



Intruding into a conversation: how behavioral manipulation could support management of *Xylella fastidiosa* and its insect vectors

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Abstract

Behavioral manipulation (BM) is a multimodal control approach based on the interference with the stimuli mediating insect perception and interaction with the surroundings. BM could represent a win–win strategy for the management of vector-borne plant pathogens as the bacterium *Xylella fastidiosa*, since it could reduce the number of vectors alighting on host plants and, consequently, the chances for transmission to occur. In this review, we summarized current knowledge and highlighted gaps in information on (i) how insect vectors of *X. fastidiosa* in general, and more specifically the meadow spittlebug *Philaenus spumarius*, locate and accept the host plant; and (ii) how behavioral manipulation techniques could be applied to disrupt the vector–host plant interaction. Finally, we discussed how diverse BM strategies could be combined with other integrated pest management tools to protect olive groves from inoculation with the fastidious bacterium.

Keywords Olive · Spittlebugs · Sharpshooters · Transmission · Vector-borne plant pathogens

Introduction

Native to the Americas, the gram-negative, xylem-limited bacterium *Xylella fastidiosa* is a colonizer of both plants and insects and can infect more than 650 plant species (Almeida 2016; Sicard et al. 2018; Morelli et al. 2021).

Xylella fastidiosa is characterized by various phylogenetic clades, each with a limited host range, and only particular bacterial genotypes cause specific plant diseases. The current main grouping comprises the subspecies *fastidiosa*, *multiplex*, and *pauca* (Morelli et al. 2021). The bacterium is transmitted only by xylem-sap feeding insects, such as sharpshooters (Hemiptera: Cicadellidae: Cicadellinae) and spittlebugs (Hemiptera: Aphrophoridae). The inoculation of

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bacterial cells may occur few minutes upon stylets insertion into the host plant tissues and contact with a xylem vessel (Cornara et al. 2020, 2022).

Invasions of new areas and continents largely depend on trade of plant material, and diverse introductions recently resulted in the establishment of *X. fastidiosa* in Europe (Martelli 2016; Strona et al. 2017). The region Apulia, in south-eastern Italy, was the first area of the Old World where a *X. fastidiosa* outbreak was reported; the strain ST53, belonging to the subspecies *pauca*, likely introduced around 2008, was demonstrated to be the causal agent of the olive quick decline syndrome (Saponari et al. 2017; Vanhove et al. 2019). The Italian outbreak could be thought as a “perfect storm” in which the combination of several factors resulted in an unprecedented spread of the fastidious bacterium and the loss of millions of olive trees, and, as a consequence, in economic and social turmoil. Firstly, *X. fastidiosa* was accidentally introduced into an environment (Apulia) where a native, competent, and polyphagous vector, the meadow spittlebug *Philaenus spumarius* (L.) (Hemiptera Aphrophoridae), is very abundant (Cornara et al. 2018a). Secondly, olive trees, hosts of both the spittlebug and the strain ST53, cover the area, forming an almost continuous forest interspersed with Mediterranean maquis sheltering the vectors during hot and dry summers (Cornara et al. 2018a; Bodino et al. 2019). Thirdly, pest management efforts were belated because symptoms of the disease can show one-to-two years after infection and due to the difficulties in uprooting infected trees, which represent a cultural heritage for the local residents (Almeida et al. 2019; Saponari et al. 2019). Currently, the main control strategies against *P. spumarius* in olive orchards consist in tilling, which is aimed at reducing the herbaceous cover hosting the spittlebug juveniles, and in mandatory pesticide applications (Saponari et al. 2017, 2019; Lago et al. 2021, 2022). Notwithstanding these efforts, *X. fastidiosa* infections continue to expand, with a yearly rate of movement of the invasion front of about 10 km, leaving devastation in its wake (Saponari et al. 2019). As a fact, the bacterium is causing immeasurable environmental losses and is rapidly accelerating the desertification of the region, due to tree removal and drawbacks of vector control measures, which pose a risk to biodiversity (Sánchez-Bayo and Wyckhuys 2019; Ali et al. 2021). New strategies that do not threaten the environment and that should be compatible with other integrated pest management techniques are urgently needed for the long-term management of the bacterium and its vector.

As mentioned above, *X. fastidiosa* can be theoretically transmitted by any xylem feeder, but the relevance of a vector in the bacterium epidemiology depends on its ecological attributes (e.g., vector density, distribution and dispersal), among which host selection plays a pivotal role. By understanding the stimuli underlying the behaviors leading to host

plant location and acceptance by the insect vector, it would be possible to develop behavioral control strategies aimed at disrupting one or more aspects of these processes (Foster and Harris 1997; Mazzoni and Anfora 2021). Behavioral manipulation could represent a win–win strategy in the fight against *X. fastidiosa* because it could decrease both the vector-borne spread of the bacterium and reliance on pesticides (Mazzoni and Anfora 2021).

In this review, we summarize current knowledge and highlight information gaps on i) how insect vectors of *X. fastidiosa* in general, and more specifically the meadow spittlebug *Philaenus spumarius*, locate and accept the host plant; and ii) how behavioral manipulation techniques could be applied to disrupt the vector–host plant interaction.

Introducing behavioral manipulation

Behavioral manipulation (BM) methods for pest control are based on techniques aimed at interfering with crucial behaviors of target pests, in order to reduce their impact on crop production (Foster and Harris 1997; Cowles 2004; Gut et al. 2004; Mazzoni and Anfora 2021). BM may affect both intra- and interspecific communication; typical examples of it are semiochemical-based techniques such as mating disruption, which is largely adopted to control a wide range of crop pests (Benelli et al. 2019; Cardé 2021; Nieri et al. 2022). Usually, BM strategies do not eradicate the pest, but tend to reduce the density of its population, decreasing direct damages to crops and/or the transmission of vector-borne pathogens (Hooks and Fereres 2006). Even if BM does not offer a quick or definitive suppression of pests compared to insecticides, it provides long-term and area-wide control, often lasting throughout the lifecycle of the crop–pest interaction (Foster and Harris 1997; Cowles 2004). In addition, limitations of BM are counterbalanced by its sustainability and compatibility with other pest management strategies, such as biological control (Foster and Harris 1997; Cowles 2004; Pecenka et al. 2021).

Alteration of behaviors related to plant–insect interaction (i.e., host finding and feeding) may seem more advantageous than mating disruption, which reduces local populations but does not guarantee plant protection, especially considering potential immigration of pests from outside the crop (Foster and Harris 1997). In the case of vector-borne plant pathogens, BM might reduce the transmission rate by lowering the contacts between the pest and the target crop (Miller and Strickler 1984; Todd and Nault 1990; Cowles 2004; Almeida et al. 2005; Hooks and Fereres 2006; Hu, Mou and Tsai 2020).

In this context, to control a vector-borne bacterium as *X. fastidiosa*, the prerequisite for an efficient BM strategy is knowledge regarding the exogenous and endogenous factors

governing the vector's host plant selection, which can be divided into host finding (thus, orientation and landing) and host acceptance (e.g., probing, feeding and oviposition) (Schoonhoven 1968; Visser 1983, 1986). Intraspecific communication, particularly mating behavior, will be also treated within the present review, since it is crucial to better understand the insect behavioral ecology once landed on the host plant. In this perspective, studying how the pest selects its hosts and communicates can provide insights regarding how to interfere with its landing, settling and permanency on the plant (i.e., by reducing mate and host finding, by impairing feeding by means of vibrational stimuli and/or by genome editing (Mazzoni and Anfora 2021; Salvagnin et al. 2018)).

Host finding

The search for a new host is generally triggered by changes in environmental factors or by modifications of the insect's physiology such as food deprivation or egg maturation. On the other hand, landing is driven by the right stimulus or set of stimuli, which may include abiotic and biotic factors such as host plant-mediated and non-host cues (i.e., wind, rain, the presence of hetero- and conspecifics, etc.) as well as learning (Miller and Strickler 1984; Visser 1986; Bernays 1996; Finch and Collier 2000; Cowles 2004; Hodkinson 2009; Döring 2014). In the last decade, an impressive number of works regarding host finding and acceptance in phytophagous insects has been published. However, information regarding how these insects perceive and evaluate their environment is rather fragmented (Prokopy and Owens 1978, 1983; Todd and Nault 1990; Stenberg and Ericson 2007; Döring 2014). The majority of published works suggests that two main sensory modalities govern this process: vision and olfaction (Prokopy and Owens 1983; Miller and Strickler 1984; Dicke 2000; Beyaert and Hilker 2013; Ben-Yakir et al. 2020). All *X. fastidiosa* competent vectors presumably use semiophysicals (namely, visual and vibrational cues) and semiochemicals (odors) for host finding (Krugner et al. 2019; Nieri et al. 2022). In particular, visual cues are likely critical in host detection, while volatiles and xylem-sap metabolites, are key components of host acceptance.

Vision

Among herbivorous insects (especially auchenorrhynchs), vision is probably the sensory modality driving host localization at long distances. For instance, in the leafhopper *Empoasca vitis*, the suppression of opsin genes within the eyes was sufficient to hinder tropism toward hosts, especially at relatively long distances from the plant (Zhang et al. 2018). Phytophagous insects elaborate visual cues in function of i) their distance from the plant, and ii) their position

in vicinity of the potential host (i.e., nearby or inside the canopy). Thereby, distant plants are presumably perceived as indistinct shapes against the horizon, while, as the insect approaches, the visual quality of the foliage is used to identify hosts and triggers landing. Once inside the crop or the canopy, visual cues such as shape, size, color, brightness and polarization, guide the insect toward the preferred plant and/or structure (Prokopy and Owens 1983). For instance, Moericke (1955) and Kennedy and colleagues (1961) described how insects, in this case aphids, respond to ultraviolet and human-visible light, which govern attack flights or trivial flights involving landing on green plants or long migratory flights, respectively.

Color is a key factor driving host finding and landing in herbivorous insects. Color is composed of different spectral characteristics: hue is the dominant wavelength, brightness the total amount of light reflected, and saturation the spectral purity of the reflected light. Insects may utilize any of these cues in different combinations, and many have true color vision, which is defined as intensity-independent discrimination of objects, based on their spectral properties (Van der Kooi et al. 2021). Yet, the way in which insects perceive colors differs fundamentally from humans (Chittka and Döring 2007). To the best of our knowledge, a systematic understanding of behavioral responses to colors in spittlebugs and related *taxa* is missing, together with data on spectral reflectance of traps used in behavioral experiments. Nonetheless, mechanisms discovered in other hemipteran insects such as aphids (Döring 2014; Döring and Kirchner 2022) may help to guide the interpretation of experiments with spittlebugs or closely related species. This approach may also be used to compare behavioral differences between species, which may be remarkable. For example, green is attractive to most leafhoppers (i.e., *Empoasca* spp.), which prefer bright colors corresponding to young leaves (Zhang et al. 2018; Bian et al. 2020), while whiteflies such as *Bemisia tabaci* prefer yellow (Blackmer and Byrne 1993) and thrips (e.g., *Frankliniella occidentalis*) are extremely sensitive to blue (Blackmer and Byrne 1993; Zhang et al. 2018; Ren et al. 2020). Differences occur even between sexes, as in the leafhopper *Scaphoideus titanus*, in which males are mostly attracted from yellow, while females seem to prefer red, probably because this color recalls the grapevine bark, thus oviposition sites (Mazzoni et al. 2011). This example suggests the presence of another spectral channel (and consequently, receptors), maximally sensitive in the orange or red range. Similar preferences have been observed in some Australian hemipterans as well (Farnier et al. 2014).

Multichromatic vision do not likely play an important role in the discrimination of different plant colors (Prokopy and Owens 1983), considering that many plants share similar spectral characteristics (Farnier et al. 2014). Light, scattered from or transmitted through leaves, is most intense around

500–580 nm, in the green-yellow part of the spectrum, resulting in green-yellow objects being extremely attractive for phytophagous insects seeking for vegetation (Prokopy and Owens 1983). Given that information is currently scarce on behavioral or physiological responses of spittlebugs to this color range, we may only speculate what colored stimuli are used by these insects. For many herbivorous insects, yellow colors indicate young leaves rich in nitrogen, which is a limiting factor in many plants (Mooney and Gulmon 1982). It must be said, however, that yellow leaf color is not necessarily an indicator of high quality (Döring and Kirchner 2022). Future research should therefore assess whether specific spectral properties of leaves of these plants are related to food quality and are consequently relevant for xylem feeders. In this regard, research on behavioral and electrophysiological responses to colors is needed, as it would facilitate the development of new trapping devices for the control of spittlebug and sharpshooter vectors in the field.

In the case of *P. spumarius*, the sole study that investigated the effectiveness of differently colored sticky traps dates back to 1967 and demonstrated that yellow is the most attractive color compared to the others tested, which included white, blue, green, orange, red and pink (it must be noted that these were the colors as perceived by human observers). A low number of *P. spumarius* was recorded on white, blue and pink traps, whereas intermediate numbers were found on green, orange and red traps (Wilson and Shade 1967). However, the yellow sticky traps currently employed in the field do not efficiently trap spittlebugs, especially in olive groves, suggesting that there are other attractive cues (different wavelengths, saturation, shape or factors other than color) involved (Morente et al. 2018). For instance, insects can detect the linear polarization of light, which represents the oscillation of incident photons in a common plane. Light, reflected from the shiny, waxy cuticle of leaves, becomes linearly polarized (Wehner 2001). The observer perceives this light together with the diffuse, unpolarized light, scattered from leaves or reflected through leaves. The ratio between the polarized and unpolarized light depends on the chemical and physical properties of the cuticle and the leaf parenchyma, and it could therefore be used by insects to detect or evaluate potential hosts. For instance, polarized reflections are exploited by butterflies to evaluate and identify host plants (Kelber et al. 2001), in that they choose oviposition sites based on the degree of polarization of reflected light (Blake et al. 2019). Aquatic bugs have photoreceptors optimized for detecting water bodies using polarization vision as well (Schwindt 1984a, 1984b), proving that hemipterans possess a object-directed polarization vision that could be used to select targets.

The life cycle of *P. spumarius* potentially influences the way insects perceive and process visual stimuli, considering that the transition to adulthood means passing from a

sedentary, semiaquatic lifestyle to a dry and free-living one (Halkka et al. 1977; Keskinen and Meyer-Rochow 2004; Cornara et al. 2018a). In this univoltine species, eggs are laid on straw very close to the soil, while nymphs crawl on plants in the surrounding ground cover after hatching. Nymphs likely do not seek specific host plants given that they may thrive on hundreds of herbaceous species, while the production of a watery foam is essential for their survival as it avoids desiccation. The life of the nymph is consequently rather sedentary until adulthood. On the other hand, the adult spittlebug emerges from the foam covered by an exoskeleton protective against sunlight and provided with wings and legs capable of impressive jumps. They are hence ready to explore the outside world and find shelters if the herbaceous cover dries out in summer (Yurtsever 2000; Cornara et al. 2018a; Bodino et al. 2020). In this perspective, the eyes of *P. spumarius* are expected to undergo significant changes during adult molting giving that adults walk, jump and fly to find hosts. They need appropriate visual acuity, achieved during metamorphosis by an increase in size and number of facets within the compound eye. The cornea thickens and the rhabdoms become thinner, making the adult eyes tougher and improving vision compared to juveniles (Keskinen and Meyer-Rochow 2004). Nothing is known, however, about how *P. spumarius* eyes respond to specific visual requirements, and what stimuli, attractive or repellant, might be involved in orientation and behavioral changes.

If visual cues are pivotal, repellant stimuli could be used to reduce host finding by the spittlebug and integrated with attractive stimuli to develop push-and-pull strategies. Some plant species evolve resistant traits that help reduce detection by pests, even when this implies a lower reflection of optimum light wavelengths. For example, plants can reduce aphid landing by reflecting wavelengths other than the yellow or green—in the UV spectrum—or by producing waxless and glossy leaves (Eigenbrode and Espelie 1995; Stapleton and Summers 2002; Moharramipour et al. 1997; Smith and Chuang 2014).

Visual background appearance is another driving force guiding insects toward vegetated ground surfaces that may be used for vector management (Döring and Röhrig 2016). The marked contrast in the light spectrum between plants and soil is attractive to insects, especially when substantial amounts of bare soil surround a plant or a crop (Prokopy and Owens 1978, 1983; A'Brook 1968). A comparable situation occurs in the olive orchards ravaged by *X. fastidiosa* in southern Italy, where the herbaceous cover dries out in summer, leaving olive trees and a few evergreen shrubs surrounded by bare red soil (Fig. 1) (Cornara et al. 2018a; Bodino et al. 2019; Saponari et al. 2019). As noted above, current control techniques aimed at reducing vector populations involve removal of the ground cover in olive orchards.

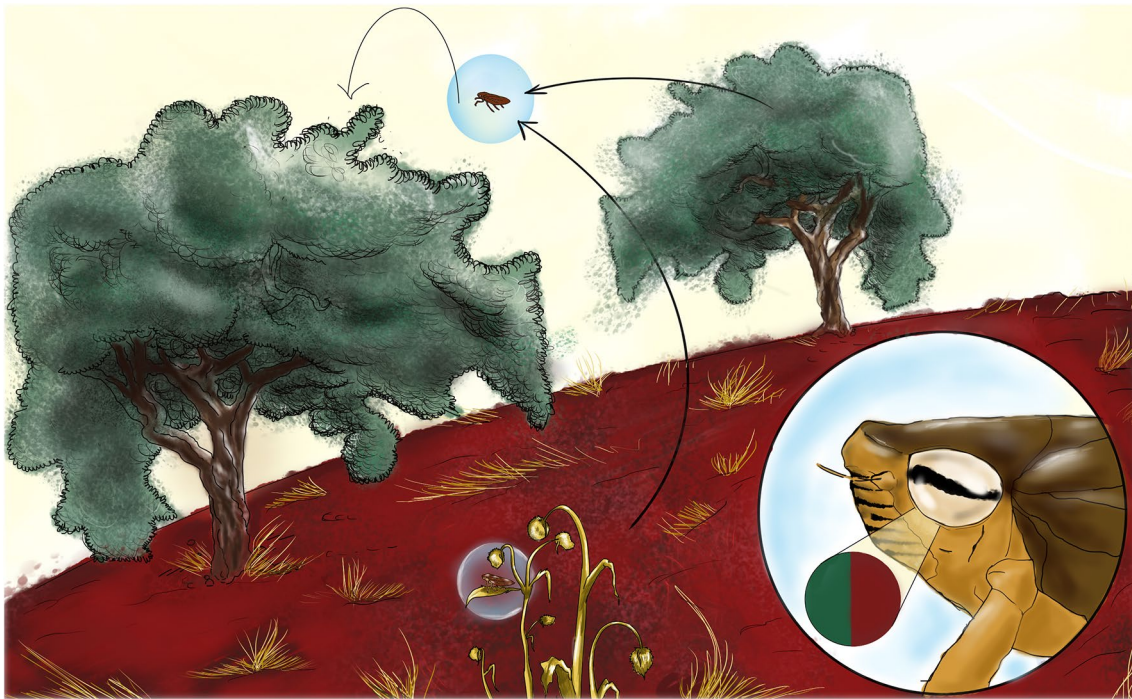


Fig. 1 Visual cues may govern the movement of the spittlebug *Philaenus spumarius* toward olive plants, considering contrast of colors between the red bare soil and the green olive canopy. The spit-

tlebug may move from the drying herbaceous vegetation or from surrounding olive/wild trees

Even if this tillage decreases the number of nymphs developing on the understory, it could potentially increase the risk of attracting adult spittlebugs from outside the orchard. In this regard, even if the dispersal of *P. spumarius* seems limited in olive orchards, it is influenced by several factors, such as agroecosystem structure and landscape composition (Santoemma et al. 2019; Bodino et al. 2021b). As reported by Lago et al. (2022), interplant movements could occur during night or dusk, suggesting that also the time of the day should be considered. Provided that visual stimuli are available for *P. spumarius*, imagine a spittlebug adult searching for a host in proximity of a tilled plot: would not be the leafy and green canopy of an olive tree easy to spot against the red bare soil? Even though this is only a hypothesis, it would be of paramount importance to investigate the role of color background in host localization by this insect, especially considering that similar information could provide novel insights regarding the relation between ground cover removal and spittlebug abundance on olive canopies.

Finally, it has been noted that xylem feeders discriminate against plants showing symptoms of severe water stress and/or of bacterial infection (Marucci et al. 2005; Mizell et al. 2008; Rashed et al. 2011; Daugherty et al. 2011; Krugner et al. 2014). In particular, visual stimuli influence host selection by sharpshooter vectors of *X. fastidiosa* in the Americas, as these insects discriminate against infected grapevines,

which are subjected to water stress and presumably represent a low-quality food source (Daugherty et al. 2011, 2017; Del Cid et al. 2018). *Philaenus spumarius* may show a similar preference, which would affect pathogen acquisition and, consequently, the spread of the olive disease caused by the fastidious bacterium. As pointed out by Daugherty and colleagues (2011), when investigating whether alternate hosts in the field represent pathogen reservoirs, it is important to study how vectors respond to infection in these plant species. In fact, *X. fastidiosa* infection level and symptom severity differ among different host species, and trends in quality over time may influence host phenotype and, as a consequence, vector behaviors (Hill & Purcell 1995; Purcell, 1997; Daugherty et al. 2011, 2017). Considering that *X. fastidiosa*, *H. vitripennis* and *P. spumarius* have broad host ranges (Krugner et al. 2019; Almeida et al. 2005; Cornara et al. 2018a, b), it would be crucial to unveil how infection and symptom expression impact the acceptance of different host plants by vectors. Similar information would, in our opinion, allow to better characterize *X. fastidiosa* epidemiology and develop strategies aimed at reducing vectors landing on host plants.

Olfaction

Plants emit volatile organic compounds (VOCs) that can be detected by phytophagous insects during flight and landing via olfactory receptors on their antennae, or with other sensilla on tarsi and mouthparts (Visser 1986; Andersson et al. 2015). Depending on the species, either host-specific volatiles or specific ratios of ubiquitous plant odors (such as green-leaf volatiles) are used by insects to find preferred hosts (Bruce et al. 2005; Riffell et al. 2009; Bruce and Pickett 2011). Extensive research has proven that odors are crucial components in long- and short-range localization of food sources within insect *taxa* such as Lepidoptera and Diptera, as well among some hemipterans, such as stinkbugs (Pentatomidae). Electrophysiological and behavioral tests on sternorrhynchans such as aphids (Aphidoidea), whiteflies (Aleyrodoidea) and psyllids (Psylloidea) demonstrated not only that odors trigger physiological responses, but also that they influence the orienting behavior of these insects, even if solely at short distances from the plant (Bruce et al. 2005; Coutinho-Abreu et al. 2014).

In contrast, auchenorrhynchans (cicadas, spittlebugs, leaf-, plant- and treehoppers) have small antennae, and most studies suggest that olfaction has little role in mate and host finding, although exceptions have been reported (e.g., Mazzoni et al. 2009; Ranieri et al. 2016; Zhang et al. 2018). For instance, the cixid planthopper *Hyalesthes obsoletus* has sensible sensilla that are finely tuned to perceive preferred hosts (Riolo et al. 2012). In many leafhopper and planthopper species, chemical stimuli such as plant volatiles are similarly associated to host detection, though in most cases odors just increase responsiveness to visual stimuli (Obata et al. 1981; Todd et al. 1990; Cook and Denno 1994; Fereres and Moreno 2009; Mazzoni et al. 2009; Rossi Stacconi et al. 2014; Darshanee et al. 2017; Grange et al. 2017). Enhanced responses to visual cues attributable to plant volatiles have also been observed in the sharpshooter *Homalodisca vitripennis*, a *X. fastidiosa* vector in North America (Patt and Sétamou 2007; Krugner et al. 2019). Among these and other xylem feeders, a variety of cues are presumably used to track the physiological state of host plants and consequently assess whether they can provide adequate nutrients (Mizell and French 1987; Andersen et al. 1992; Brodbeck et al. 1999; Redak et al. 2004).

The evidence produced so far on the relevance of olfactory cues in long- and short-range host plant location by *P. spumarius* is fragmentary and inconclusive. Morphological studies showed that the antennae of *P. spumarius* bear a lower number of antennal sensory structures than leafhoppers and planthoppers (Ranieri et al. 2016). The morphology of *P. spumarius* sensilla suggests that their main function is thermo/hygroreception, notable considering that humidity plays a pivotal role in the life cycle of spittlebugs (Weaver

and King 1954; Tichy and Loftus 1996; Ranieri et al. 2016; Cornara et al. 2018a). At any rate, the general organization of some basiconic and coeloconic sensilla is consistent with an olfactory function (Ranieri et al. 2016), and electroantennographic (EAG) studies confirmed that the antennae of both *P. spumarius* males and females respond to a wide range of VOCs belonging to different chemical classes (Germinara et al. 2017). Recent experiments also proved that spittlebugs are attracted and/or repelled by different aromatic plants, and that the response depends on the sex of the insect and on the distance from the odor source (Ganassi et al. 2020). Cascone and colleagues (2022) observed a negative correlation between the amount of limonene, 3-octanone, camphor, geraniol, and (-)-myrtenol and attractiveness toward *P. spumarius* females. Among EAG-active host plant volatiles, spittlebug females were apparently attracted only by (+)-camphor, cis-3-hexenyl-acetate and cis-3-hexen-1-ol (Anastasaki et al. 2021; Rodrigues et al. 2022). With regard to olive, females were attracted by the blend of VOCs emitted by varieties susceptible to *X. fastidiosa* (Ogliarola, Rotondella and Frantoio) and repelled by a resistant one (FS-17), while males were totally unresponsive (Cascone et al. 2022).

Besides the evidence produced so far, literature on spittlebug species others than *P. spumarius* suggest that there is room for repellent compounds to be found and exploited. The Neotropical spittlebug pest *Mahanarva spectabilis*, for instance, likely used olfactory cues to distinguish among sugarcane cultivars and pasture grasses, both under greenhouse and field conditions. While attractive cultivars were most susceptible to nymphs and adults, volatiles emitted by a resistant cultivar had a repellent effect, suggesting that host suitability may be discriminated through odor cues (Aua and De Resende 2018; Silva et al. 2019). By identifying odors that are less attractive for pest insects, it might be possible to develop resistant varieties emitting repellent volatiles, or to identify plant volatiles that could be used to develop repellent tools. Novel techniques in the field of genome editing may also be employed to protect plants, considering that the plant susceptibility to pest attacks may be reduced by modifying its emission of kairomones, as suggested by Salvagnin and colleagues (2018).

Host acceptance

Despite decades of effort, knowledge on the biochemical and biophysical factors driving the acceptance of host plants by xylem feeders is still scattered. Once on a plant, the insect proceeds through a sequence of brief stereotypical behaviors aimed at discriminating whether the plant could be an acceptable food source or oviposition substrate. Each behavioral step is composed of overlapping fixed action patterns,

and behavioral responses proceeding to completion without sensory feedback are triggered by a specific stimulus or set of stimuli (Backus 1985). Host acceptance therefore depends on a threshold of positive sensory inputs to the central nervous system that triggers stylets insertion (probing) and tasting/testing ingestion and maintains ingestion and swallowing. The factors determining host plant acceptance include i) intensity of olfactory and gustatory feeding stimulants, ii) intensity of deterrents and repellents, iii) metabolic state of the insect, including degree of deprivation of specific dietary factors and iv) learning resulting from previous feeding experience (Fig. 2) (Dethier 1982).

The first step of the acceptance process is exploration of plant after landing. Among piercing-sucking insects, auchenorrhynchans exhibit a unique behavior, namely dabbing (the insect repeatedly touches the plant with the tip of the labium, which bears chemo- and mechanoreceptors). Simultaneously, chemicals in the plant's waxy cuticle solubilize in the

insect's saliva, producing a chemical mixture that is sensed by labial sensilla (Backus 1985). Basiconic sensilla with supposed olfactory function have recently been described on the labium of *P. spumarius* (Ranieri et al. 2020).

Besides chemical cues, the tissue topography of the plant is another essential cue in the process of recognizing a suitable host. While sharpshooters and aphids insert their stylets through flat surfaces, spittlebugs prefer a rounded support to grab with the forelegs, pulling it toward their labium while pushing the stylets in (Cornara et al. 2019). Besides providing stimuli for host recognition and acceptance, the plant anatomy could represent a first line of defense against spittlebug settling. For example, glandular trichomes function as feeding barriers in the case of *P. spumarius* nymphs (Hoffman and McEvoy 1985; Smith and Chuang 2014). On the other hand, once the insect has access to the plant, probing occurs, in that the stylets are inserted into the plant tissues searching for gustatory cues driving ingestion and

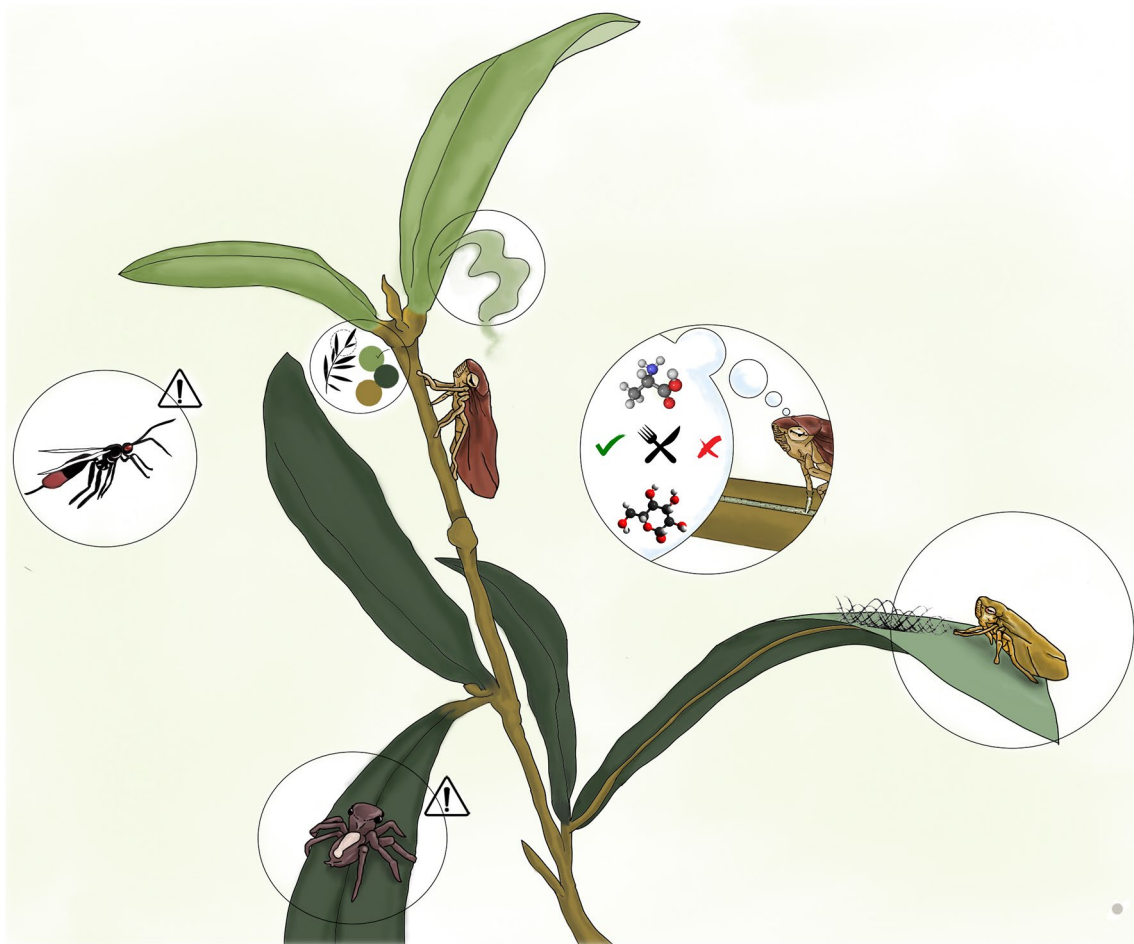


Fig. 2 The image depicts some of the cues that may influence the settling of the spittlebug *Philaenus spumarius* on a plant. Semiochemicals include plant volatiles **A** and composition of the xylem sap **B**, which provide information regarding the suitability of the plant as

food source. Semiophysicals comprise vibrational signals emitted by **C** conspecifics and **D** predators, as well as acoustic signals produced by approaching parasitoids **E** and **F** visual cues such as color and plant structure and shape

final acceptance. It is important to point out that probing and feeding should be considered separate behaviors since each is triggered by a primary set of specific gustatory stimuli (Sogawa 1976). Among *X. fastidiosa* vectors, trial ingestion and sensing/tasting of xylem sap through the sensilla lining the precibarium are pivotal steps underlying host plant acceptance (Backus and McLean 1985; Cornara et al. 2018b; Ranieri et al. 2020). If the plant is not considered an “acceptable host” after probing, the stylets are withdrawn and feeding does not occur.

Precibarial sensilla are crucial for host acceptance as they detect extremely diluted metabolites, such as amino acids, organic acids and sugars, present in the xylem sap (Prokopy and Owens 1983; Miller and Strickler 1984; Visser 1986). The latter is an incredibly challenging food source, given that it is dilute, nutritionally unbalanced and under negative tension. Unique features permit xylem feeders to live on this nutritionally poor diet, including i) capacity of ingesting voluminous throughput; ii) ability of efficiently extracting organic nutrients; iii) assets of symbionts that reprocess the amino acid repertoire; and iv) mechanisms for disposal of excess nitrogen. As an example, large sucking pump (cibarial) muscles allow xylem feeders to process hundreds of body weight equivalents of xylem fluid daily. This high throughput is then secreted from the anus and is used by spittlebugs nymphs to produce the spittle mass, while adults (and nymphs of other species) excrete the liquid as a succession of droplets. The flow is so rapid and evident that sharpshooters owe their name to this behavior. Besides managing the voluminous input of sap, efficient extraction of nutrients is crucial and is accomplished by means of a bypass. The filter chamber, in which the anterior and posterior extremities of the midgut are closely apposed, shuts most xylem sap into the lower reaches of the digestive track. This permits the intestines to extract remaining organic compounds more efficiently, resulting in assimilation of more than 99% of the nutrients (Andersen et al. 1989). In addition, to cope with the fact that xylem-sap organics are dominated by a handful of nonessential amino acids, typically glutamine and asparagine, xylem feeders have evolved close symbiotic relationships with bacteria that convert these compounds into essential amino acids (Ankrah et al. 2020a). The carbon skeletons of these organic nitrogen compounds are source of energy and building blocks for carbohydrates and fats. Overall, these factors enable xylem feeders, despite the low absolute levels of nitrogen in xylem sap, to have a surfeit of nitrogen which they dispose in form of ammonia, a toxic compound. However, diluted ammonia is excreted within the copious fluid output (the process is known as ammonotelism and is common among insects’ aquatic forms) (Ankrah et al. 2020b).

Even if xylem sap is a challenging feeding source, polyphagy and frequent host switching enable xylem feeders to

take advantage of the temporal and spatial dynamic of rapidly changing xylem stream nutrients (Mizell III et al. 2008). Once a xylem vessel is reached and sap flows through the food canal and the precibarium, chemical components of the xylem sap should trigger the ingestion, acting as phagostimulants. Several studies on both sharpshooters and spittlebugs point toward amino acids, particularly the amides glutamine and asparagine, as the main drivers of host plant acceptance, shaping xylem-feeders’ abundance and feeding patterns (Brodbeck et al. 1990; Andersen et al. 1992; Thompson 1994, 2004). Availability and ratios of amides are potentially the most relevant indicators of a host’s nutritional value in xylem feeders and other species as well (Andersen et al. 1992). Glutamine, for instance, is an essential component of insect artificial diets, while asparagine deficiencies likely represent a host resistance mechanism against brown planthoppers (Auclair and Cartier 1963; Mittler 1972). Although not essential, proline can influence feeding preferences as well, because it is presumably indispensable for flying (Weeda et al. 1979).

Xylem feeders have to overcome another obstacle: xylem sap is energetically costly to extract, due to negative pressure within xylem vessels (Raven 1983). Studies on the relationship between xylem-sap tension and feeding in *P. spumarius* suggest that negative tension may not be a limiting factor, as far as the ratio between the volumetric energy density of sap ingested and the energy spent to withdraw and ingest it remains positive. Moreover, cibarial dilator muscles are able to overcome tensions up to -15 bar, well above the normal range of tensions spittlebugs are expected to encounter under field conditions (Bergman et al. 2021). In addition, Beckett et al. (2019) reported that the metabolic rate of actively feeding *P. spumarius* is just 20% greater than during resting, indicating a relatively low cost of xylem-sap extraction. Similarly, xylem tension does not seem to affect the feeding rates of *H. vitripennis*, provided that the nutritional value of the host exceeds the costs of feeding under xylem negative pressures (Brodbeck et al. 1990; Andersen et al. 1992). The net result is that xylem feeders profitably extract the exceptionally large quantities of xylem sap required for adequate nutrition, as attested by their evolutionary success and status as abundant and consequential pests and vectors.

Overall, more precise knowledge of the sensory perception and specific stimuli that mediate feeding may aid plant geneticists in designing cultivars resistant to spittlebugs and sharpshooters. Moreover, the role played by xylem-sap metabolites in shaping host plant acceptance opens the possibility for managing populations of xylem feeders by manipulating exogenous factors (such as water, fertilizers, etc.) that might influence xylem-sap chemistry, potentially reducing the host suitability for the insects.

Substrate-borne vibrational signals as semiophysicals

From a vibrational point of view, plants are noisy environments, where both biotic and abiotic factors provide specific constraints that shape insect communication systems and host preferences (Šturm et al. 2022). Many arthropods use substrate-borne vibrations in combination with other modalities to gather information from the environment, and it is estimated that at least 150,000 insect species rely exclusively on vibrational communication (Virant-Doberlet and Cokl 2004; Cocco and Rodríguez 2005). As noted above, this is the case in Auchenorrhyncha, whose mechanoreceptors are tuned to perceive species-specific signals emitted by co- and heterospecifics (Virant-Doberlet and Cokl 2004; Hill and Wessel 2016). Consequently, substrate-borne vibrations are semiophysicals that travel through plants and convey essential information regarding the environment (e.g., for determining whether the plant is a favorable host for living, feeding, mating and ovipositing), while reducing the risks of being predated (Cocco and Rodríguez 2005; Virant-Doberlet et al. 2019; Nieri et al. 2021).

Given that communication can take place only when signal prevails over noise (Wiley 1983), the signal transmission properties of plants can ultimately influence how insects select and use their hosts (Joyce et al. 2014; Mortimer 2017). In fact, even if wind and rain are ubiquitous sources of abiotic noise, the vibrations that they induce in the plant structure can differ depending on the plant species or even between parts of the same plant (Barth et al. 1988; McVean and Field 1996). A plant influences insect communication not only by conveying noise but also by acting as a signal filter, framing which signal features are transmitted and how (Michelsen et al. 1982; Magal et al. 2000). In some cases, closely related insect species or subspecies have evolved distinct signals as a result of adaptation to host plants with different signal transmission properties (McNett and Cocco 2008). Indeed, such coevolution between insects and plants mechanical features usually occurs in insect specialist species, whose life cycle occurs on the same host (Čokl et al. 2005).

Given the wide and varied nature of their hosts, polyphagous species such as *P. spumarius* are likely not adapted to particular plant structures. While other biotic factors are important in shaping the relationships between the spittlebug and plants, the presence of signaling co- and heterospecifics could be used by *P. spumarius* to evaluate the suitability of plants as hosts, not only as a food source, but also as mating and oviposition sites. In this species, mating success accordingly depends upon the establishment of a vibrational duet between a male and a female, in that female vibrational signals trigger pair formation and guide the male toward

the partner (Avosani et al. 2020). Even so, females call only when sexually mature, thus after the breakage of the ovarian diapause, when eggs start to develop in their ovaries. Depending on the geographical range, the sexual maturity occurs from late summer or autumn until oviposition and death of the female (Avosani et al. 2021b; Cornara et al. 2018a). Given that female signals may influence the persistence of males on plant substrates, especially at the end of summer, they could be used in the framework of BM approaches. Moreover, female could use signals emitted by other females on the same plant to evaluate suitable oviposition sites given that aggregation could be common even among *P. spumarius* adults, and not only among nymphs aggregating and sharing their spittle to enhance their probability of survival (Mangan and Wutz 1983; Wise et al. 2006; Bodino et al. 2021a, b). Even if a recent study indicates a prevailing role of intraspecific volatiles in aggregating ovipositing females (Sevarika et al. 2022), we cannot exclude that vibrational signals could concur to it. Likewise, if vibrational signals could attract or hold spittlebugs on plants, it might be possible to keep infective spittlebugs inside “trap” crops, reducing their movement toward olive trees, especially when applied to plants that are preferred by *P. spumarius*. In this regard, it has been shown that *Lavandula angustifolia* and, in particular, *Taraxacum officinale* are more suitable hosts for spittlebugs nymphs and adults compared to other species common in olive groves (Morente et al. 2022). The authors suggested avoiding the two plant species as ground cover plants in crops vulnerable to *X. fastidiosa*, but there could be room for evaluating them as trap crop, potentially integrating other (e.g., vibrational) stimuli.

Another possible approach is to interfere with the mating communication in order to reduce male–female encounters. Attempt of vibrational mating disruption already proved to be effective in several leafhoppers and planthoppers in laboratory conditions but also at the field level, as in the case of the leafhoppers *S. titanus* and *H. vitripennis* (Krugner and Gordon 2018; Mazzoni et al. 2019, Nieri and Mazzoni 2019, Feng et al. 2022). Similarly, trials conducted under laboratory conditions demonstrated a significant reduction of *P. spumarius* mating when virgin pairs were exposed to synthetic vibrational signals that masked the frequency pattern of the natural mating signals (Avosani et al. 2022). Given the promising results, research should unveil whether the synthetic vibrational signal affects multiple behaviors simultaneously, as in the case of *S. titanus*, in which the disturbance noise used for mating disruption significantly decreased the time spent by males and females on vibrated plants and reduced oviposition (Zaffaroni Caorsi et al. 2022).

These approaches based on vibrations are promising because they manipulate highly conserved communication modalities that mediate behaviors crucial for the species survival, such as reproduction. However, a deep knowledge of

insect phenology in association with the vibrational behavior of the species are required. As mentioned before, in *P. spumarius* vibrational signals have different roles in the course of the summer because females start to be active and sensitive to male signals only in correspondence of the ovariole development (Akassou et al. 2021; Avosani et al. 2021a). For this reason, methods of interference and/or capture are more likely to succeed only if applied in the proper time windows, similarly to semiochemicals in field applications (Suckling 2000a, 2000b).

As mentioned above, the plant is an intricate network of signaling and eavesdropping arthropods, thus an insect has to overcome the noise coming from conspecifics and heterospecifics, while avoiding being detected by unwanted receivers such as predators and parasitoids (Virant-Doberlet et al. 2011, 2019). In some species, vibrations are used to cooperate, while in others to compete, or to mediate spacing (Greenfield 1994, 2014). Though parasitoids and predators can exploit vibrations emitted by preys to locate them, the opposite is also true (Virant-Doberlet et al. 2019): prey can discriminate between approaching predators and non-predators and respond accordingly. Depending on the species, escaping a predator could mean jumping or dropping off the plant, startling the predator, freezing or engaging in warning displays (Tsubaki et al. 2014; Kang et al. 2017; Takanashi et al. 2019). *Philaenus spumarius* is equipped with a large and complex array of abdominal mechanoreceptors that may serve to perceive environmental vibrations (Ehlers et al. 2022). If *P. spumarius* detects predators through vibrations and avoids them by leaving the host plant, similar vibrational signals could be used as repellent stimuli, potentially reducing the suitability of hosts. For instance, nonspecific vibrations (white noise) induce aphids to leave host plants consistently reducing the population density (Parent et al. 2022). A specific signal, such as a predator or an intraspecific distress signal, could be used to develop an effective behavioral manipulation strategy that can overcome the risk of habituation (Foster and Harris 1997), although even predator signals, not coupled with actual threat, could be soon become ineffective, as suggested by Afitto and Thaler (2020). Overall, the combination of attractive and repellent substrate-borne signals could lead to the development of push-and-pull vibrational approaches to reduce the settling of adult spittlebugs into olive trees.

Interestingly, in addition to deterring permanent settlement on the plant, substrate-borne vibrations could affect spittlebugs probing and feeding behaviors, as recently demonstrated by Avosani et al. (2021b). In their pioneering study, vibrational stimuli employed against *P. spumarius* reduced its feeding activity on an herbaceous plant, although the same stimuli had no effect when applied to olive plantlets, probably because the signal was filtered differently by the olives structure. Nonetheless, this proof-of-concept

demonstrated that the spittlebug host acceptance is susceptible to vibrational interference, and paves the way for further research (Avosani et al. 2021b). Considering that *P. spumarius* is a native and abundant species in all the Palearctic region, a feeding deterrent strategy is promising in light of the fight against *X. fastidiosa*, as it could reduce the transmission of the bacterium by lowering the number of vectors feeding on the plant and the contact between insect stylets and plant xylem. The signal used by Avosani and colleagues (2021a) consisted in a modified female distress signal, but it would be interesting to assess whether a fright stimulus, such as vibrations coming from a predator, could be even more effective in deterring feeding or in repelling *P. spumarius* from hosts.

Conclusions

The aim of this review was to outline the primary interactions between host plants and pests that govern attraction toward the host, acceptance and settling, and to suggest approaches to disrupt these interactions in the frame of an integrated pest management strategy. We were particularly interested in profiling environmentally and economically sustainable strategies that could prevent further spread of the bacterium *X. fastidiosa* in Europe based on the interference with the processes governing host finding and settling in its vector, *P. spumarius*.

As mentioned before, the epidemiology of the *X. fastidiosa* depends on the completion of steps (host plant detection, acceptance and feeding) by its insect vectors in order to spread to healthy plants and, consequently, to survive and evolve (Chatterjee et al. 2008; Retchless et al. 2014; Sicard et al. 2018). Transmission of the bacterium is mainly associated with two factors, namely vector transmission efficiency and vector activity, the latter being the combination of the abundance of insect vectors on the host plant and their time of permanence. Considering the transmission of the strain ST53 to olive by the meadow spittlebug, a relatively low efficiency is compensated by high population densities residing on olive canopies for months (Cornara et al. 2017; Bodino et al. 2019, 2021a). Another aspect to consider is that bacterial cells inoculation seems to occur a few minutes after stylets insertion into the host plant and contact with a xylem vessel (Cornara et al. 2020). Therefore, a successful and sustainable strategy aimed at disrupting *X. fastidiosa* transmission and spread should aim at (i) avoiding vector-host plant contact, and (ii) reducing host plant suitability.

Compelling evidence suggests that odors might indeed play a role in host localization by adult spittlebugs, even though developing attractive semiochemicals and trapping devices seems still challenging, considering that more information are needed regarding the candidate compounds'

active space and concentration needed to successfully guide *P. spumarius* toward the odor source (Ranieri et al. 2016; Anastasaki et al. 2021; Cascone et al. 2022; Sevarika et al. 2022). On the other hand, if repellent or deterrent odors are identified (i.e., from emissions of plants unsuitable for *P. spumarius*), there is room for designing push-and-pull techniques, even if practical aspects such as application and persistence of the chemical compounds on the olive canopy and/or coexisting alternative hosts must be ascertained.

Visual stimuli might be essential within host finding and have been greatly neglected in the case of *X. fastidiosa* vectors. For example, yellow sticky traps are inadequate for monitoring *P. spumarius* in olive orchards, especially if insect densities are low (Morente et al. 2018). Instead of focusing on colors as perceived by humans, sticky traps could be improved by changing the shape, the use of contrasting colors, and spectral reflectance relevant for the insects (Farnier et al. 2014). Furthermore, the landscape composition of olive orchards could contribute to orientating *P. spumarius* toward the host plants. In our opinion, it would be crucial to assess whether the contrast between the bare soil and the plant canopy could encourage adult spittlebugs to move toward olive trees and other woody plants when the ground cover is removed. In such scenario, the practice of removing the herbaceous cover to reduce nymphal populations may be a further trigger for spittlebug dispersal toward olive canopies. If this is the case, diverse types of mulches could be tested in olive groves, in order to evaluate if any of them could lower the number of adult spittlebugs landing on olive trees. Mulches within the olive orchards could be for example coupled with colored sticky traps and other attractants designed to draw *P. spumarius* out of the orchards.

Another interesting approach to test is represented by intercropping, since it may potentially reduce the colonization of plants susceptible to *X. fastidiosa* by adult spittlebugs, as the latter could find shelter and feeding sources alternative to olive trees. At any rate, woody hosts that tolerate summer drought, and are not hosts of the bacterium would be the most suitable ones. An additional benefit of intercropping relies on the potential increase in predators and parasitoids within the orchard (Ju et al. 2019), which could enhance biocontrol and/or reduce settling of spittlebugs. Even so, intercropping may influence pest management in truly diverse ways, based on local conditions and specific interactions within the agroecosystem. Tests are therefore needed to assess whether this would be a feasible approach for the European outbreaks, and whether it could be used to reduce the transmission of *X. fastidiosa*.

Besides interfering with host plant location and landing, effective BM strategies should include measures aimed at reducing the chances for a spittlebug to settle on the target plant. If chemical compounds are not used by *P. spumarius*

as olfactory cues in host localization, they likely convey pivotal information on host suitability during probing. There may be deterrent compounds involved in host resistance that reduce suitability of certain plant species or cultivars, thus decreasing vector feeding activities and bacterium transmission. By elucidating the compounds and the mechanisms involved in resistance to both *X. fastidiosa* and the vector, it may be possible to breed resistant or tolerant olive varieties or to stimulate similar responses in susceptible cultivars. Screening for resistant genotypes is of crucial importance, as olive cultivars expressing repellent and deterrent traits are urgently needed to allow infected areas to be replanted and us to witness the blossoming of new olive trees resistant to the vector, the pathogen, or both. Several decades of effort to breed pasture grass cultivars resistant to Neotropical spittlebug pests offers a note of caution. Although there was some success in breeding and screening for nymph resistant strains, this resistance did not carry over to adults (Aguirre et al. 2013). In practice, succession of new tolerant and resistant plantings in pastures did not result in control of spittlebugs, partly because tolerance engendered high pest populations. The case of *P. spumarius* is not directly analogous, since this spittlebug function as a vector and neither it harms directly by feeding nor olives are nymphal hosts. Nonetheless, the large literature on Neotropical spittlebug pests of sugarcane and cultivated pasture grasses probably harbors useful lessons for *P. spumarius* control in Europe.

Finally, vibrations, as well as chemical compounds, play a key role in the short-range communication and host acceptance of insects (Strauß et al. 2021). As suggested by several authors, hi-jacking insect vibrational communication makes it possible to manipulate behaviors, including mating, permanence on hosts, oviposition and feeding (Eriksson et al. 2012; Takanashi et al. 2019; Avosani et al. 2021a, b; Nieri et al. 2021; Zaffaroni-Caorsi et al. 2022). *Philaenus spumarius* relies on substrate-borne vibrations to communicate with conspecifics, to perceive the environment and, potentially, to detect natural enemies. By achieving deeper knowledge regarding the role of vibrations in determining host suitability, it may be possible to identify semiophysicals that can be used in concomitance to other cues to attract spittlebugs toward trap crops, repel them from olive trees and/or deter feeding, overall reducing interactions with the plant and constraining the spread of *X. fastidiosa*.

To conclude, there are diverse BM strategies targeting insect–plant interactions that can be evaluated in the future and that could, if effective, be combined with other integrated pest management tools and approaches, such as biocontrol, biopesticides and cultural practices, to protect olive groves from inoculation with the fastidious bacterium.

Author contribution

SA and DC wrote the first draft. SA prepared the figures. All the authors edited and reviewed the manuscript. DC coordinated the review.

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Declarations

Conflict of interest The authors declare no competing interests.

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