

## Bioecological Traits of Spittlebugs and Their Implications for the Epidemiology and Control of the *Xylella fastidiosa* Epidemic in Apulia (Southern Italy)

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### Abstract

Spatial-temporal dynamics of spittlebug populations, together with transmission biology, are of major importance to outline the disease epidemiology of *Xylella fastidiosa* subsp. *pauca* in Apulian olive groves. The spread rate of *X. fastidiosa* is mainly influenced by (i) the pathogen colonization of the host plant; (ii) the acquisition of the pathogen by the vector from an infected plant, and its inoculation to healthy plants; (iii) the vector population dynamics and abundance at different spatial scales; and (iv) the dispersal of the vector. In this contribution we summarize the recent advances in research on insect vectors' traits—points ii, iii, and iv—focusing on those most relevant to *X. fastidiosa* epidemic in Apulia. Among the vectors' bioecological traits influencing the *X. fastidiosa* epidemic in olive trees, we emphasize the following: natural infectivity and transmission efficiency, phenological timing of both nymphal and adult stage, the role of seminatural vegetation as a vector reservoir in the agroecosystem and landscape, and preferential and directional dispersal capabilities. Despite the research on *X. fastidiosa* vectors carried out in Europe in the last decade, key uncertainties on insect vectors remain, hampering a thorough understanding of pathogen epidemiology and the development of effective and targeted management strategies. Our goal is to provide a structured and contextualized review of knowledge on *X. fastidiosa* vectors' key traits in the Apulian epidemic, highlighting information gaps and stimulating novel research pathways on *X. fastidiosa* pathosystems in Europe.

**Keywords:** insect vector, *Philaenus spumarius*, plant pathogenic bacterium, transmission biology, vector-borne plant disease

Vector-borne plant diseases rely on organisms—mainly hemipteran insects—for their spread; thus the rate and extent of the incidence of a disease depend on the bioecological traits of the vectors, for example, population dynamics, conditional behaviors, and pathogen transmission biology (Cator et al. 2020; Jeger et al. 2004; Shaw et al. 2017; Spence 2001). The importance of vector traits and their spatiotemporal variability in disease epidemiology is generally accepted (Smith et al. 2014), although both empirical and theoretical models usually include only a few such traits, if any, and rarely account for their spatial, temporal, and behavioral variability (Cator

et al. 2020; Jeger 2020). Moreover, most research on the importance of the vectors' traits in plant pathogen epidemiology has been carried out on virus vectors, while the relevance of such traits for bacteria–insect vector pathosystems is often neglected (Jeger 2000; Orlovskis et al. 2015; Tamborindeguy et al. 2017). The pathosystems that emerged in Europe upon the introduction of the exotic bacterium *Xylella fastidiosa* Wells et al. (Xanthomonadaceae) are no exception, as the relationships between bioecological traits of the insect vectors and epidemiological dynamics have not yet been fully investigated.

The xylem-limited bacterium *X. fastidiosa* is the causal agent of several plant diseases that have mainly been reported in the New World (Sicard et al. 2018), for example, Pierce's disease (PD) on grapevines, citrus variegated chlorosis, and leaf scorch disease on almond (Coletta-Filho et al. 2020; EPPO 2019; Sicard et al. 2018; Vanhove et al. 2019). The global increase in the exchange of goods and plant materials has led to the current worldwide expansion of the bacterium, which, at the moment of the preparation of this review, has been reported outside the Americas in Italy, Spain, France, Portugal, Taiwan, Israel, and Iran (EPPO 2022; Landa et al. 2020; Morelli et al. 2021; Zecharia et al. 2022).

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The first detected outbreak of *X. fastidiosa* in Europe was reported in 2013 on olive trees in the Apulia region of Italy, where *X. fastidiosa* subsp. *pauca* sequence type ST53 was found to be the causal agent of a new plant disease, the olive quick decline syndrome (OQDS) (Loconsole et al. 2016; Saponari et al. 2017). The pathogen found suitable epidemiological conditions in this area (Strona et al. 2017) and, after initially being restricted to the Salento peninsula, quickly spread over the Apulia region, thus leading to a massive dieback of susceptible olive trees (EFSA Panel on Plant Health [PLH] et al. 2019; Kottelenberg et al. 2021). *X. fastidiosa*-induced diseases are the outcome of the bacterial colonization of xylem vessels, which causes a significant reduction of the sap flow through diffuse bacterial aggregates, alterations of the xylem cell wall and pit membranes (Montilon et al. 2022), and vessel occlusions as part of the host plant defense mechanisms (e.g., production of tyloses) (Baccari and Lindow 2011; Cardinale et al. 2018; Chatterjee et al. 2008; Newman et al. 2003; Rapicavoli et al. 2018). A reduction in xylem sap flow often causes symptoms similar to those of water-stressed plants, that is, marginal leaf necrosis, leaf scorching, and shoot dieback, which in turn can lead to extensive desiccation of the canopy (Castro et al. 2021; Newman et al. 2003).

*X. fastidiosa* is transmitted by xylem sap-feeding insects (Hemiptera: Cicadomorpha) from two distinct taxonomic groups: leafhoppers (Hemiptera: Cicadellinae, Cicadellini and Proconiini tribes) and spittlebugs (Hemiptera: Cercopoidea) (Cornara et al. 2019). Xylem-sap feeder communities in American agroecosystems are dominated by sharpshooters, while spittlebugs are prevalent in European agroecosystems. These two taxonomic groups share the same xylem sap-feeding trait but have notable biological and ecological differences (for further details, see, e.g., Cornara et al. 2019; Krugner et al. 2019; Markheiser et al. 2022). Hence, information obtained from studies on bioecology traits of *X. fastidiosa* vectors in the Americas and their implications for plant epidemics are not necessarily transferrable to a European scenario.

The role of insect vectors in the spread of the bacterium and the lack of curative applications upon persistent systemic infections of crop plants make insect vectors the primary target of control strategies to counteract the impact of the *X. fastidiosa* epidemics. As such, when OQDS first emerged in Apulia, resources were devoted to advancing the knowledge on *X. fastidiosa* insect vectors in Europe. Spittlebugs were unambiguously identified as the main species responsible for the OQDS epidemic, as well as for the spread of the bacterium in the outbreaks in Corsica, Balearic Islands, and mainland Spain (Cornara et al. 2017b; Cruaud et al. 2018; EFSA 2018; Olmo et al. 2017). The spittlebug *Philaenus spumarius* (L.) was ascertained to be the key vector species in the Apulian olive *X. fastidiosa* subsp. *pauca* pathosystem (Cavaliere et al. 2019; Cornara et al. 2017b). Two other spittlebug species—*Neophilaenus campestris* (Fallén) and *Philaenus italosignus* Drosopoulos & Remane—transmit *X. fastidiosa*, although their role in the *X. fastidiosa* subsp. *pauca* epidemic is likely negligible, given the low numbers of these species observed on olive trees and/or their low transmission efficiency (Cavaliere et al. 2019).

The mandatory control strategies against the spread of *X. fastidiosa* epidemic in Apulia involve (i) identification and roguing of infected plants in the buffer zone, (ii) mechanical management of nymphal stages of the vector species through mowing and/or tilling, and (iii) control of adult populations through insecticide applications (EFSA Panel on Plant Health [PLH] et al. 2019; European Union 2020). Despite the effectiveness of these agronomic practices in suppressing the spittlebug nymphal populations in olive groves, the difficulties in the implementation of these interventions at the regional level are most likely the reason for its limited impact on the reduction of *X. fastidiosa* epidemic spread in the Apulian olive groves (EFSA Panel on Plant Health [PLH] et al. 2019; Kottelenberg et al. 2021; Sanna et al. 2021).

Several models have been developed concerning the epidemiology, distribution, and possible spread of *X. fastidiosa* throughout Apulia, Italy, and Europe (Brunetti et al. 2020; Kottelenberg et al. 2021; Signes-Pont et al. 2020; Strona et al. 2020; White et al. 2020). Some of these, such as assessing the optimal width of the buffer zone and eradication measures (White et al. 2017, 2020), have directly influenced the management strategies of the epidemic. However, most of these models rely on poor knowledge of possible key epidemiological parameters (Occhibove et al. 2020), although there have been efforts to include vectors' traits in epidemiological models (Gilioli et al. 2023; Giménez-Romero et al. 2023). Indeed, the predictive and explanatory abilities of such models are highly dependent on the accuracy of spatiotemporal epidemiological data and directly measured parameters, which are typically lacking for emerging diseases (Parnell et al. 2017). Moreover, the traits of insect vectors (e.g., transmission biology, dispersal/movements, abundance/density) are rarely explicitly included in epidemiological models for plant pathologies, despite often being considered of key importance (Kyrkou et al. 2018). Even when parameters regarding the vectors, such as infection rate and abundance, are incorporated in models, they are usually included as constants, although they vary to a great extent over time and space, with possible significant impact on the outcomes of the epidemic (Cator et al. 2020). The absence and/or scarce implementation of knowledge on the traits of the vectors hampers the development of both reliable epidemiological models and effective control strategies.

Work by Jeger and Bragard (2018) and Occhibove et al. (2020) emphasized the key role of vector transmission in determining disease dynamics and highlighted the most important uncertainties concerning *X. fastidiosa* pathosystems that impact the accuracy of epidemiological predictions for disease prevention and control strategies, identifying the most urgent knowledge gaps that need to be filled. Some of the more conspicuous uncertainties concern insect vectors, specifically: (i) dispersal, (ii) density and distribution (at different spatial scales), (iii) transmission biology, and (iv) bioecology.

In consideration of the abovementioned *X. fastidiosa* research frameworks and guidelines, the aim of this article is to synthesize the recent advances in the research on bioecology of *X. fastidiosa* vectors in Europe, with a particular focus on the *X. fastidiosa* subsp. *pauca* ST53 epidemic in Apulia. Providing an exhaustive review of the literature on spittlebugs and other *X. fastidiosa* vectors is beyond the scope of this work (Cornara et al. 2018a, 2019; Krugner et al. 2019; Redak et al. 2004); our intention is to present an overview of the current knowledge on the spittlebugs' traits that primarily influence the *X. fastidiosa* epidemic in Apulia—and possibly in other European foci—and to discuss their implications for the understanding of the *X. fastidiosa* epidemiology and on the development of effective management strategies.

## Transmission Biology of Insect Vectors

The transmission of insect-borne plant pathogens relies to a great extent on both the acquisition/inoculation performances and the feeding behavior of the vectors; these vector traits may thus affect the epidemiological dynamics and outcomes (Eigenbrode et al. 2018). The transmission biology of vectors of American *X. fastidiosa* pathosystems has been studied in depth, especially for PD of grapevine. However, it is beyond the scope of this review to deal with the great amount of research conducted on sharpshooter vectors (e.g., see the reviews of Backus and Shih 2020; Krugner et al. 2019; Redak et al. 2004), although key characteristics of *X. fastidiosa* transmission that stem from studies on sharpshooters have also been confirmed for spittlebugs in Europe. The biology of *X. fastidiosa* transmission by insects is peculiar among vector-borne plant pathogens, as it is persistent and propagative but not circulative (Hill and Purcell 1995). Briefly, (i) *X. fastidiosa* presents

no transstadial or vertical transmission (i.e., intergenerational) in its insect vectors (Freitag 1951); (ii) *X. fastidiosa* colonization of insect hosts is limited to the foregut, and thus the infectivity of vectors is lost during molting (Almeida and Purcell 2003; Hill and Purcell 1995); and (iii) there is no detectable latency period from acquisition to inoculation, and no biofilm formation is necessary for an effective inoculation (Purcell and Finlay 1979). However, some critical transmission biology characteristics may change drastically between vector species–host plant species combinations (Almeida et al. 2005). Because of the novel combination of vector species, *X. fastidiosa* strain, and host plant in the Apulian pathosystem, specific research is of great relevance to understand the spread dynamics of this epidemic.

### Natural Infectivity

The first parameter investigated in the Apulian epidemic area was that of natural infectivity, that is, the prevalence of infected field-collected insects. The natural infectivity of *P. spumarius* in infected olive groves, expressed as a percentage of *X. fastidiosa*-positive individuals in field-collected populations, was estimated to be in a 15 to 70% range, although significant differences have emerged over the years (Ben Moussa et al. 2016; Cornara et al. 2017b; Saponari et al. 2014). In general, a lower prevalence ( $\approx 20$  to 25%) of *X. fastidiosa*-positive individuals was observed in May, soon after adult spittlebug emergence, followed by a marked increase during summer, on average by around 50%, with peaks of *X. fastidiosa*-positive individuals occasionally reaching 70 to 100% on different vegetation compartments (olive canopies, ground vegetation, and shrubs bordering the olive groves) (Cornara et al. 2017a, b). The increasing occurrence of dead olive trees in the epidemic area, coupled with the prohibition of planting new olive groves (except for resistant cultivars), is possibly reducing the bacterial reservoir and the natural infectivity of the insects (M. Saponari, unpublished data). Surveys performed in 2022 in the epidemic area indeed showed a lower prevalence of *X. fastidiosa*-positive individuals (9 to 42%) (V. Cavalieri, unpublished data) compared with that reported in previous studies.

Data on the natural infectivity of spittlebugs in Europe are also available from surveys carried out in Corsica (France), showing somewhat similar infectivity rates of *P. spumarius* in June (up to 43.7%) and October (12.5 to 34.4%), with no significant seasonal variation, although surveys were only carried out in these 2 months (Cruaud et al. 2018). The overall rate of *X. fastidiosa*-positive insects observed in a larger survey in Corsica was 8% (100 positive out of 1,200 sampled), as obtained from 39 locations sampled from 2016 to 2019 (Farigoule et al. 2022) (Table 1). Field surveys conducted in the Balearic Islands in 2017 to 2020 showed an average natural infectivity of 23.8% for *P. spumarius* and 21.3% for *N. campestris*, with isolates of different subspecies being detected in the *X. fastidiosa*-positive spittlebugs (López-Mercadal et al. 2021). To the best of our knowledge, no estimation of the natural infectivity of potential vector species in *X. fastidiosa* outbreaks in mainland Spain has been published.

### Efficiency

Efficiency, that is, how often a vector transmits a pathogen over time or per transmission opportunity, is an important characteristic of vector transmission, and hence it is the main transmission parameter implemented in epidemiological and control models (Purcell and Almeida 2005). Transmission competence and efficiency have been studied for *P. spumarius* and other potential insect vectors of in the Apulian pathosystem. Here we report the transmission efficiencies recalculated from original papers to allow easier comparisons, that is, acquisition efficiency is reported as the percentage of *X. fastidiosa*-positive insects after an acquisition trial, while inocula-

tion efficiency of an insect vector is considered to be the percentage of infected recipient plants per *X. fastidiosa*-positive insect per day (Table 1).

According to different studies, acquisition efficiency of *P. spumarius* from field olive trees (susceptible cultivar: ‘Cellina di Nardò’) varied from 15 to 20% to 60 to 80% (Bodino et al. 2021b; Cavalieri et al. 2019; Cornara et al. 2017a) (Table 1). The acquisition efficiency of *P. spumarius* from naturally infected field olive trees can change over the year, and it is lower in late spring to early summer (June to July, 30 to 60%) and higher in late summer (September, 55 to 83%). Once the bacterium has been acquired, *P. spumarius* adults remain *X. fastidiosa*-positive throughout their life span, that is, up to 78 days post-acquisition (late October to November) (Bodino et al. 2021b).

The inoculation efficiency of *X. fastidiosa* subsp. *pauca* by *P. spumarius* adults on olive trees is quite low. Inoculation rate estimates are about 6 to 11% of plants infected per *X. fastidiosa*-positive insect per day, after testing spittlebugs previously isolated on infected field olive trees for acquisition (Bodino et al. 2021b; Cavalieri et al. 2019; Cornara et al. 2017a). The inoculation rates are even lower when insects collected directly in olive groves with a high prevalence of *X. fastidiosa*-infected plants (i.e., natural infectivity) are considered (Cornara et al. 2017a) (Table 1). Inoculation efficiency on olive seedlings is quite constant throughout the year and at different post-acquisition times, at least under controlled conditions, without any significant changes in the transmission rate, even long after acquisition (Bodino et al. 2021b).

The spread rate of *X. fastidiosa* subsp. *pauca* can change significantly according to the seasonal and environmental variables (Bodino et al. 2021b). In a vector transmission experiment within an experimental olive seedling population, *X. fastidiosa* subsp. *pauca* spread faster (i.e., a higher proportion of plants infected during the same access period) under controlled conditions than under seminatural conditions, and faster in autumn than in summer. The observed differential spread rate could be due to several environmental and experimental variables, for example, the more constant climatic variables present under controlled conditions may favor a longer survival, a higher mobility propensity, or differences in individual inoculation rates. Indeed, the faster *X. fastidiosa* subsp. *pauca* spread rate in fall seems to correspond to a higher propensity and frequency of movement by *P. spumarius* adults late in the season, as observed in the dispersal studies conducted by Casarin et al. (2023) and Lago et al. (2021a) (see Movement Capabilities and Dispersal Ecology section). However, the drivers of variability of *X. fastidiosa* subsp. *pauca* transmission efficiency are still a matter of speculation, and further studies are needed to identify them and their role in disease epidemics. Such knowledge is crucial, considering the important effects of climate, seasonality, and water stress of host plants on vector transmission and epidemiology observed in other *X. fastidiosa* pathosystems (Daugherty and Almeida 2019; Daugherty et al. 2009, 2017; Del Cid et al. 2018).

Alternative host plants for both the bacterium and the insect vectors may play pivotal roles in the spread of *X. fastidiosa*, thereby potentially hampering the success of control strategies applied to crops and target agroecosystems, even though the OQDS epidemic seems to have been mainly driven by a secondary (olive-to-olive) spread (Cornara et al. 2017b). It is thus important to elucidate the transmission capabilities of polyphagous insect vectors, such as *P. spumarius*, from and to alternative host plant species. Experiments have been conducted under controlled conditions to test the acquisition efficiency from several naturally infected plant species. Insect vectors acquiring *X. fastidiosa* subsp. *pauca* from milkwort, almond, and cherry are competent for *X. fastidiosa* subsp. *pauca* inoculation of recipient plants (periwinkle) (Table 1). Oleander and *Acacia saligna* may instead be partial sink plants, that is, *P. spumarius* can inoculate them and occasionally acquire *X. fastidiosa* subsp. *pauca* from them, but is then unable to successfully re-inoculate

**TABLE 1**  
**Collection and summary of data on *Xylella fastidiosa* transmission biology, bionomics, and dispersal capabilities of *Philaenus spumarius* from relevant studies carried out in Apulia, Italy, and Europe**

Transmission biology	Apulia <sup>a</sup>	Italy	Europe	References
Natural <i>X. fastidiosa</i> prevalence (%)	15–70		Corsica: 12.5–34.4 Spain (Balearic): 20.8–27.3	Cavaliere et al. 2019; Cornara et al. 2017a; Cruaud et al. 2018; Farigoule et al. 2022; López-Mercadal et al. 2021
Seasonality	10–25 in May 50–70 (100) in summer			Cavaliere et al. 2019; Cornara et al. 2017b
Acquisition rate (%)				
Olive (field)	15–20 to 60–80			Cavaliere et al. 2019; Cornara et al. 2017a, b
Milkwort	21–50			Cavaliere et al. 2019; Cornara et al. 2017a
Almond	23			Cornara et al. 2017a
Oleander	20			Cornara et al. 2017a, b
Periwinkle	0–20			Bodino et al. 2022; Cornara et al. 2017a
Grape	0			Cornara et al. 2017a
Inoculation rate (%) <sup>b</sup>				
Olive seedlings	6–11 (3.1–5.6) [4]			Cavaliere et al. 2019; Cornara et al. 2017a, b
Oleander	0 (from oleander) [7.8–12]			Cornara et al. 2017a, b
Periwinkle	37.6 (from periwinkle) 5 [0–3.9]			Bodino et al. 2022; Cornara et al. 2017a, b
Almond/stone fruit	0 7.6 (from almond)			Cornara et al. 2017a, b
Milkwort	4.9 7.9 (from milkwort)			Cavaliere et al. 2019; Cornara et al. 2017a, b
Grape	0			Cornara et al. 2017b; Moralejo et al. 2019
Bionomics				
DD nymphal peak <sup>c</sup>	180–369	267–294		Bodino et al. 2019
DD adult emergence <sup>c</sup>	278–547	273–626		Bodino et al. 2019
Nymphal density (individuals/m <sup>2</sup> ) <sup>d</sup>	5–40	Liguria: 31–68 Basilicata: 3–15 Trentino: 3.5–12.4	Spain: 2–3.5 Portugal: 0.8–30	Avosani et al. 2022; Bodino et al. 2019; Morente et al. 2018; Trotta et al. 2021; Villa et al. 2020
Adult density (individuals/sweep) <sup>d</sup>				
Seasonal peaks				
Olive	0.15–0.7	0.1–0.15		
Weeds	0.05–0.5	0.3–0.75		
Wild woody hosts	0.05–0.45	0.04–0.15		

(Continued on next page)

<sup>a</sup> Data in square brackets are from inoculation trial using naturally infected *P. spumarius* individuals. Inoculation rate data are from insects acquiring from olive trees, unless otherwise stated.

<sup>b</sup> Inoculation rate (efficiency) = % of plants infected by single *X. fastidiosa*-positive insect per day, calculated by the formula adapted from Swallow (1985):

$$E = 1 - (1 - \alpha)^{1 / (\frac{\beta k}{n})}$$

in which  $\alpha$  = proportion of infected plants,  $\beta$  = proportion of infectious insects,  $k$  = number of individuals used per tested plants, and  $n$  = duration of inoculation access period (IAP) in days.

<sup>c</sup> 10°C threshold.

<sup>d</sup> Density data were, when needed, transformed from the original data into individuals/m<sup>2</sup> (nymphs) or individuals/sweep (adults); transformation of adult sampling data to a real density (number on a given surface) was not attempted, as the surface actually sampled by a sweep net may greatly vary based on operator, vegetation type, and status.

other recipient plants with the bacterium. *P. spumarius* naturally infected or fed on field-infected olive trees can successfully inoculate oleander, milkwort, periwinkle, and citrus with *X. fastidiosa* subsp. *pauca* (Table 1). No successful inoculations have been recorded for grape, almond, or cherry (Cavaliere et al. 2019; Cornara et al. 2017a).

Some other xylem sap-feeding insects are present in Apulian olive groves, although usually at lower densities than *P. spumarius*, and/or rarely on olive canopies (see the dedicated section below). The spittlebug *P. italosignus* can reach relatively high densities in olive groves whose herbaceous cover is dominated by its nymphal host plant, asphodel (*Asphodelus* spp.) (Panzavolta et al. 2019). Although it is able to acquire *X. fastidiosa* subsp. *pauca* from field-infected olives with a similar efficiency to *P. spumarius* (16 to 24%), its inoculation efficiency for olives is much lower than that of *P. spumarius* (1.6 to 2.1%). The spittlebug *N. campestris* shows low acquisition (5 to 10%) and inoculation (0 to 2%) rates on olive (Cavaliere et al. 2019). Other (occasional) xylem-sap feeders have seldom been able to acquire *X. fastidiosa* subsp. *pauca* in field or controlled trials—that is, cicadas (*Cicada orni* L. [Hemiptera: Cicadidae]: 0.6 to 1.8%), leafhoppers (*Euscelis variegatus* Kirschbaum [Hemiptera: Cicadellidae]: up to 40%), and Issidae (*Latilica tunetana* [Matsumura] [Hemiptera: Issidae]: 2.7%)—but they have never successfully inoculated the bacterium to recipient plants (Ben Moussa et al. 2016; Cavaliere et al. 2019; Cornara et al. 2020b; Elbeaino et al. 2014).

The only widespread and locally abundant sharpshooter species in Europe is *Cicadella viridis* (L.) (Cornara et al. 2019; Nickel 2003). Preliminary experiments performed in Apulia showed that this sharpshooter may seldom acquire *X. fastidiosa* subsp. *pauca* from a few experimental plant species (myrtle-leaf milkwort, lavender), and never from olive tree or alfalfa, while only a single transmission event has been reported from milkwort to periwinkle (Bodino et al. 2022). The sharpshooter *Draeculacephala robinsoni* Hamilton—a potential *X. fastidiosa* vector—has recently been reported to have a limited distribution in France and Spain (Rösch et al. 2022). In short, despite the presence of other xylem-sap feed-

ers, only *P. spumarius* currently seems to transmit *X. fastidiosa* subsp. *pauca* at epidemiologically significant levels in the Apulian pathosystems.

## *X. fastidiosa* Load in Vectors

The size of the *X. fastidiosa* population in a vector's foregut is to some extent related to transmission success, although the causal link between these two parameters is still being debated (Almeida and Purcell 2003, 2006; Bodino et al. 2021b; Cornara et al. 2016). Indeed, transmission events can also occur from vectors with a low number of *X. fastidiosa* cells in their foregut (Almeida and Purcell 2003; Severin 1950). Many research efforts have been dedicated to deciphering the molecular mechanisms of adhesion of *X. fastidiosa* on foregut walls as a prerequisite to reducing their transmission capabilities (Bossi Esteves et al. 2020; Feitosa-Junior et al. 2022; Killiny and Almeida 2009; Killiny et al. 2012; Labroussaa et al. 2016, 2017).

An *X. fastidiosa* population in *P. spumarius* can reach an average size comparable with those observed in sharpshooter vectors, that is,  $10^4$  cells, as also predicted from anatomic and physiological studies comparing *P. spumarius* and *Graphocephala atropunctata* (Signoret) (Bodino et al. 2021b; Ranieri et al. 2020). However, the median bacterial load is usually higher in the foregut of sharpshooters, where it often reaches  $10^5$  cells (Almeida and Purcell 2003; Hill and Purcell 1995; Killiny and Almeida 2009). Some preliminary results on *P. spumarius* reported significantly lower *X. fastidiosa* populations ( $10^2$  cells) (Cavaliere et al. 2019; Cornara et al. 2017b), but these were probably due to both methodological differences in the acquisition trials and to the PCR tests being performed after short times post-acquisition only, thereby not allowing enough time for the growth of the bacterial population. Indeed, the size of the *X. fastidiosa* population in *P. spumarius* tends to increase from  $10^2$  to  $10^3$  to  $10^4$  cells during the first 2 to 3 weeks after acquisition and then reaches a plateau (Bodino et al. 2021b). The *X. fastidiosa* population in *P. spumarius* vectors (i.e., number of bacterial cells) can influence the successful inoculation rate, with insects having

**TABLE 1**  
(Continued from previous page)

Transmission biology	Apulia <sup>a</sup>	Italy	Europe	References
Dispersal				
Nymphs	No significant dispersal capabilities avg. 38 cm (max. 89 cm) in 20 min—60 cm max.			Albre et al. 2021; Halkka et al. 1967
Adult				
Diffusion coefficient	166.3	306.1 (ground cover)		Bodino et al. 2021a
Distance (m)				
Actual recapture (max.)	120 (olive canopy) 155 (ground cover)	200 (ground cover)	Belgium: 32	Bodino et al. 2021a; Casarin et al. 2023
Model daily (median)	26	35	Belgium: 1.5	Bodino et al. 2021a; Casarin et al. 2023
Model tot life (mean)	374	507		Bodino et al. 2021a
Model tot life (max., 98% CI)	748	1,014		Bodino et al. 2021a
Flight mill: Single flight (mean)			Spain: 460 Belgium: 102	Casarin et al. 2023; Lago et al. 2021a
Flight mill: Single flight (max.)			Spain: 5,468 (326 min) Belgium: 1,542 (150 min)	Casarin et al. 2023; Lago et al. 2021a
Flight propensity (%)			Spain: 57–62.5 Belgium: 20–47	Casarin et al. 2023; Lago et al. 2021a
Speed (mean) (m/s)			Spain: 0.24 Belgium: 0.01	Casarin et al. 2023; Lago et al. 2021a

higher bacterial populations in the foregut being more likely to inoculate the pathogen to recipient plants. An increase of one order of magnitude ( $10^2$  to  $10^3$ ) in the average *X. fastidiosa* load of inoculative *P. spumarius* leads to a significant increase (greater than threefold) in the likelihood of a successful transmission. Similar results have been reported for *P. spumarius* transmitting *X. fastidiosa* subsp. *fastidiosa* to grapevine in California (Cornara et al. 2016).

### *X. fastidiosa* Load in Source Plants

The size and distribution of an *X. fastidiosa* population in source plants affect the acquisition efficiency in sharpshooters to a great extent (Hill and Purcell 1997). However, there is still a lack of information regarding the acquisition efficiency of the *X. fastidiosa* population in source plants for European pathosystems. Bodino et al. (2021b) found that differences in *X. fastidiosa*-positive *P. spumarius* after acquisition could not be related to differences in the *X. fastidiosa* loads in source olive plants, because the latter were similar across the seasons. Indeed, given the difficulties involved in isolating growing cells from olives, the estimation of the bacterial population is but an indirect estimation performed by quantitative PCR, which provides no differentiation between DNA of viable and nonviable bacterial cells. However, significant differences in acquisition efficiency were found when spittlebugs were confined to olive trees of susceptible or resistant cultivars (Cavaliere et al. 2021), the latter of which are known to harbor lower bacterial populations (Giampetruzzi et al. 2020).

### Feeding Behavior

The feeding behavior and preferential plant choice of vectors play a direct role in transmission of *X. fastidiosa*, influencing the probability of a vector transmitting the pathogen to recipient plants. Mouthparts movements probably affect—together with the flow velocity in the foregut—the success of *X. fastidiosa* cell acquisition, retention, and inoculation (Backus and Shih 2020; Cornara et al. 2020a; Ranieri et al. 2020).

Experiments using electrical penetration graph techniques have shown that *X. fastidiosa* subsp. *pauca*-infected *P. spumarius* individuals differed for some feeding behaviors from healthy individuals (Cornara et al. 2018b, 2020a). In fact, *X. fastidiosa*-positive individuals performed fewer sustained ingestions and consequently had a shorter xylem ingestion and longer non-probing period, and they required a longer time to perform the first probe. Such behaviors suggest infective *P. spumarius* individuals may have some difficulties in feeding, possibly caused by a partial obstruction of the food canal (Cornara et al. 2020a). Indeed, the potential physical reduction in volume and the corresponding higher sap-sucking flow velocity tend to significantly increase the net pressure needed to maintain the flow in the precibarium, even though this effect seems more relevant for a sharpshooter (*G. atropunctata*) than for *P. spumarius* (Ranieri et al. 2020). Cornara et al. (2020a) also noted a specific behavior (named *Xe*) associated with the inoculation of *X. fastidiosa* that may be linked to egestion due to the fluttering of the precibarial valve caused by a phagostimulation failure. This feeding pattern was unusual on olive, but it can occur after a short feeding time (a few minutes), partly explaining the somewhat inefficient *X. fastidiosa* transmission of *P. spumarius* and the modest effect of longer inoculation periods on the transmission rates observed during transmission trials.

The feeding behavior of sap-sucking insects can change dramatically because of many variables, for example, host plant species, cultivar, control strategies, daytime/season, environmental and climatic conditions (Brodbeck et al. 2011; Krugner et al. 2012; Lago et al. 2022; Miranda et al. 2013). No information is yet available on the variation of feeding behavior of *P. spumarius* on different olive cultivars or for different periods of the year or for plants with

different water-stress status, although such variations may have a significant impact on transmission capabilities and possibly on *X. fastidiosa* subsp. *pauca* epidemiology in the olive groves in Apulia.

Finally, conditional plant choice by insect vector, for both inoculation and acquisition, can significantly impact the transmission efficiency at the population level. Sharpshooter vectors in American pathosystems tend to prefer fully irrigated and asymptomatic plants, which could lead to significant epidemiological outcomes, for example, an increase in the encounter rate with healthy plant hosts, resulting in a faster spread of the bacterium throughout the agroecosystem (Daugherty et al. 2011; Del Cid et al. 2018). To the best of our knowledge, no studies have been carried out in European *X. fastidiosa* pathosystems to investigate similar effects.

### Biological Traits

Deciphering the biology of spittlebugs in olive groves has been one of the research priorities since the first infected spittlebugs were found in the Apulian region (Saponari et al. 2014, 2016). The bionomics, life cycle, and spatiotemporal density of insect vectors on both crops and other agroecosystem vegetation compartments are key issues for understanding the epidemiological dynamics of *X. fastidiosa* (Almeida et al. 2005; Jeger and Bragard 2018). Consequently, several surveys have been conducted on the biology and ecology of spittlebugs in Europe in recent years (Albre et al. 2021; Antonatos et al. 2019; Bodino et al. 2019; Di Serio et al. 2019; Dongiovanni et al. 2019; Hasbroucq et al. 2020; Morente et al. 2018; Villa et al. 2020). Here, we only highlight the most important data on the biology of the vectors that are relevant for the Apulian epidemic, while a wider collection on the bionomics of *P. spumarius* and other *X. fastidiosa* vectors can be found in Cornara et al. (2018a, 2019).

#### *P. spumarius*

European true spittlebugs (Hemiptera: Aphrophoridae) are typically univoltine (one generation per year), overwintering as egg. They present five nymphal instars that develop on host plants protected by a characteristic foam that forms a protective barrier against predation, dehydration, and solar radiation (Chen et al. 2018; Halkka et al. 1967; Henderson et al. 1990; Whittaker 1970). In the Mediterranean area, nymphal instars of *P. spumarius* emerge in February/March from eggs oviposited during the previous fall on dead plant material (Weaver and King 1954). The nymphal population peak is observed in early/mid-April (Bodino et al. 2019). The density of *P. spumarius* nymphs in Apulian olive groves varies greatly from locality to locality and over the sampling years, with a maximum average density during the population peak of about 40 nymphs/m<sup>2</sup> (Table 1).

Early adults emerge in late April/early May, and reach high densities on herbaceous cover, that is, up to 0.5 individuals/sweep (entomological sweep net, about 40-cm diameter). The adult population then colonizes the crop canopy, reaching high densities on olive trees 2 to 3 weeks after emergence (late May/early June). The spittlebug density on olive trees peaks at 0.15 individuals/sweep (Bodino et al. 2019; Cavaliere et al. 2019), although, average densities as high as 0.7 individuals/sweep can be reached in some cases (Cornara et al. 2017b). Spittlebug abundance within olive groves is generally low during the summer period, especially on the ground cover, where it often occurs that no insects are sampled from late June to September, likely due to the desiccation of herbaceous vegetation. The number of spittlebugs on olive trees also decreases steeply in the summer period to well below 0.1 individuals/sweep. In some olive groves, wild woody host plants represent an important reservoir for spittlebugs in summer, with densities often greater than 0.1 to 0.2 individuals/sweep, especially during June and July.

*P. spumarius* adults are sampled at higher densities in the fall than in the summer period, especially on ground cover (up to 0.45 individuals/sweep) (Bodino et al. 2019; Cornara et al. 2017b). This is likely due to the oviposition behavior of females, who lay eggs at the ground level on straw, stubble, or other dead plant material, usually between two apposed surfaces (Weaver and King 1954). During the oviposition period (October to November), sex ratio is female-biased ( $\approx 0.55$  to  $0.75$ ), that is, most of the individuals present in the olive agroecosystem are potentially ovipositing females, with an estimated female density on herbaceous cover from 0.05 to 0.37 individuals/sweep.

A similar life cycle has been confirmed in several Mediterranean areas, although generally lower spittlebug densities have been observed, particularly in Spanish olive groves (López-Mercadal et al. 2021; Morente et al. 2018; Tsagkarakis et al. 2018). A potentially important epidemiological aspect has been observed in olive groves in northern Italy (Liguria region), where an extended period of the presence of adult *P. spumarius* on olive canopies was recorded over 3 months (from June to early September) compared with the 1- to 2-month visiting period registered in Apulia during the same study (Bodino et al. 2019). If confirmed—as other studies in the Trentino region in Italy suggest, see Avosani et al. (2022)—a longer time frame for the vectors' presence on olive trees could be a key parameter in epidemic dynamics of potential *X. fastidiosa* foci in northern Mediterranean areas.

*P. spumarius* is an extremely polyphagous insect, with a host plant range that probably exceeds 1,000 species from several botanical families (Cornara et al. 2018a; Stewart and Lees 1996; Weaver and King 1954; Yurtsever 2000). In Apulian olive groves, *P. spumarius* nymphal stages may be found on most of the plant species commonly present in herbaceous ground cover. However, some patterns of preferential selection have been highlighted, that is, density of insects was higher on some plant taxa compared with their relative abundance in the sampled area (Bodino et al. 2020; Dongiovanni et al. 2019). *P. spumarius* nymphs were sampled on about 50 plant genera in olive groves, mostly belonging to the Asteraceae and Fabaceae botanical families. The plant genera hosting the highest number of nymphs were *Picris*, *Sonchus*, and *Crepis* (Asteraceae) and *Medicago*, *Trifolium*, and *Vicia* (Fabaceae). Conversely, other botanical families, such as Brassicaceae, Paveraceae, Fumariaceae, and Chenopodiaceae, were negatively selected, that is, avoided.

To the best of our knowledge, no information is available on the preferential distribution of spittlebug adults on ground cover in Europe. The *P. spumarius* adult stage is frequently and locally abundant on wild woody plants, especially in early summer (Bodino et al. 2019). Some woody plant species seem to be preferentially selected, such as oaks (*Quercus* spp.) and mastich (*Pistacia lentiscus* L., *Pistacia terebinthus* L.) (Bodino et al. 2020; Cornara et al. 2021). The seasonal dynamics of wild woody host plant selection may also be influenced by variations in the xylem-sap nutrient content, which is affected in different ways by temperature and drought stress in diverse plant species (Brodbeck et al. 1990, 2011). Spittlebugs in particular seem to be preferentially associated with ectomycorrhizal-associated trees, given their enhanced levels of nitrogen, and thus organic compounds, in the xylem (Thompson 2022).

### *N. campestris*

*N. campestris* is a common and locally abundant species in Apulian olive groves; its nymphal instars are mainly associated with Poaceae (Bodino et al. 2020; Cornara et al. 2019; Whittaker 1965). *N. campestris* shows seasonal phenology and population dynamics similar to those of *P. spumarius* in Apulian olive groves. Indeed, the nymphal stages emerge and develop in the same period as those of *P. spumarius*, although the population peak occurs slightly later (late April/early May). Adults emerge in mid-May and are mostly associated with herbaceous cover, on which they can reach densities

of up to 0.25 individuals/sweep. *N. campestris* adults can be found on olive and other wild woody plants within and in the surroundings of olive groves, especially soon after emergence, but rarely reach densities higher than 0.1 individuals/sweep. The time period during which *N. campestris* frequent olive canopies is shorter than that of *P. spumarius* and is usually restricted to 2 weeks immediately after adult emergence (Bodino et al. 2019). *N. campestris* adults appear to mostly be associated with coniferous plants during the summer months and can move for quite long distances to locate them (Cornara et al. 2019; Di Serio et al. 2019; Morente et al. 2018). The epidemiological outcomes of such medium/long-distance movements should be carefully investigated (see Strona et al. 2020). Given the low transmission efficiency (described previously) and densities recorded on *X. fastidiosa*-susceptible plants, the epidemiological role of this vector species is thought to be negligible in the Apulian epidemic (Cavalieri et al. 2019).

## Movement Capabilities and Dispersal Ecology

The dispersal of the vectors plays a significant role in *X. fastidiosa* spread, as demonstrated for different sharpshooter species in American pathosystems (Blackmer et al. 2006; Coviella et al. 2006; Krugner et al. 2019) and also predicted in Europe by modeling studies (Strona et al. 2020; White et al. 2017). Nonetheless, few studies have investigated the movement and dispersal potentials of *X. fastidiosa* vectors in Europe using two different methodologies—mark-release-recapture (MRR) and flight mill—and providing different estimations.

Bodino et al. (2021a) carried out a dispersal study of *P. spumarius* in olive groves in Apulia using the MRR methodology. *P. spumarius* adult individuals were released onto olive canopies in several separate trials during a 2-year study and then recaptured, using sweep nets, at distances of up to 200 m from the release point. Their dispersal capability was then estimated using a dispersal kernel in which Brownian movement was assumed. The median dispersal capability of *P. spumarius* in olive groves was estimated as 26 m/day, equivalent to a median dispersal of ca. 350 m during the entire adult life. Most of the spittlebug population (98% CI) would remain within 750 m from the release point, although a few individuals could move farther away during the year. Interestingly, in the same study, higher dispersal rates were estimated for *P. spumarius* released in a grassland environment (open space) in northern Italy, that is, 35 m/day, with a 500-m median dispersal throughout adult life.

Casarin et al. (2023) combined data, from both MRR and flight mill experiments performed in Belgium on *P. spumarius* and another spittlebug that is not present in the olive groves in southern Italy, *Aphrophora salicina* (Goeze). Their estimation of *P. spumarius* dispersal was 1.5 m/day, with a maximum distance from the starting point of 20 to 32 m over 100 days. These estimates are much lower than the ones obtained in the Apulian MRR experiments. Conversely, Lago et al. (2021a), testing *P. spumarius* using flight mill in Spain, observed much longer flight distances: an average of 460 m in  $\approx 30$  min, with a maximum of 5 km traveled during a 5-h assay. Moreover, in a previous MRR study carried out in Spain, *N. campestris* adults were recaptured at quite long distances from the release point, that is, up to 2.4 km, 45 days after release (Lago et al. 2021b).

Conditional movement and dispersal by *P. spumarius* were investigated by Lago et al. (2021a) and Casarin et al. (2023). Both studies showed that *P. spumarius* adults display different flight performances according to sex, season/physiological state, and time of day. According to Casarin et al. (2023), females showed a better flight performance than males in the early season, and both female and male adults fly farther soon after emergence compared with later in the season. In a flight mill experiment, *P. spumarius* females traveled longer distances during the night and morning than during the afternoon (Lago et al. 2021a).

## Density and Distribution at Different Spatial Scales

The distribution, presence, and density of spittlebugs are highly variable at different spatial scales, and it is usually difficult to accurately predict the presence and abundance of spittlebugs in a specific location. Dramatic differences in spittlebug density have been observed during entomological surveys in olive groves in different Mediterranean countries. The olive groves located in the *X. fastidiosa* subsp. *pauca* epidemic area in southern Apulia usually show high densities of *P. spumarius* and, on a smaller scale, of *N. campestris*, as described earlier (see “Biological Traits” section). The observed average abundance of spittlebugs observed in olive groves in the Iberian Peninsula (Spain and Portugal) was lower, at both the nymphal and adult stages, and *N. campestris* was locally more abundant than *P. spumarius* (Lopes et al. 2014; Morente et al. 2018; Villa et al. 2020). The adult densities of spittlebugs were generally lower in Greek olive groves than in the Apulian ones, although *P. spumarius* may occasionally reach similar densities on weeds as those registered in Italy, for example, 0.5 individuals/sweep (Antonatos et al. 2019) (Table 1). High densities of spittlebugs—in some cases higher than the ones in Apulia (e.g., 60 nymphs/m<sup>2</sup>, 1.3 adults/sweep) were registered in northern Italian olive groves (Liguria) and vineyards (Piedmont), although the observed spittlebug abundance in a different northern region (Trentino) was generally lower (Avosani et al. 2022; Bodino et al. 2019, 2021c).

Regional surveys of insect vector populations have highlighted that spittlebug densities in Apulian olive groves were among the highest observed at both the Mediterranean and the European level. In fact, the dramatic plant epidemic in Apulia was caused by the introduction of *X. fastidiosa* subsp. *pauca* in an area that has a landscape dominated by susceptible crop plants and very high populations of a competent insect vector. However, it is difficult to clearly assess the differences in spittlebug abundance at a regional/country level, given the high inter-orchard variability, even at short distances, and considering that most surveys have investigated a limited number of sites. Environmental drivers can significantly affect the observed differences in the presence and abundance of spittlebugs, but knowledge about them is still limited, although it is crucial to produce more accurate predictions on the density of vectors and to implement them in epidemiological models of *X. fastidiosa*. The most prominent drivers of the distribution of spittlebugs—and the only ones investigated so far—are considered to be landscape composition/structure and climate.

Few studies have been performed on the effect of the landscape on the distribution and abundance of spittlebugs, and none of them were carried out in the Apulian region. The presence and abundance of *P. spumarius* adults in olive groves in the Abruzzo region in Italy were positively associated with the proportion of olive groves and negatively with that of vineyards at a small spatial scale (125 to 250 m) (Santoiemma et al. 2019). The presence of *P. spumarius* (i.e., detection) in the olive groves and vineyards of the Trentino region in Italy was negatively correlated with the proportion of woodlands in the surroundings at a similar spatial scale (200 m) and positively correlated with weed height (Avosani et al. 2022). The directional movement of the populations of the *P. spumarius* adults in the agricultural landscape in Abruzzo has been found to be high throughout the season between olive groves, quite high during spring and fall from grasslands, and high from woodlands to olive groves in summer and fall (Cappellari et al. 2022). The positive role of woodlands (agroforestry systems, broadleaved and sclerophyllous vegetation) in maintaining a high density level of *P. spumarius* in the landscape has also been observed in southwest Spain, as has a negative correlation with coniferous forests (Godefroid and Durán 2022).

Climate variables may have profound effects on spittlebug populations (Halkka et al. 2006; Whittaker and Tribe 2013). Recent macroclimatic studies using bioclimatic species distribution models

highlighted that (theoretical) distribution of *P. spumarius* is mainly influenced by the maximum temperature in spring and humidity in the fall to winter period (Godefroid et al. 2021). Such models indicate that southern Apulia, like many other relatively moist areas in spring in the Mediterranean region, presents a high level of suitability. Conversely, large areas of Spain are rather unsuitable for *P. spumarius*, which can partially explain the low abundances recorded in different surveys conducted in Spain, as described earlier. However, the present distribution and abundances of *P. spumarius* and other spittlebugs could dramatically shift following the predicted climate change in Europe, given that suitability of the Mediterranean region would on average decrease for these vectors (Godefroid et al. 2021).

## Bioecological Traits of Insect Vectors and Research Perspectives of Paramount Importance for the Management of the *X. fastidiosa* subsp. *pauca* Epidemic

The bioecological characteristics of the key insect vectors may significantly influence disease dynamics (Cator et al. 2020; Daugherty and Almeida 2009; Sicard et al. 2018; Wonham et al. 2006). A limited number of traits usually play a paramount role in driving pathogen transmission and spread; thus, highlighting the key vectors' parameters is crucial to maximize effectiveness of epidemiological models and disease management strategies with limited resources. Here, we have attempted to outline the most important bioecological characteristics of the vectors of the *X. fastidiosa* subsp. *pauca* epidemic in Apulia. The transmission biology parameters of the insect vectors that mainly affect the spread of *X. fastidiosa* subsp. *pauca* in Apulia are (i) natural infectivity of vectors in the epidemic area, (ii) transmission (acquisition/inoculation) efficiency, and (iii) feeding behavior and time spent feeding on crop (Fig. 1).

Data on natural infectivity (i) of *P. spumarius* and other xylem-sap feeders are available for Apulia, although only at a local scale. Natural infectivity currently seems to be decreasing in the epidemic area (V. Cavaliere, unpublished data), although a similar trend should be carefully monitored to be confirmed. Apart from *P. spumarius*, the transmission capabilities of cicadas should also be further investigated, given the high number of cicadas in Apulian olive groves, to confirm the negligible role of these insects in the spread of *X. fastidiosa* subsp. *pauca*, as suggested in the study of Cornara et al. (2020b).

The transmission efficiency (ii), for both acquisition and inoculation, has been investigated for the Apulian pathosystem. However, the drivers of spatiotemporal variability of transmission efficiency are still largely unknown. Apart from the study by Bodino et al. (2021b), no information on the effects on the transmission outcomes of climatic conditions, water stress, plant infection status, or insect behavior—all variables demonstrated to significantly affect several American pathosystems—is available yet for European *X. fastidiosa* epidemics.

The feeding behavior (iii) of *P. spumarius* has recently been studied, and a specific behavior has been co-associated with the inoculation of *X. fastidiosa* (Cornara et al. 2020a). Knowledge on these aspects is far from being conclusive, and experiments based on a larger number of insects might produce significant correlative and causal results. Furthermore, studies on the effects of insecticides on spittlebug feeding and transmission are just beginning (Lago et al. 2022). Clarifying these aspects, as well as those related to the temporal variations in feeding behavior that may be linked to transmission efficiency, could have important consequences from an epidemiological and transmission control perspective.

The biological traits of spittlebugs of paramount importance in the *X. fastidiosa* subsp. *pauca* epidemiology are (i) timing of nymphal peak and adult emergence, (ii) timing and intensity of



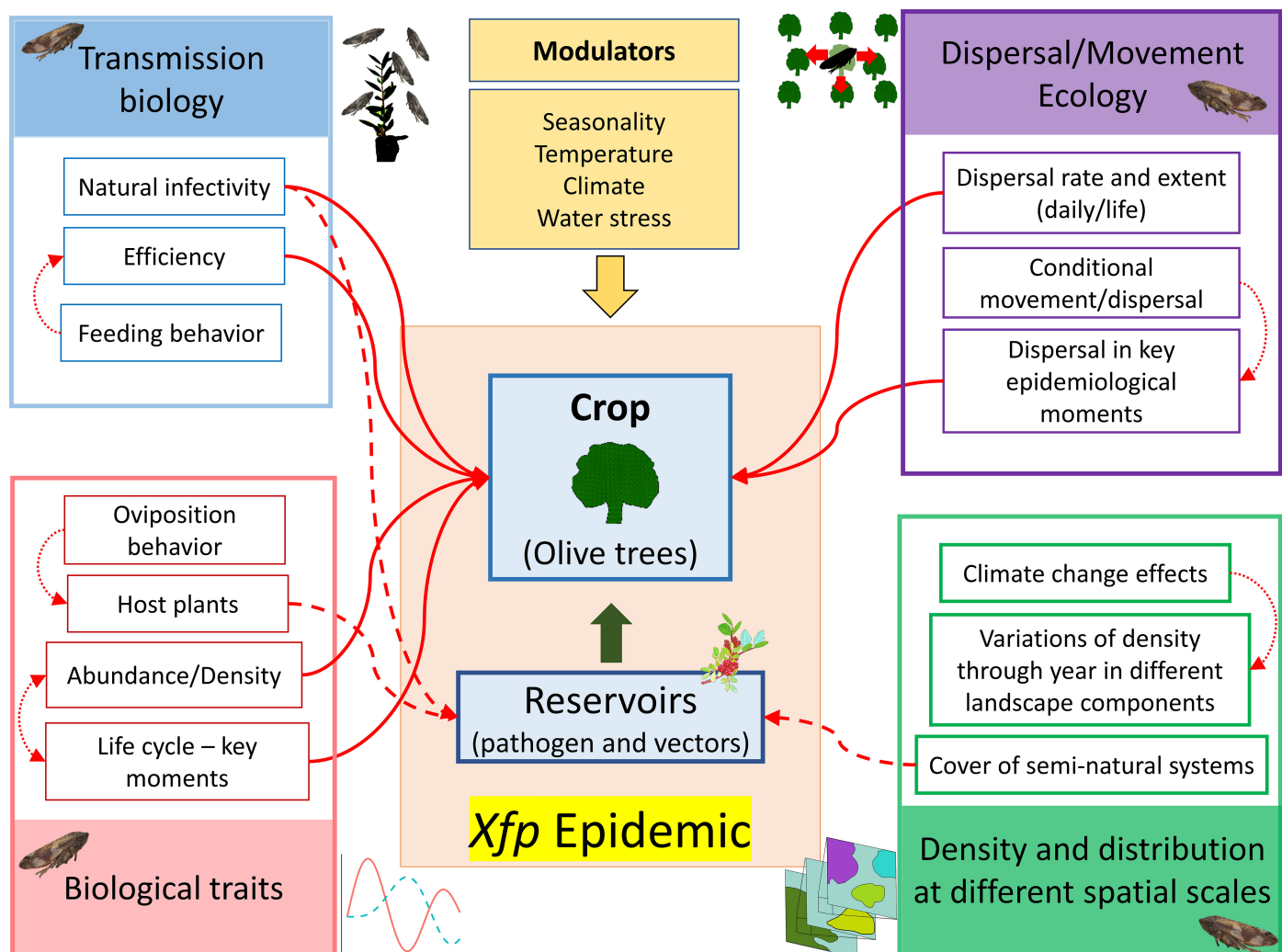
population peaks on olive canopy and on other vegetation compartments in the olive agroecosystem, (iii) timing of oviposition and reproductive behavior, and (iv) presence of weeds and wild woody plants as vector/pathogen reservoirs.

The nymphal peak and adult emergence (i) are key parameters to accurately define the temporal window to achieve effective control strategies targeting the nymphal population, the most susceptible stages, and thus reducing the population size of the adults that emerge in an agroecosystem. The timing and intensity of population density peaks on olive canopy (ii) is a key vector parameter that is directly linked to the transmission and spread of *X. fastidiosa*, and its seasonal pattern should be considered in epidemiological models to derive an accurate average  $R_0$  (basic reproduction number). The olive canopies in Apulia in fact serve as suitable refuge for adults during the first part of the summer, acting as a source of inoculum for a quick *X. fastidiosa* spread, but the spittlebug density on the crop tends to drop in late summer. Moreover, the dynamics of spittlebug density in non-crop reservoirs within or close to olive agroecosystems should be addressed, and their consequences for *X. fastidiosa* subsp. *pauca* epidemiology should be further evaluated (Fig. 1).

The size of the adult female population during the oviposition period, their reproductive behavior, and the oviposition site preferences (iii) determine the number of nymphs that emerge in the

agroecosystem in the following year and thus the interannual population dynamics of insect vectors. No studies have addressed the population dynamics and reproductive behavior of spittlebugs in Apulia. However, *P. spumarius* females in Apulia seem to show lower fertility than those in northern Italy (Di Serio et al. 2019). A similar trend could be associated with the observed absence of the symbiont *Wolbachia* Hertig in *P. spumarius* populations in southern Italy, which are present in the populations in northern Italy, because some strains of *Wolbachia* might be beneficial for the host, as they could increase fecundity (Formisano et al. 2022). This discovery leads to the possibility of exploiting *Wolbachia*, through the incompatible insect technique, for the control of *P. spumarius*, although its feasibility in the field has not yet been explored.

An interesting exploitation of the oviposition site preferences of spittlebugs for population control involves habitat manipulation to implement push–pull management strategies in olive agroecosystems. Morente et al. (2022) showed that, in Spain, some plants (e.g., *Anthriscus cerefolium* [L.] Hoffm., *Sinapis alba* L.) can attract females searching for oviposition sites, but are associated with a low survival rate of nymphs, and could therefore be used as trap crops, while others (e.g., *Diplotaxis tenuifolia* [L.] DC.) are neither chosen for oviposition nor adapted for nymphal development, and could be exploited to create repellent plant covers in olive groves.



**FIGURE 1**

Main biocological traits of vectors affecting the *Xylella fastidiosa* subsp. *pauca* (*Xfp*) epidemic. Arrows depict the most significant vector traits influencing the olive crop (solid line), reservoirs (dashed line), and other insect vector traits (dotted line).

The dispersal parameters of vectors are of paramount importance for *X. fastidiosa* epidemiology (Jeger and Bragard 2018; White et al. 2020). We emphasize a few of these parameters: (i) daily dispersal rate; (ii) total dispersal capabilities of an adult during its entire life; (iii) dispersal during the key transmission periods, for example, in moments of high attraction to olive trees or high transmission efficiency; and (iv) preferential directions of movement and dispersal, as based on seasonal or climatic factors, host plant selection, or on physiological stage throughout the year.

Data regarding the first two parameters are now available for the Apulian olive agroecosystem (Bodino et al. 2021a) (Table 1). However, it is worth noting that other studies on *P. spumarius* dispersal in Europe obtained strikingly different estimates for dispersal capabilities of spittlebugs, reporting both lower and higher dispersal values (Casarin et al. 2023; Lago et al. 2021a). Thus, these estimates should be regarded with caution and only implemented in epidemiological models and control strategies after taking into consideration their high variability. Such high variability is likely due to a plethora of environmental and physiological drivers of spittlebug movement and dispersal that are still largely unexplored (e.g., traits iii and iv). That said, the actual diffusion of *X. fastidiosa* subsp. *pauca* in Apulia is faster ( $\approx 10$  km/year) than even the highest vector dispersal estimates obtained so far (Kottelenberg et al. 2021). Therefore, it is likely that the *X. fastidiosa* epidemic at the regional and country levels is mainly explained by long-range dispersal, which is likely driven by a human-mediated spread (e.g., hitchhiking of infective insects or transportation of *X. fastidiosa*-positive plant material) (Strona et al. 2020; White et al. 2020). These two human-mediated spreading patterns should be studied in depth to clarify their actual contribution to the progress of the epidemic.

The distribution and density of vectors are key parameters for vector-borne epidemiological models, because their presence and abundance drive the spread of the disease (Jeger et al. 2004). These parameters are very variable and difficult to generalize, because of the variability of the vector population levels at different spatial scales (agroecosystem, landscape, regional). The following can be mentioned: (i) high spittlebug densities are present in the southern Apulian olive groves; (ii) spittlebug populations are highly variable across the Mediterranean region and usually lower than those registered in the Apulian olive groves; (iii) the proportion of low-input agricultural (e.g., olive groves in Apulia) or seminatural systems in the landscape tends to increase spittlebug presence and abundance; (iv) the density varies in the landscape across the year, with a high number of spittlebug adults moving between and to olive groves; and (v) climatic variables (winter humidity and spring temperature) drive the presence and abundance of *P. spumarius*, with a possible future significant reduction of optimal areas in the Mediterranean region due to climate change. The current and future changes in cropping systems in the epidemic area should take into account the particular intrinsic features of the Apulian agricultural landscapes and possibly favor management strategies, at different spatial levels, that suppress natural spittlebug populations.

## Conclusions

In this review, we summarized the most relevant data—from an *X. fastidiosa* epidemic perspective—on the bioecological characteristics of *X. fastidiosa* vector species in Europe. Although far from being exhaustive, this work aimed at extracting the most relevant data from the literature and at inserting them into the context of the *X. fastidiosa* subsp. *pauca* epidemic in Apulia and its control.

A decade after its discovery in Italy, *X. fastidiosa* subsp. *pauca* is still spreading in the Apulia region, thus potentially threatening, in the near future, other important olive production areas in the Mediterranean region (Godefroid et al. 2019; Schneider et al. 2020). The current mandatory control strategies involve the removal of in-

fecting plants in the buffer zone and mechanical/chemical control of the insect vectors (EFSA Panel on Plant Health [PLH] et al. 2019; European Union 2020). Despite the effectiveness of the agronomic practices in suppressing the spittlebug nymphal populations in olive groves, the difficulties in the implementation of these interventions at a large-scale and wide regional level are most likely the reason for the scarce impact registered on the reduction of *X. fastidiosa* epidemic spread in the Apulian olive groves (EFSA Panel on Plant Health [PLH] et al. 2019; Kottelenberg et al. 2021; Morelli et al. 2021; Sanna et al. 2021). Changes in the cropping system and the replacement of infected orchards of highly susceptible olive cultivars with resistant ones are currently the most promising strategies to cope with this pathogen, which is now endemic (Saponari et al. 2017, 2019). However, innovative control strategies that target the different components of the pathosystem should be developed, possibly tailored to the specific epidemiological characteristics of the disease in Apulia, which is influenced to a great extent by the local agricultural landscape. An environmental and economically sustainable area-wide suppression of spittlebugs should be pursued from a vector control perspective. Gathering detailed knowledge of the bioecology of insects and its effects on the spread and epidemiology of *X. fastidiosa* subsp. *pauca* is key to developing targeted, timely, and effective control measures against spittlebugs to reduce the incidence and spread of the disease.

Following several European-level research projects, basic and applied knowledge of *X. fastidiosa* epidemiology and insect vectors in the Mediterranean region has greatly increased in the last few years. However, several characteristics pertaining to insect vector biology and ecology—highly relevant for *X. fastidiosa* epidemiology—are still unclear and/or have not been considered in depth as drivers of the spread of *X. fastidiosa*. This in turn means that the bioecology of vectors has not been used enough to inform and develop new integrated and effective control methods. A recent modeling study, in which some of the authors collaborated, has explicitly implemented some biological processes, including some insect vector characteristics, in a mechanistic epidemiological model focused on disease management (Gilioli et al. 2023). We consider this to be a first step in the integration of knowledge on vectors' traits in the control strategies for the *X. fastidiosa* subsp. *pauca* epidemic. We hope that the present compendium of the current state of the art of the research on *X. fastidiosa* subsp. *pauca* vector bionomics will foster attention on the important aspects of insect vector bioecology in an *X. fastidiosa* epidemic context, thereby helping researchers in different fields—even those without particular entomological knowledge, such as epidemiologists, modelers, and experts in integrated pest management strategies—to improve the comprehension and the management of European *X. fastidiosa* pathosystems.

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