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Role of spittlebugs in *Xylella fastidiosa* subsp. *fastidiosa* sequence type 1 (ST1) epidemiology in Southern Italian vineyards

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1 **Role of spittlebugs in *Xylella fastidiosa* subsp. *fastidiosa* sequence type 1 (ST1) epidemiology in**
2 **Southern Italian vineyards**

3

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18

Abstract

19 The recent finding of *Xylella fastidiosa fastidiosa* ST1 (*Xff*) in almond, grapevine, and cherry plants
20 in South-Eastern Italy, and specifically in one of the most economically relevant table grape districts
21 worldwide, urgently calls for data on insect vectors involved in bacterium spread for informing
22 management strategies. A survey of potential vector species was conducted from April to October
23 2024 in five table-grape vineyards using the “tendone” system and five mixed plots (wine grapevines,
24 olives, almonds, and other plants) located in the municipality of Triggiano (Bari, Italy). Data were
25 collected on: i) presence and abundance throughout the year of xylem-sap feeding species, i.e.
26 competent vectors of the bacterium; ii) host plants for both juveniles and adults; iii) infectious status
27 of the plants the adults were collected from; iv) vector infectivity throughout the year. The two species
28 competent for the bacterium transmission present in the surveyed area were *Philaenus spumarius* and
29 *Neophilaenus campestris*. The data collected suggest *N. campestris* could be responsible for both
30 secondary "almond-to-almond" and primary "almond-to-grapevine" transmission, while *P. spumarius*
31 could be the main driver of the secondary "grapevine-to-grapevine" *Xff* transmission. However, the
32 data presented here refer to a single year of sampling in the epicenter of the outbreak; therefore, spatial
33 and temporal sampling limitations do not permit to draw definitive conclusions about vector-driven
34 *Xff* epidemiology. Nevertheless, our preliminary findings are crucial for informing containment
35 strategies and attempts to eradicate the outbreak.

36

37 Running title: Spittlebug vectors *Xylella fastidiosa* in vineyards

38

39 **Keywords:** Vector-borne plant pathogens; Outbreaks; Table grape; Almond; Tendone vineyards.

Introduction

40 Native to the Americas, the gram-negative xylem-limited bacterium *Xylella fastidiosa* is the
41 etiological agent of some of the most devastating diseases of plants of economic importance
42 worldwide (Sicard et al. 2018). For its spread over short distances, the bacterium relies on xylem-sap
43 feeding insects, notably sharpshooter leafhoppers (Hemiptera: Cicadellidae) and spittlebugs
44 (Hemiptera: Aphrophoridae). The meadow spittlebug *Philaenus spumarius* Linnaeus, 1758
45 (Hemiptera: Aphrophoridae) emerged as the main vector of the sequence type (ST) 53 (*X. fastidiosa*
46 subsp. *pauca*) to olive in Southern Italy and is supposed to play a relevant epidemiological role in all
47 the bacterium outbreaks described in Europe so far (Cornara et al. 2019). To date, all the research
48 efforts have been mainly dedicated to the olive pathosystem, overlooking other bacterium-vector-host
49 plant associations. There is therefore a significant knowledge gap on vector activity in agro-
50 ecosystems other than the olive one and for other xylem-feeders widespread in Europe, as well as on
51 the spittlebugs' transmission biology of *Xylella* genotypes different than ST53.

52 During the vector monitoring program for the strain ST53 conducted in the Apulia region in 2022 and
53 2023, a total of 15 *P. spumarius* adults (2 in 2022, and 13 in 2023) were found positive to *X. fastidiosa*
54 in an important table-grape district few kms away from the city of Bari, the capital of Apulia
55 (Southern Italy) where the main vine training system is the "tendone". Further multi-locus sequence
56 typing (MLST) analysis confirmed the bacterial genotype retrieved in the insects belonged to the
57 sequence type ST1, subspecies *fastidiosa* (*Xff*-ST1). The finding prompted a thorough monitoring
58 campaign with the collection and testing of several host plants possibly hosting the bacterium, that
59 led to the detection of almond, grapevine and cherry plants infected with *Xff*-ST1. The finding of *Xff*-
60 ST1 in Apulia follows the one in cherry, grapes and almond in Mallorca (Balearic Islands, Spain)
61 (Olmo et al. 2021), and the report in almond and grapes in Israel (Zecharia et al. 2022). During this
62 first preliminary survey in Apulia, grapevine plants found infected with *Xff*-ST1 were mainly located
63 on external rows of the vineyards, often close to infected almond trees (Cornara et al. 2025). This
64 spatial distribution suggests an *Xff*-ST1 pattern of spread similar to the one observed in Northern
65 California vineyards, i.e. primary transmissions occurring from reservoirs outside the vineyards
66 followed by secondary grape-to-grape transmission (Daugherty et al. 2025). The meadow spittlebug
67 *Philaenus spumarius*, i.e. the spittlebug species found positive for the bacterium, together with the
68 other xylem feeder common in the area, namely the spittlebug *Neophilaenus campestris* Fallen, 1805
69 (Hemiptera: Aphrophoridae), could possibly be the two drivers of *Xff*-ST1 spread. *Philaenus*
70 *spumarius* has been reported to be competent for the transmission of *Xff* to grapevine, with a
71 grapevine-to-grapevine transmission efficiency per individual per day of ~15%, similar to the value
72 reported for the sharpshooter *Homalodisca vitripennis* Germar, 1821 (Severin 1950; Cornara et al.

73 2016; Beal et al. 2021). Despite the apparent similarities, previous knowledge generated from
74 California Pierce's disease (PD) pathosystem should be cautiously transferred to the Apulian and
75 European scenarios. There are indeed three main differences between PD in California vineyards and
76 the *Xff*-ST1 pathosystem in Apulia. First, the "tendone" training system has unique conditions that
77 might influence the insect-bacterium-plant interactions, and, to the best of our knowledge, no
78 investigations on PD spread in tendone vineyards have ever been carried out. Second, PD research
79 has primarily focused on wine grape cultivars under field conditions, whereas table grape is
80 widespread in the area of the Apulian region where *Xff*-ST1 was detected. Notably, table grape
81 cultivars are more susceptible to the disease (Rashed et al. 2011; Deyett et al. 2019). Third, the
82 primary vectors of Xf in European outbreaks—spittlebugs—differ significantly from the
83 sharpshooters that spread PD in North American vineyards. These differences in phenology, ecology,
84 and behavior may also affect vector-mediated bacterial spread.

85 These differences and the related knowledge gaps urgently call for research on insect vectors dynamic
86 and vector-mediated *Xff* spread in one of the most important table-grape districts worldwide, to
87 promptly inform containment strategies and eradication attempts.

Materials and methods

Study area and sampling sites

88 The study area was located in the municipality of Triggiano (Bari, Italy), where *Xff*-ST1
89 positive plants were detected, mainly almond, grapevine and cherry (Cornara *et al.* 2025) (Table 1).
90 The survey was carried out from early April until the end of October 2024 in 10 sites approximately
91 1 ha each (Figure 1). Five sites were characterized by “tendone” table grape vineyards, bordered by
92 semi-natural habitats and almond trees. The remaining five sites were termed as “mixed orchards”,
93 composed by wine grapevines trained using the trellis system, in addition to olive, almond, stone
94 fruit, mulberry, fig, and wild plants, surrounded by semi-natural habitats. Inside each site, vector
95 sampling was carried out every two weeks always on the same plants, that were marked with bands
96 and metal tags.

97

Population dynamics of juvenile stages of insects and host plants

98 Spittlebug nymphs were monitored in both the “tendone” and “mixed orchard” plots with the
99 quadrat sampling method, using five 100x25 cm transects per sampling site. For each transect, host
100 and non-host plant species of the juvenile stages were identified in accordance with the guidelines of
101 Pignatti (2019). In instances where identification at the species level was not possible due to the
102 absence of clear taxonomic characteristics, the plant species were identified at the genus or family
103 level. An assessment was conducted of the population dynamics of nymphs, the host plants of the
104 juvenile stages, and the adults’ emergence period. The number of individuals per each juvenile instar
105 was determined, with the first and second merged into a single group since the first two instars are
106 hard to differentiate in the field (Bodino *et al.* 2019).

107

Samples collection of adult insects and plants

108 Adult insects were sampled from four compartments: i) ground cover; ii) grapevine plants; iii)
109 almond plants; iv) trees and shrubs other than grapevine and almonds.

110 In the “tendone” vineyards, insects were collected from the ground cover using nets with a
111 diameter of 38 centimeters. Each sample was composed by all the insects collected during four
112 consecutive sweeps performed over a 1mq transect (quadrat sampling). Five samples were collected
113 from the ground cover adjacent to the vineyards and five from inside the vineyards. Xylem feeder’s

114 presence, abundance and dynamic on the grapevine were monitored by enclosing a randomly selected
 115 shoot per grape in a plastic bag and vigorously shaking the shoot, on a total of nine blocks of
 116 grapevines per vineyard each constituted by four plants. Three blocks were selected per row,
 117 monitoring plants at the border of the vineyard, plants on the 4th-6th rows, and plants on the 9th-11th
 118 rows. Consequently, in each vineyard, xylem-feeding insects were collected by bagging shoots from
 119 36 plants (one shoot per plant). All the insects collected from the four shoots/plants constituting the
 120 block were pooled in a single sample, i.e. nine samples per vineyard were collected.

121 For trees and shrubs bordering each tendone, including almonds, insects were collected using
 122 sweep nets and electric portable aspirators. Ten consecutive sweeps/plants were made around the
 123 plant canopy.

124 In “mixed orchards”, adult xylem-feeders were collected from the ground cover by quadrat
 125 sampling (five quadrats per site) using the sweep nets. For trees and shrubs, sweep nets were used,
 126 with ten sweeps per plant. For wine grapes when present, insects were collected by shoots-bagging
 127 (explained above), with five samples (each constituted by insects collected from four grapevine
 128 shoots) per plot.

129 Upon collection, the insects were stored in EtOH 99.8% at -20°C before being identified at
 130 the species level using the taxonomic key provided by Ossiannilsson et al. (1981) and tested for *X.*
 131 *fastidiosa* by real-time PCR (RT-PCR). In instances when positive insects were present on a plant,
 132 the plant portion from which insects were sampled was collected and tested for *X. fastidiosa* by RT-
 133 PCR.

134

***Xylella fastidiosa* subsp *fastidiosa* detection in insects and plants**

135 Total DNA extraction and RT-PCR of insects were performed according to the EPPO
 136 diagnostic standard PM 7/24 (5) (EPPO 2023). Insect heads were severed with a sterile scalpel and
 137 homogenized singly with stainless steel beads (5 mm in diameter) using a TissueLyser LT (QIAGEN,
 138 Hilden, Germany). Total DNA was extracted following the CTAB procedure. The pellet was
 139 resuspended in 50 µl of DNA-se/RNA-se free water. The quantity of the DNA extract was assessed
 140 with a Qubit 4 Fluorometer (ThermoFisher Scientific, USA). Then, RT-PCR was performed using the
 141 *Xylella*-specific primers/probe designed by Harper et al. (2010). Samples yielding doubtful RT-PCR
 142 results were re-amplified in direct and nested PCR assays targeting *holC* gene, according to Cruaud
 143 et al. (2018). The samples displaying the specific band on agarose gel were then considered positive.

144 Leaf petioles and main veins were cut using a sterile scalpel (0.5-1 g per plant), homogenized
145 inside extraction bags (Bioreba, Reinach, Switzerland) containing 4 ml of CTAB lysis buffer
146 (AppliChem GmbH, Darmstadt, Germany) by using a semi-automated homogenizer (Homex 6,
147 Bioreba, Reinach, Switzerland). Total DNA was extracted following the procedure PM 7/24 (5)
148 (EPPO 2023). The quality of DNA extract is assessed with a Qubit 4 Fluorometer (ThermoFisher
149 Scientific, USA). Then, RT-PCR was performed using the *Xylella*-specific primers/probe designed by
150 Harper et al. (2010). Samples yielding positive results were subjected to Multilocus sequence typing
151 (MLST) and blast sequence analyses using the dedicated PubMLST database
152 (<https://pubmlst.org/organisms/xylella-fastidiosa>) to confirm whether the allelic profile of all typed
153 positive samples corresponded to the ST1.

154

Data analysis

155 To compare data on xylem-feeders' relative abundance across grapevines, trees, and shrubs,
156 we accounted for differences in monitoring methods across compartments (ground cover, almond,
157 grapevine, and other species) by using the ratio of spittlebugs collected per compartment per date.
158 Namely, for the ground cover, we calculated the total number of spittlebugs collected per transect
159 (1mq). For almond and other woody hosts, we considered the number of insects per plant. For
160 grapevine, we considered the number of spittlebugs collected per block, each composed of four plants
161 (four randomly selected shoots per block).

162 Infectivity was expressed as the number of insects testing positive to *X. fastidiosa* by RT-PCR
163 over the total number of insects collected per compartment per date.

164 Statistical analyses were conducted using R version 4.1.3 (R Core 2020). Generalized Linear
165 Mixed Models (GLMM) were employed to evaluate the differences in spittlebugs relative abundance
166 between mixed orchards and tendone plots, among compartments, among the grapevine blocks in the
167 tendone (to evaluate a possible border effect), and the abundance trends throughout the year. Data
168 were transformed with $\ln(x+1)$ or \sqrt{x} when necessary to reduce heteroscedasticity and improve
169 normal distribution. Models were run using the “glmmTMB” package (Venables and Ripley 2013),
170 while residual distribution was checked using the “DHARMA” package (Fox and Weisberg 2018). In
171 case of a statistically significant effect ($p < 0.05$), pairwise comparisons were conducted by Tukey's
172 HSD (honest significant differences) test using “emmeans” package (Lenth 2021). Given the
173 relatively low number of *Xff*-positive insects collected in the surveyed plots, infectivity data are only
174 summarized in the results section and figures.

175

Results

Spittlebug nymphs' population dynamic and host plants

176 The monitoring of spittlebugs nymphs was conducted in mixed orchards and on ground
 177 vegetation surrounding tendone, given the presence of a limited number of herbaceous plants inside
 178 the tendone plots. At the beginning of the survey (April 15th, 2024), the main pre-imaginal instars
 179 present were the fifth instar for *P. spumarius* (0.83 ± 0.33 individuals/transect; mean \pm se) and the third
 180 instar for *N. campestris* (0.65 ± 0.44 individuals/transect). No nymphs have been found from May 13th
 181 on.

182 During the season, spittlebugs nymphs were observed on 25 over 46 herbaceous plant species
 183 inside the transects, of which 44 identified at species level (Supplementary Table 1); plants belonging
 184 to the genus *Crepis L.* and all the species belonging to the family *Poaceae L.* were identified at the
 185 genus and the family level, respectively. Among all those inspected, the most prevalent herbaceous
 186 plant species in the surveyed plots were *Poaceae* spp., which were observed in 55.9% of the total
 187 transects examined. Other species that were observed with high frequency included *Glebionis*
 188 *coronaria L.* (19%), *Sonchus tenerrimus L.* (15.6%), *Medicago polymorpha L.* (14.4%), and
 189 *Scorpiurus muricatus L.* (12.7%) (Figure 2). Regarding vector abundance, *Neophilaenus campestris*
 190 was mainly present on *Poaceae* spp., with ca. 1.2 ± 0.25 nymphs/transect. In contrast, *Glebionis*
 191 *coronaria* was identified as the main host species for *P. spumarius*, with a frequency of ca. 2.3 ± 0.40
 192 nymphs/transect. No nymphs were observed on *S. muricatus*.

193 Data on nymphal instars abundance per herbaceous plant species are reported in Figure 2 and
 194 Supplementary Table 1.

195

Spittlebugs abundance in mixed orchards and tendone vineyards

196 The two xylem-sap feeding insect species present in the surveyed area, thus the two species
 197 competent for *Xff* transmission, were *P. spumarius* and *N. campestris*.

198 When the survey started (April 15th), the first adults of *P. spumarius* and *N. campestris* had
 199 already emerged, and all individuals were collected from the ground cover. No adults were found on
 200 trees or shrubs. Adult spittlebugs peak on the ground cover was observed at the end of April, with
 201 0.96 ± 0.23 *P. spumarius*/transect and 1.67 ± 0.79 *N. campestris*/transect. Thereafter, spittlebugs'
 202 abundance on the ground cover steadily decreased.

203 The abundance of spittlebugs in mixed orchards was found to be significantly higher than in
 204 tendone plots, regardless of the compartment, for both *P. spumarius* ($t=3.029$, $p=0.003$) and *N.*
 205 *campestris* ($t=3.994$, $p<0.001$).

206 Considering the data from both mixed orchards and tendone plots, *P. spumarius* relative
 207 abundance per sample was significantly higher on the ground cover (0.25 ± 0.06 individuals/transect)
 208 compared to almond (0.08 ± 0.02 individuals per plant) ($t=3.160$, $p=0.010$) and grapevine (0.08 ± 0.02
 209 individuals per block of four plants) ($t=3.148$, $p=0.011$). The abundance of individuals on the ground
 210 cover compared to other trees and shrubs, including olive, was overall similar (0.17 ± 0.03 individual
 211 per plant).

212 For *N. campestris*, the average abundance was significantly lower on grapevine (0.02 ± 0.01)
 213 compared to the ground cover (0.33 ± 0.12) ($t=3.603$, $p=0.002$) and other species (0.19 ± 0.05) ($t=3.271$,
 214 $p=0.007$). The population abundance of individuals on almond plants (0.09 ± 0.03) was overall similar
 215 to other compartments.

216 The relative abundance of the two spittlebugs tended to decrease throughout the season in all
 217 the compartments, both in the mixed orchards or in the tendone plots (*P. spumarius*: $z=3.720$,
 218 $p<0.001$; *N. campestris*: $z=3.994$, $p>0.001$).

219 On almond plants, both in mixed orchards and tendone, *P. spumarius* was collected from the
 220 first half of April, i.e. during fruit growth, to the beginning of September, i.e. when natural defoliation
 221 started, with two peaks during fruit growth: a first peak at the end of May (0.19 ± 0.06) and a second
 222 peak in the last decade of June (0.23 ± 0.09) (Figure 3). A significantly higher relative abundance was
 223 observed during fruit growth and ripening compared to the later phase (hulls split and leaves fell)
 224 ($t=2.557$, $p=0.011$).

225 *Neophilaenus campestris* was collected from almond plants from the second half of April to
 226 the end of September, when most leaves had fallen, with a population peak from the end of May to
 227 mid-June (0.46 ± 0.27) (Figure 3). In this case, the relative abundance during fruit growth was
 228 significantly higher compared to the period of fruit ripening ($t=2.834$, $p=0.03$), and to the period of
 229 the hulls split ($t=3.815$, $p=0.001$) and leaves fall ($t=3.832$, $p=0.001$). Furthermore, the relative
 230 abundance of the insect during ripening was significantly higher compared to the period from the
 231 hulls split ($t=2.820$, $p=0.03$) and to leaves fall ($t=3.602$, $p=0.002$).

232 Considering the tendone vineyards, the two spittlebug species were collected from grapes
 233 from mid-May to the end of October, i.e. from the end of the flowering to post-harvest. For both
 234 species, a first peak in relative abundance was measured at the end of May during cluster growth (*P.*
 235 *spumarius* 0.24 ± 0.11 and *N. campestris* 0.13 ± 0.06), and a second peak between the end of July and

236 the beginning of August during ripening and veraison (*P. spumarius* 0.22 ± 0.08 and *N. campestris*
 237 0.13 ± 0.05). *Neophilenus campestris* abundance on grapevine was relatively (but non-statistically
 238 significantly) lower than *P. spumarius* (Figure 3). The relative abundance of *P. spumarius* tended to
 239 increase on plants in internal rows (9th to 11th rows) throughout the season, while remaining constant
 240 on border plants ($t=3.146$, $p=0.005$). No differences in *N. campestris* relative abundance were found
 241 between the rows, with a negative gradient from the border to the center of the vineyard (raw data).

242

Spittlebugs infectivity in mixed orchards and tendone vineyards

243 The only plants testing positive by RT-PCR for *Xff* were almond (6 *Xff*-positive plants out of
 244 the 60 tested) and grapevine (3/232) (Table 2). The MLST analysis confirmed that the bacterial
 245 sequence type found was ST1.

246 The first spittlebugs testing positive for *Xff* among the ones collected in 2024 two *N.*
 247 *campestris*, one male and one female, collected from an infected almond tree in one of the monitored
 248 mixed orchard plots on May 27th. On June 10th, another female of *N. campestris* collected from an
 249 *Xff*-positive almond plant bordering a tendone vineyard tested positive for *Xff* (Figure 4). Considering
 250 all the spittlebugs collected from almond plants in the ten plots surveyed in 2024, the mean *N.*
 251 *campestris* infectivity was 16.05% (13 out of 81 individuals tested positive to *Xff*). In contrast, none
 252 of the 67 *P. spumarius* collected from almonds was found harboring *Xff*.

253 The first *Xff*-positive insect collected on grapevine within a tendone plot was a *N. campestris*
 254 male; the individual was collected on June 22nd from one of the grapevine blocks on a border row.
 255 The four plants of the block were found to be *Xff*-free. The first *P. spumarius* positive for the
 256 bacterium (female) was collected from a border block of *Xff*-free grapevines on July 3rd (Figure 4).
 257 Approximately one and a half months (on August 6th) after the collection from negative grapevines
 258 of the first positive *N. campestris* one of the four grapevine plants of the block tested positive for *Xff*.

259 The average infectivity for spittlebugs collected from tendone vineyards throughout the year
 260 was 9.52% for *N. campestris* (2/21) and 9.09% for *P. spumarius* (5/55). The *Xff*-positive *N. campestris*
 261 individuals were collected from grapevine plants from the third decade of June to the third decade of
 262 July, during the fruit veraison, exclusively on border grapes. In contrast, *Xff*-positive *P. spumarius*
 263 individuals were collected from grapevine from the beginning of July (i.e. veraison period) to the end
 264 of September (i.e. post-harvest period). For *P. spumarius*, the infectivity tended to increase during the
 265 season, ranging from 12% to 50%. *Xff*-positive *P. spumarius* were collected from the border and
 266 inside the vineyard (Figure 4).

267 Data on total number of samples collected and tested per plant species, number of positive
268 plants, number of spittlebugs collected per plant species, and number of insects positive to *Xff*, are
269 reported in Supplementary Materials Table 2.

270

Discussion

271 The finding of the *Xylella fastidiosa fastidiosa* sequence type ST1 (*Xff*), i.e. a genotype which
272 can cause Pierce's disease of grapevine, in one of the most important table grape-producing districts
273 worldwide (Cornara et al. 2025) urgently called for investigations about possible bacterium patterns
274 of spread and vector species involved, in order to timely inform containment strategies and current
275 attempts to eradicate the bacterium.

276 Our survey revealed that two insect species competent for *Xff* transmission are possibly
277 involved in bacterial spread within the monitored area, namely *Neophilaenus campestris* and
278 *Philaenus spumarius*. According to the data collected, *N. campestris* could putatively be responsible
279 for either the secondary almond-to-almond bacterial spread or the primary almond-to-grape
280 transmission. On the other hand, the meadow spittlebug *P. spumarius* could be the main driver of the
281 secondary grape-to-grape *Xff* spread. However, our conclusions should be taken with caution, given
282 the temporally and spatially limited dataset.

283 In the US, since the last decades of the 1800s, several outbreaks of Pierce's disease have been
284 reported in California and Florida vineyards (Pierce 1892; Adlerz and Hopkins 1979). Sharpshooters,
285 as the native *Draeculacephala minerva* Ball, 1927 and *Graphocephala atropunctata* Signoret, 1854,
286 and the invasive *H. vitripennis*, are the most important vectors at least in agricultural settings (Blua
287 et al. 1999; Redak et al. 2004; Daugherty and Almeida 2009). In Californian vineyards, transmission
288 occurs first in spring with dispersal of overwintering infective insects from riparian vegetation
289 bordering the vineyards to grapevine plants closer to the borders. During summer, *X. fastidiosa*
290 infected grapevines serve as source of inoculum for the secondary grape-to-grape transmission. These
291 summer inoculations might not lead to systemic persistent infections either because of they occur
292 temporally close grapevine severe pruning and removal of the inoculum before the bacterium spread
293 within the plant, or for winter recovery (Feil et al. 2003; Daugherty et al. 2025). Throughout the
294 season, the sharpshooters' infectivity tends to increase, reaching the peak before the individuals move
295 to overwintering habitats (Daugherty et al. 2025; Beal et al. 2021).

296 Although the two pathosystems, namely the wine grape vineyards in California with a trellis-
297 system and table grape vineyards in Southern Italy trained using the tendone system are very different

298 from each other, there are overall some similarities worthed to highlight, thus lessons from the best
299 characterized pathosystem worldwide to be learned and possibly transferred to the European scenario.

300 The population dynamic of the two spittlebug species in the surveyed area is overall similar to
301 the one described for olive agroecosystems (Cornara et al. 2017; Morente et al. 2018; Bodino et al.
302 2019). Juveniles develop on ground vegetation, with *N. campestris* mainly on monocots and *P.*
303 *spumarius* nymphs on dicots. Adults of both species emerge in late April and readily disperse toward
304 trees and shrubs including almond and grapevine following ground cover removal and/or senescence.
305 The first spittlebug adults of both species collected in May on grapevines inside the tendone vineyards
306 possibly emerged from the few herbaceous plants remaining inside the tendone after tillage and
307 ground cover removal. Therefore, at least hypothetically, in tendone vineyards with cover crops, thus
308 without ground cover removal, the vector population could peak before than what observed in the
309 present survey carried out on tilled vineyards, i.e. end of July-mid August. Alternatively, the
310 presence of the ground cover could reduce the need for vectors to find other hosts, thus reducing the
311 frequency of dispersal toward trees and shrubs including grapevine (Morente et al. 2022).
312 Furthermore, given visual cues seem to be pivotal for host location in spittlebugs, the removal of the
313 ground cover would create a contrast between the grapevine foliage and the bare ground attracting
314 spittlebugs toward the vineyards (Lazar et al. unpublished; Avosani et al. 2024). Overall, the effect of
315 ground cover management on vector activity on grapevine is one of the factors that deserve further
316 investigations, given its relevance for *Xff* spread and management.

317 The first *Xff*-positive spittlebugs found in the surveyed area were two *N. campestris* collected
318 from an infected almond plant at the end of May. *Neophilaenus campestris* was the only species of
319 the two ones competent for the bacterium transmission retrieved in the area whose individuals were
320 found harboring *Xff*, with the highest infectivity (number of *Xff*-positive insects over the total number
321 of insects collected) around mid-July, similarly to data reported for sharpshooters in California
322 almond orchards (Cabrera La Rosa et al. 2008). Indeed, none of the *P. spumarius* collected from
323 almond plants tested positive for the fastidious bacterium. Our observations diverge from previous
324 reports on the *X. fastidiosa* subspecies *multiplex* outbreak in Alicante, with *P. spumarius* infectivity
325 in almond orchards being more than twenty-times that observed for *N. campestris* (27% and 1.2%,
326 respectively) (Cornara et al. 2019). This apparent discrepancy might be explained by the relatively
327 low number of individuals collected in the present survey (a total of 69 individuals out of 60 plants
328 throughout the season), with higher numbers of individuals collected possibly corresponding to a
329 higher probability of catching infective ones. Another possible explanation for the apparent lack of
330 *Xff*-acquisition from almond plants by *P. spumarius* might be the relatively low preference displayed
331 by the meadow spittlebug for the almond varieties (unknown) in the plots surveyed in the present

332 study compared to Alicante's almonds, with the former being less suitable for the meadow spittlebug
333 than the latter. The low suitability, thus possibly the reduced time spent by the vector on the plant,
334 would reduce the probability the plant serves as both source and recipient host for the bacterium
335 (Irwin and Ruesink 1986; Daugherty et al. 2009). *Philaenus spumarius* was demonstrated to
336 efficiently acquire the bacterium from almond plants and inoculate both almond and grapevine in
337 transmission trials carried out under greenhouse conditions (Purcell 1980). However, in classic
338 transmission trials, which are of paramount importance for characterizing the transmission biology
339 of vector-borne plant pathogens, the insect is forced to feed on the source/recipient plants it is caged
340 on, overlooking insect's behavior and preference. On the other hand, if offered a choice, the insect
341 could avoid the source/recipient plant it had to feed on when forced, thus potentially leading to
342 different results in terms of acquisition and inoculation efficiency. Furthermore, apart from the host
343 plant species, xylem-sap feeders' preference for certain varieties over others is another factor that
344 should be taken into account given its relevance in shaping bacterium transmission and disease
345 prevalence (Rashed et al. 2011; Cornara et al. 2025).

346 Infective *N. campestris* individuals, possibly acquiring the bacterium from infected almond
347 plants bordering the tendone vineyards, were collected from grapevine in the last decade of June.
348 Therefore we speculate that *Xff*-positive almonds possibly serve as source either for the secondary
349 almond-to-almond transmission, or for the primary transmission almond-to-grape, with *N. campestris*
350 playing a role in the spillover. Therefore, according to our preliminary data, *N. campestris*, whose
351 importance in the *X. fastidiosa* ST53 epidemiology in olive orchards is deemed to be negligible
352 (Cornara et al. 2017; Cavalieri et al. 2019), might play a role in *X. fastidiosa* ST1 pathosystem.
353 Although occasionally collected on olive, grapevine, and other cultivated plants, this spittlebug
354 species displayed a marked preference for weeds and conifers (Morente et al. 2018; Cornara et al.
355 2021). *Neophilaenus campestris* presence on grapevine plants inside the tendone plots was indeed
356 limited to a short period between the end of June and the beginning of July, apparently enough to
357 inoculate plants at the border of the tendone with *Xff*. This pattern of spread is again similar to the
358 one observed for *D. minerva*-mediated *X. fastidiosa* transmission to almond and grapevine in
359 California, with bacterium spread from border plants driven by a species preferring pastures and
360 seminatural habitats but transiently moving to cultivated plants in late spring-early summer (Cabrera
361 La Rosa et al. 2008; Daane et al. 2011).

362 While the presence of *N. campestris* in vineyards was transient and limited to border plants,
363 the meadow spittlebugs *P. spumarius* abundance tended to increase from the beginning of July on,
364 apparently moving progressively from border plants to the center of the tendone. Furthermore, the
365 first *Xff*-positive *P. spumarius* among all the surveyed plots was collected inside a vineyard, and the

366 infectivity for individuals collected from grapevine showed an increasing trend with a peak at the end
367 of the season (post-harvest). Although we cannot exclude *Xff*-positive spittlebugs could have acquired
368 the bacterium from plants external to the tendone before moving to grapevine (as well as from
369 grapevine inside the tendone that were not sampled and tested for *Xff*), the meadow spittlebug
370 population dynamic and infectivity trend inside the tendone, combined with the apparent lack of
371 acquisition from almond, suggest *P. spumarius* could be the main driver of the secondary grape-to-
372 grape bacterium transmission. Our observations, although preliminary, are in line with data reported
373 for both spittlebugs and sharpshooters in US vineyards. In Beal et al. (2021) wine-grape vineyards
374 survey, the population abundance of *P. spumarius* on grapevine increased slowly throughout the
375 season. The first bacterium-positive meadow spittlebugs on grapevine plants in Californian vineyards
376 were observed from mid-June on, with a gradual increase in infectivity (Cornara et al. 2016; Beal et
377 al. 2021). Similar infectivity trends were observed also for sharpshooters as *H. vitripennis* and
378 *Oncometopia nigricans* Walker, 1851 (Hemiptera: Cicadellidae) in Florida vineyards (Adlerz and
379 Hopkins 1979). The blue-green sharpshooter *G. atropunctata* in California, whose first generation
380 is responsible for *X. fastidiosa* primary spread from wild riparian plants to grapevines at the border
381 of the vineyards, also displayed an increase in *Xf*-positive individuals, likely acquiring the bacterium
382 from infected grapevines, after the end of September (Purcell 1975; Daugherty et al. 2025). Adlerz
383 and Hopkins (1979) in Florida, Freitag and Frazier (1954) and Sisterson et al. (2020) also reported
384 the highest transmission efficiency by different species of field-collected sharpshooters occurring
385 during summer-fall in Northern California vineyards. Therefore, according to our preliminary data,
386 we speculate *P. spumarius* could play a relevant role in secondary grape-to-grape bacterial spread,
387 i.e. acquisition from and inoculation to grapevine, with the transmission probability increasing as the
388 season progresses. Factors other than the vector-bacterium-plant interaction, as climate (winter
389 recovery) and pruning would then contribute determining the probability of inoculation events to end
390 up in persistent systemic infections.

391 Future research efforts should address crucial factors potentially affecting the bacterial spread
392 in European vineyards as: i) impact of training system, cover crops, and plastic tarps on vectors
393 population dynamics, comparing tendone and trellis systems; ii) plant-bacterium-vector interaction
394 for European wine and table grapes, mainly aimed at finding sources of resistance to both the insect
395 vectors and the bacterium.

396 Eventually, one-year sampling in the epicenter of the outbreak does not allow us to provide a
397 conclusive and detailed picture of the population dynamic of the insect vectors and their role in *Xff*
398 epidemiology in vineyards. On the other hand, although preliminary, the data we present here are
399 crucial for timely informing bacterium containment strategies; further sampling is currently hampered

400 by plants removal in the frame of the current ST1 eradication plan undertaken by the Apulian
401 Regional Plant Protection Service ([Emergenza Xylella - Sito Ufficiale - Regione Puglia](#)).

402

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412

Authors contribution statement:

413 Conceptualization: PP and DC. Survey: PP, NT, GS, GR. Analysis: MM, MLV, NS, GS. Data curation:
414 PP, MM, NS, MLV, MC, DC. Formal analysis: PP, MM, NS, GS, DC. Methodology: PP, NS, MC,
415 DC. Funding acquisition: VV, DC. Project administration: DC and VV. Supervision: DC. Writing
416 original draft: PP, MM, MS, DC. Writing, review & editing: All the co-authors.

417

Conflicts of interest

418 The authors have no conflicts of interest to declare.

419

Data availability statement

420 Additional data are available from the corresponding author (daniele.cornara@uniba.it) upon request

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584 **Tables**

585 **Table 1:** Overview of the monitoring sites. The table column report: i) Type of site; ii) Site code; iii) Site coordinates in Degrees and Decimal Minutes
 586 (DDM); iv) Scientific name of the predominant species inside the site; v) Common name of the predominant species inside the site; vi) Cultivar.

587

Type	Code	Coordinates (DDM)	Predominant species	Common name	Cultivar
Mixed orchard	O1	41°04'26.7"N 16°56'20.2"E	<i>Prunus dulcis</i> Batsch	Almond	NA
Mixed orchard	O2	41°04'29.7"N 16°56'26.5"E	<i>Olea europea</i> L.	Olive	NA
Mixed orchard	O3	41°04'27.4"N 16°56'29.7"E	<i>Olea europea</i> L.	Olive	NA
Tendone	A1	41°04'31.1"N 16°56'46.8"E	<i>Vitis vinifera</i> L.	Grapevine	Vittoria
Tendone	A2	41°04'29.4"N 16°56'46.4"E	<i>Vitis vinifera</i> L.	Grapevine	Vittoria
Tendone	A3	41°04'25.2"N 16°56'42.3"E	<i>Vitis vinifera</i> L.	Grapevine	Summer Royal
Tendone	A4	41°04'25.8"N 16°56'36.9"E	<i>Vitis vinifera</i> L.	Grapevine	Summer Royal
Mixed orchard	R1	41°04'11.0"N 16°56'29.2"E	<i>Prunus dulcis</i> Batsch	Almond	NA
Mixed orchard	T1	41°04'38.5"N 16°57'41.9"E	<i>Prunus dulcis</i> Batsch	Almond	NA
Tendone	T2	41°04'39.3"N 16°57'45.7"E	<i>Vitis vinifera</i> L.	Grapevine	Unknown

588

589

590 **Table 1:** Almond and grapevine plants sampled and tested for *Xff* during the 2024 survey. The table reports: i) Common name of the plant; ii) Scientific
 591 name of the plant; iii) Cultivar; iv) Kind of plot; v) Total number of plants sampled; vi) Total number of *Xff*-positive plants; vii) Total number of *P.*
 592 *spumarius* (*Ps*) collected on plants; viii) Total number of *Ps* positive for *Xff*; ix) Total number of *N. campestris* (*Nc*) collected on plants; x) Total number
 593 of *Nc* positive to *Xff*.

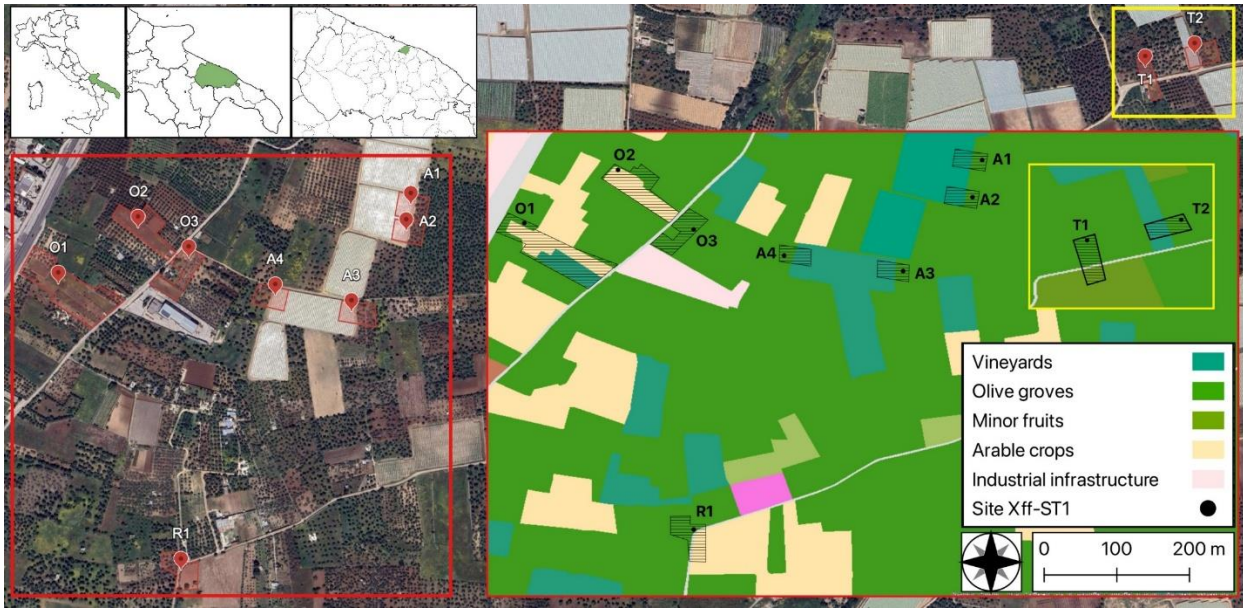
594

Common name	Scientific name	Cultivar	Plot (mixed/tendone)	n° plants sampled	n° plants positive	n° <i>Ps</i>	n° <i>Ps</i> pos	n° <i>Nc</i>	n° <i>Nc</i> pos
Almond	<i>Prunus dulcis</i> Batsch	-	mixed/tendone	60	6	67	0	81	13
Grape	<i>Vitis vinifera</i> L.	Vittoria	tendone	72	2	14	3	6	2
Grape	<i>Vitis vinifera</i> L.	Summer Royal	tendone	72	0	13	2	5	0
Grape	<i>Vitis vinifera</i> L.	Unknown	tendone	36	1	28	0	12	0
Grape	<i>Vitis vinifera</i> L.	Primitivo	mixed	9	0	14	0	3	0
Grape	<i>Vitis vinifera</i> L.	Unknown	mixed	5	0	10	0	1	0

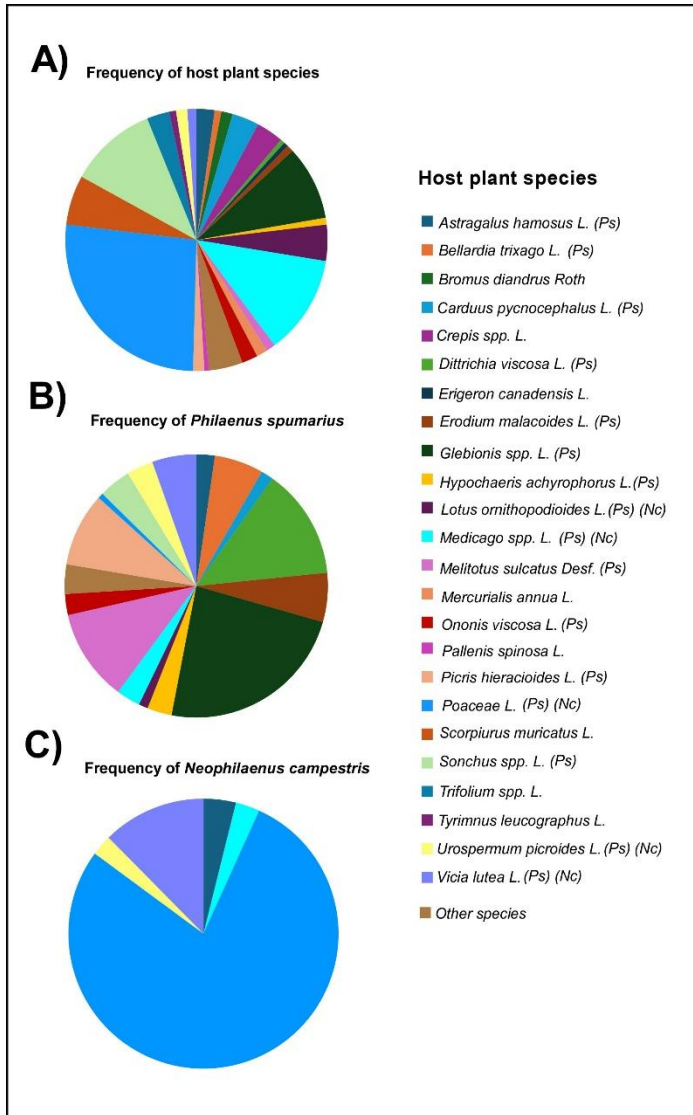
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596 **Figures**

597 **Figure 1:** Map of all the monitoring sites with land use.



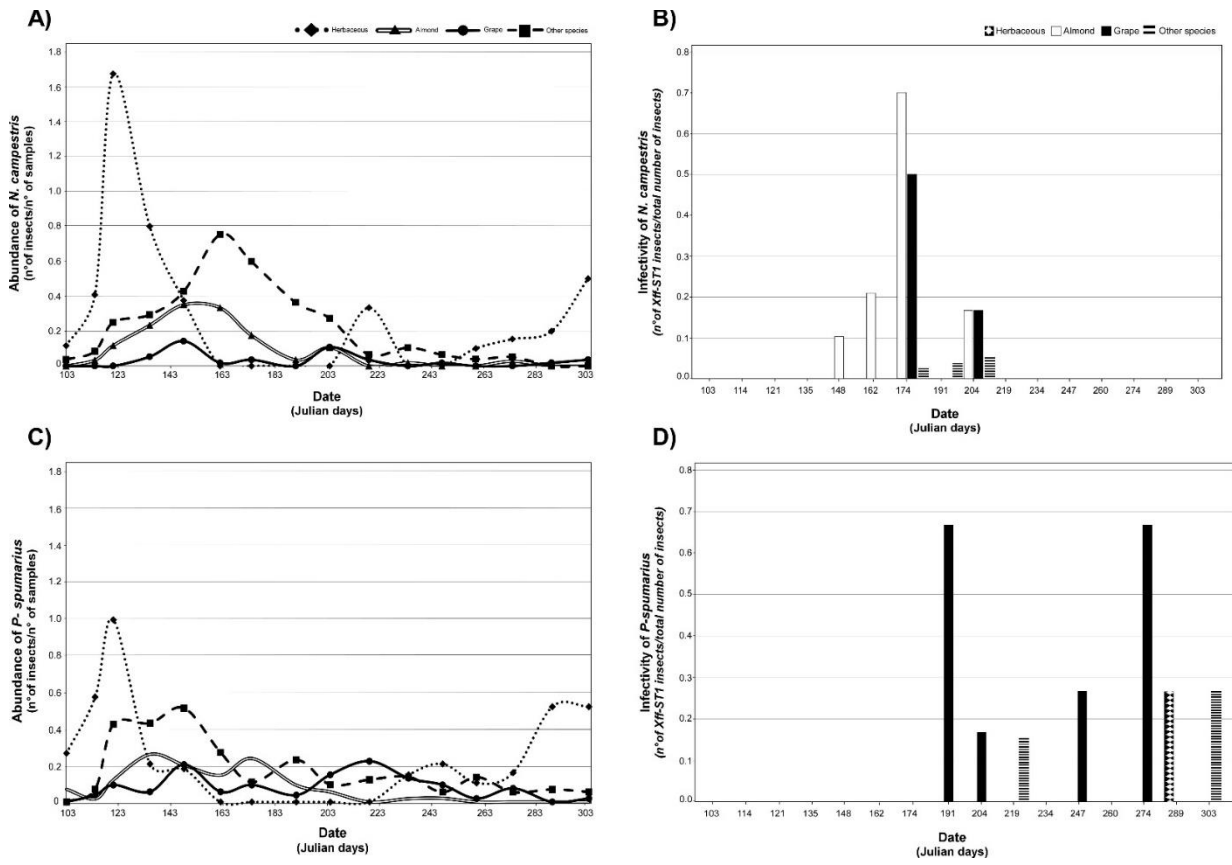
600 **Figure 2:** Observation on presence/absence of host species and nymphs of both species. A) Frequency
 601 of herbaceous host species observed during the nymph survey; B) Frequency of *P. spumarius* nymphs
 602 on herbaceous host species; C) Frequency of *N. campestris* nymphs on herbaceous host species.



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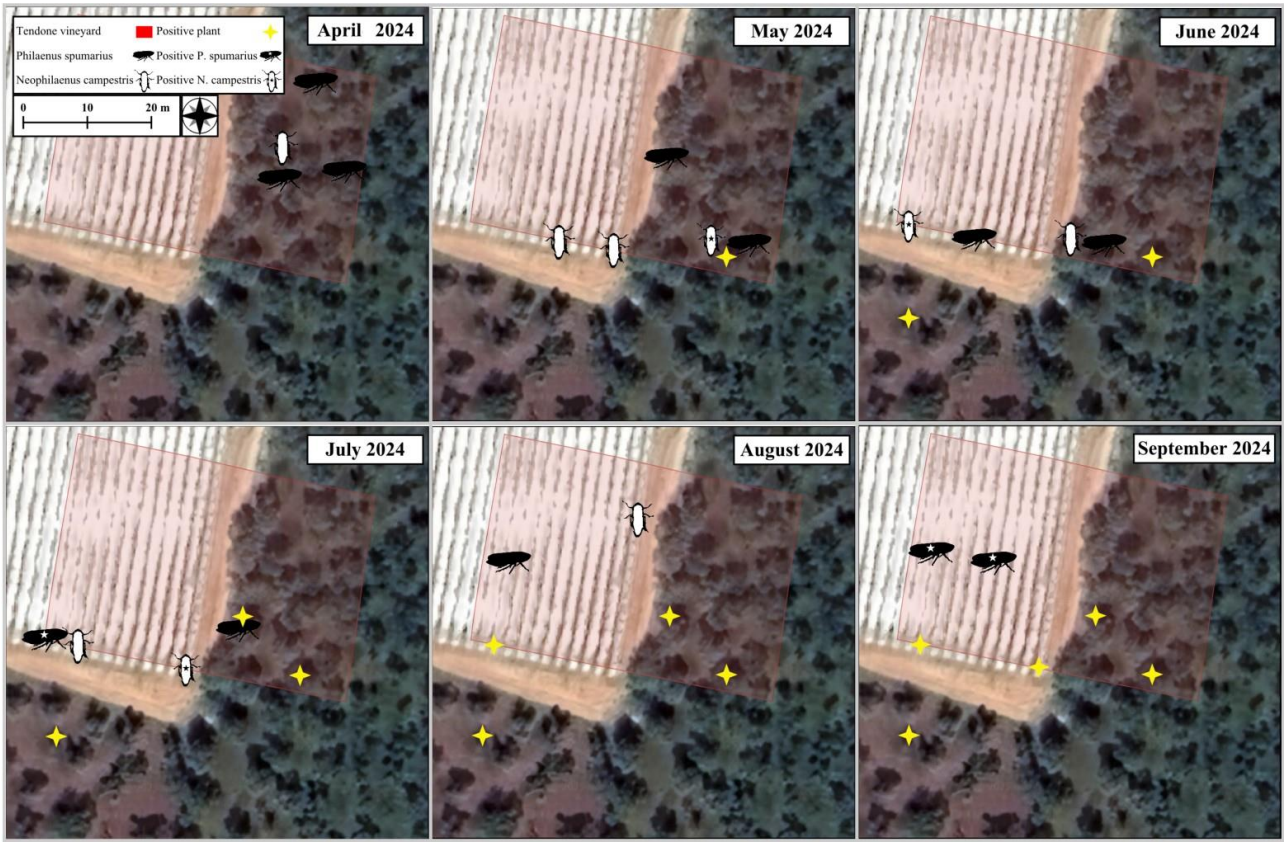
605 **Figure 3:** Relative abundance and infectivity of the two main vectors, considering the different
 606 compartments. A) Abundance and B) infectivity of *N. campestris* and C) abundance and D) infectivity
 607 of *P. spumarius*. Regarding vector abundance in vineyard, the relative abundance of *P. spumarius* and
 608 *N. campestris* refers only to tendone vineyards.



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610

611 Figure 4: Seasonal distribution patterns of the two main vectors of the bacterium in a tendone
612 vineyard.



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614
615