous and economically important cultivated plants such as grapevine and cherry, which are important *X. fastidiosa* hosts (Markheiser et al., 2020). In Spain, on the Balearic Islands, *P. spumarius* is the main and most widespread vector of *X. fastidiosa* (López-Mercadal et al., 2021), and managed to transfer this bacterium from almond to almond and from grapevine to grapevine under experimental conditions (Olmo et al., 2021). Successful transmission of *X. fastidiosa* by *P. spumarius* to different hosts was also confirmed by Cornara et al. (2017a, 2017b), while Cuntly et al. (2020) identified 1,000 hosts (mostly dicotyledonous plants) of this insect.

Cornara et al. (2018) provided a detailed description of the biology of *P. spumarius*, stating that this species overwinters in the egg stage and has one generation per year. Females mate with several males and lay eggs in autumn, in groups of up to 30 specimens, producing 350–400 eggs per mating season. Eggs are usually deposited along the edges of orchards, as well as on agricultural land after harvest, herbs, dead plant parts, plant debris, cracks and trunk bark, typically close to the soil. Egg development takes about 5–7 weeks, and the larval period lasts 35–100 days, depending on the environmental conditions. After the larvae feed on the host plants, they produce saliva, which gradually dries and hardens, allowing the formation of a cocoon in which they hibernate. Larvae hatch in spring (usually in April or May, depending on the temperatures), and adult insects (imago) appear in June, and reach maturity in July and August (Kereši et al., 2019). Adult insects live until autumn, when they are killed by low temperatures (frost), although some individuals can overwinter until spring (Cuntly et al., 2020; Kereši et al., 2019). The second generation of this pest has been identified in Greece (Di Serio et al., 2019).

N. campestris is the second most important *X. fastidiosa* vector and is widely distributed in Europe, especially in the Mediterranean region (Cavaliere et al., 2019). This insect is widespread in Spain and Portugal where it poses a significant threat, especially to commercial olive, grapevine and almond plantations (Lago et al., 2021; Morente et al., 2018). In these countries, it is mainly present on *Avena* sp.

and *Bromus* sp., as well as other plants from the *Poaceae* family (Cornara et al., 2019; Morente et al., 2018). The ability of *N. campestris* to adopt and transfer the bacterium *X. fastidiosa* under experimental conditions from infected to different host plants was reported by Cavalieri et al. (2018, 2019).

P. italosignus as a vector of the *X. fastidiosa* strain originating from the Apulia region was found to have limited presence in the southern parts of Italy and Sicily, while its greater distribution was recorded in the northern and central regions of this country, where it has a large number of different agricultural plants as potential hosts (Cavalieri et al., 2019; Panzavolta et al., 2019). Although little is known about the distribution of this pest and the plants it prefers, it has been established that the nymphs develop and females lay eggs on *Asphodelus* spp. plants. In parts of Italy where olive is the dominant plant species, the presence of this insect is rarely recorded (Cavalieri et al., 2019), while Panzavolta et al. (2019) noted a significant population of this insect in Tuscany on *Asphodelus ramosus* as well as on olives. Transmission of the bacterium by this insect to *P. myrtifolia*, olive and cherry plants under experimental conditions was also confirmed by Cavalieri et al. (2019), indicating a high risk of transmission of *X. fastidiosa* to various economically important cultivated plant species through this vector in localities where it is present.

The aforementioned finding indicates that these three cicada species are capable and present *X. fastidiosa* vectors in Europe. However, numerous studies indicate that other cicada species can be potential vectors of this dangerous phytopathogenic bacterium in Europe, such as *Cicada orni* L., *Latilica tunetana* Matsumura, *Aphrophora alni* Fallen, *Cercopis vulnerata* Rossi, *Evacanthus interruptus* L., and *E. acuminatus* Fabricius, *Cicadella viridis* L. (Cornara et al., 2019, 2020), as well as *Euscelis lineolatus* Brulle (Elbeaino et al., 2014b) and others, highlighting the importance of further research, continuous monitoring and testing of potential, new and hitherto unknown species of insects as potential *X. fastidiosa* vectors on different host plants.

X. fastidiosa Management in Europe

Current *X. fastidiosa* control strategies are mainly focused on pathogen-free propagation plant material, phytoquarantine, eradication, vector control, growth of resistant or tolerant plant cultivars, and bactericidal treatments (Commission Implementing Regulation (EU) 2020/1201; EFSA Panel on Plant Health et al., 2019a; European Food Safety Authority, 2020; Kyrkou et al., 2018; Pavan et al., 2021; Scortichini et al., 2021). For example, EU phytoquarantine

regulations mandate that, prior to export or import into the EU, any plant recognized as *X. fastidiosa* host must be tested for the presence of bacterium (European Food Safety Authority et al., 2020). Likewise, eradication proposed by Commission Implementing Regulation (EU) 2020/1201 should be applied to any new outbreak of *X. fastidiosa*, with the exception of infected zones where containment measures are authorized (e.g., South of Apulia, Corsica, and Balears). In such cases, areas in which *X. fastidiosa* infection is confirmed are demarcated, and the planting of host plants is prohibited in the infected zone (Commission Implementing Regulation (EU) 2020/1201; Pavan et al., 2021).

In the Italian legislation, further provisions are provided, whereby (1) distinction is made between “host” (species susceptible to all *X. fastidiosa* subspecies worldwide) and “specified” (species susceptible to the local *X. fastidiosa* genotype) plants; (2) “containment” rather than “eradication” is adopted as the control measure in Apulia; and (3) both infected and buffer zones are clearly demarcated (Morelli et al., 2021). The legislation further prohibits planting of susceptible hosts in infected areas (except for species or cultivars found to be resistant or tolerant), as well as movement of “host” or “specified” plants out of the demarcated areas.

Chemical control currently relies on copper compounds and several microbial biopesticides, as well as antibiotics where permitted. According to several reports, application of N-acetylcysteine (NAC) (Saponari and Boscia, 2019), copper (II) sulfate, menadione, benzethonium chloride, and abscisic acid (Ge et al., 2020; Muranaka et al., 2013; Zhang et al., 2019) as well as antibiotic (oxytetracycline) along with NAC, Zn, or Cu, and citric acid fertilizer (Scortichini et al., 2018) can achieve effective *X. fastidiosa* control under greenhouse conditions. Biocomplex Dentamet—a compound containing zinc, copper, and citric acid—can reduce *X. fastidiosa* subsp. *pauca* multiplication rate in olive trees in Salento (Apulia, Italy) by application to the canopy or injection into the trunk (Scortichini et al., 2018, 2021, 2022).

Owing to its endophytic nature, full control of *X. fastidiosa* remains challenging, as the ability of available bactericides and mineral-based compounds to access xylem vessels where the pathogen establishes is limited (EFSA Panel on Plant Health et al., 2019a; Kyrkou et al., 2018; Montesinos et al., 2022; Morelli et al., 2021; Tatulli et al., 2022). Thus, new chemical compounds are required to achieve effective disease suppression. With this aim, Baldassarre et al. (2020) studied interactions between calcium carbonate nanocrystals and bacteria cells, as well as their

application in olive to verify uptake. The authors demonstrated that these nanocrystals can be adsorbed by the roots as well as effectively translocated into the plant vessels and other tissues. These findings indicate that different compounds (phytodrugs, fertilizers) can be delivered and released into the plants using these nanocarriers. Although the authors indicated that nanoCaCO₃-based phytodrugs could potentially provide a cure for *X. fastidiosa* infections, more extensive testing needs to be carried out in the future to confirm this assertion and other potential anti-*X. fastidiosa* agents should also be investigated.

Besides chemical control, cultural practices could potentially help reduce vector activity and population density (Sanna et al., 2021). For example, for cicadas *P. spumarius*, *N. campestris* and *P. italosignus*, this may include compulsory mechanical weed control (tillage) in spring, along with the use of insecticide sprays to control adults (Cavalieri et al., 2018; Cornara et al., 2018; Pavan et al., 2021). Management of ground vegetation, as well as correct timing of soil tilling to disrupt nymph development and reduce adult emergence, have been shown by Sanna et al. (2021) to effectively control *P. spumarius* population size. However, control of adults on olives requires several insecticide applications throughout their entire feeding period. According to Dongiovanni et al. (2018), pyrethroids (deltamethrin) and neonicotinoids (acetamiprid) are the most efficacious. Soil tillage, combined with the application of pyroherbicides, herbicides, neonicotinoids and pyretroids in spring, has also been shown by Saponari and Boscia (2019) to almost eliminate the presence of juvenile *P. spumarius*. Liccardo et al. (2020) similarly reported that an inundation strategy with *Zelus renardii*—a known *P. spumarius* predator—can be an effective “green” solution to *X. fastidiosa* invasion, as it results in a pathogen incidence reduction to below 10%. According to EPPO (2020), in Apulia, elimination of weeds within and around olive groves in winter and spring reduced the abundance of both *P. spumarius* and *N. campestris* on olive trees and ground vegetation to almost zero. Moralejo et al. (2019) similarly found that weed control and soil tillage in spring may contribute to vector population reduction, which would in turn hinder *X. fastidiosa* spread.

Olive cultivar ‘Leccino’ and selection ‘FS17’ were found to be resistant to *X. fastidiosa* by several authors (Boscia et al., 2017; Saldarelli et al., 2022; Saponari and Boscia, 2019). According to Saldarelli et al. (2022), in ‘Leccino’, resistance appears to develop via a complex of mechanisms involving both genomic and physiological factors, which limit the bacterial population size. These authors also

found that ‘Leccino’ is more resilient to the *X. fastidiosa* infection as its physiological response to the water stress is not as extreme as in susceptible cultivars such as Cellina di Nardò and Ogliarola Salentina. As *X. fastidiosa* infection limits the water supply to leaves (Surano et al., 2022), physiological parameters can be used in breeding programs to ensure that olive genotypes resistant to the bacterium are chosen. For example, using simple sequence repeat marker analysis, Pavan et al. (2021) demonstrated that the olive genotypes ‘Frantoio’ and ‘Nocellara Messinese’ exhibited partial resistance. Considering that genetic resistance presents the most promising long-term *X. fastidiosa* management strategy, an intense screening program for resistance was started for more than 100 olive selections, combining natural pressure and artificial inoculation with the Apulian *X. fastidiosa* strain (Saponari and Boscia, 2019). Similarly, as a part of their study focusing on grapevine, Kyrkou et al. (2018) found that *V. vinifera* cultivars are susceptible to Pierce’s disease, as well as demonstrated resistance in other species that are not of sufficiently high quality for wine production.

Integrated pest management also includes modeling for *X. fastidiosa* spread. For example, White et al. (2017) developed a spatially-explicit simulation model for *X. fastidiosa* to provide guidance for predicting spread in the early stages of invasion and inform management strategies. Based on these simulations, the authors identified optimal control scenarios that minimize control effort while resulting in the greatest reduction in *X. fastidiosa* spread, suggesting that buffer zone width increase should be favored over surveillance efforts as control budgets increase. Their findings further highlighted the importance of non-olive hosts in increasing the disease spread rate. More recently, Brunetti et al. (2020) proposed a mathematical model ODE system for *X. fastidiosa* epidemics in the Mediterranean regions. Guided by numerical simulations, they identified the key components of this plant–insect–bacterium epidemic system that should be considered as potential long-term bio-control strategy targets. Furthermore, Kyrkou et al. (2018) developed a *X. fastidiosa* epidemiological model denoted as Xff to describe the PD dynamics in vineyards. The Xff identifies key parameters in the disease spread that should be targeted by current and future intervention strategies.

Fierro et al. (2019) developed “lattice model” while Liccardo et al. (2020) proposed a “biological control model” for managing *X. fastidiosa* vectors and infection in olive trees. Both models include three control steps, each involving one or several actions aimed at reducing vector population size and the number of adults infecting *Xylella-*

free plants (Picciotti et al., 2021). More recently, Godefroid et al. (2022) fitted bioclimatic species distribution models to empirical data to depict the macroclimatic preferences of *P. spumarius* as the major epidemiologically relevant vector currently responsible for *X. fastidiosa* spread in Europe. Finally, *X. fastidiosa* control measures also rely on minimizing other sources of stress to the host plant, such as drought, overproduction, and other diseases (EPPO, 2020).

Conclusion

This review provides a comprehensive and up-to-date assessment of the *X. fastidiosa* presence in Europe. The emergence of the bacterium throughout Italy, Spain, France and Portugal—with 174 hosts identified thus far—confirms that *X. fastidiosa* is spreading across the continent at an alarming rate. In particular, available evidence indicates that the conditions in central and southern Europe are suitable for the introduction and further spread of *X. fastidiosa*. European outbreaks of *X. fastidiosa*-related diseases present an undetectable trace in the history of plant pathology.

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

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