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1 Corresponding author: Domenico Bosco
2 DISAFA - Università degli Studi di Torino
3 Largo Paolo Braccini, 2 – 10095 Grugliasco (TO) Italy
4 Phone: +39 011 6708529
5 E-mail: domenico.bosco@unito.it
6

7 **Plant selection and population trend of spittlebug immatures (Hemiptera: Aphrophoridae) in olive groves**
8 **of the Apulia Region of Italy**

9 Crescenza Dongiovanni¹, Vincenzo Cavalieri², Nicola Bodino³, Daniele Tauro¹, Michele Di Carlo¹, Giulio
10 Fumarola¹, Giuseppe Altamura², Cesare Lasorella⁴, Domenico Bosco^{3,5}

11 ¹Centro di Ricerca, Sperimentazione e Formazione in Agricoltura Basile Caramia, Via Cisternino, 281,
12 70010 Locorotondo (Bari), Italy ²CNR – Istituto per la Protezione Sostenibile delle Piante, SS Bari, Via
13 Amendola 122/D, 70126 Bari, Italy ³CNR – Istituto per la Protezione Sostenibile delle Piante, Strada delle
14 Cacce, 73, 10135 Torino, Italy ⁴Dipartimento di Scienze agro-ambientali e territoriali – Università degli
15 Studi di Bari Aldo Moro, Via Amendola, 165/A, 70126 Bari, Italy ⁵Dipartimento di Scienze Agrarie,
16 Forestali e Alimentari – Università degli Studi di Torino, Largo Paolo Braccini, 2, 10095 Grugliasco, Italy

17 **Abstract.** The xylem-limited bacterium *Xylella fastidiosa* Wells is the causal agent of severe diseases of
18 several cultivated and wild plants. It is transmitted by xylem-sap feeder insects, such as spittlebugs
19 (Hemiptera: Cercopoidea) and sharpshooters (Hemiptera: Cicadellinae). A dramatic epidemic of *X.*
20 *fastidiosa* subspecies *paucis* Sequence Type 53 is currently affecting a large area of the Apulia Region of
21 Italy, where it is spread by *Philaenus spumarius* L. adults within olives. In 2015 and 2016, field surveys were
22 carried out in Apulian olive groves to investigate host plant selection of spittlebug nymphs, in order to
23 identify the main plant species that can act as reservoirs of the vectors. Two different sampling methods
24 were used: randomized plant sampling and quadrats sampling. Host plant selection by *P. spumarius* and
25 *Neophilaenus campestris* (Fallen) nymphs was estimated using Manly's selection index. The botanic families
26 presenting the highest number of plants infested by *P. spumarius* nymphs were Asteraceae, Fabaceae, and
27 Apiaceae. Nymphs of *P. spumarius* were sampled on 72 plant genera, and, among the most common 25

28 genera, *Sonchus*, *Knautia*, *Glebionis*, *Urospermum* (Asteraceae), *Medicago*, *Vicia*, *Melilotus* (Fabaceae) and
29 *Daucus* (Apiaceae) were the ones selected preferentially, according to Manly's index results. Populations of
30 *P. spumarius* nymphs peak in early April, with densities ranging between 10-40 nymph m⁻², and were about
31 10-fold those of *N. campestris*. Plant infestation rate by spittlebug nymphs in 2016 was significantly higher
32 in olive groves located in Lecce province (infected area) than those situated in Bari province (non-infected
33 area).

34

35 **Keywords:** insect vectors, Cercopoidea, host plant, olive

36

37 **Introduction**

38 Spittlebugs are xylem-sap feeder hemipteran insects belonging to the families Aphrophoridae, Cercopidae
39 and Clastopteridae (this latter family is absent in Europe). Nymphs of “true” spittlebugs (Aphrophoridae)
40 develop above ground and are well known for their spittle masses produced by mixing excretion, secretion
41 produced by abdominal glands and air bubbles introduced via caudal appendages, providing a protection
42 from both predation and solar radiation (Whittaker 1970, Chen et al. 2018, Cornara et al. 2018). Immatures
43 develop through five nymph instars that, with few exceptions, feed on herbaceous plants (Halkka et al. 1977,
44 Nickel and Remane 2002). The adults, generally long living, can continue to either feed on herbaceous plants
45 or move to the canopy of trees and shrubs. This host shifting behaviour is almost obligatory under the
46 conditions of warm, dry Mediterranean areas, where the ground cover vegetation almost completely
47 disappears during summer and only woody plants can sustain feeding of adults (Bodino et al. 2017).

48 The spittlebug *Philaenus spumarius* L. is by far the most common and widespread xylem-sap feeder insect in
49 Europe, and locally can reach high densities (Whittaker 1973, de Jong 2014, Rodrigues et al. 2014). It is
50 highly polyphagous, both during nymphal and adult stage, and adults are polymorphic for dorsal
51 pigmentation (Halkka et al. 1967, Drosopoulos 2003, Borges et al. 2018). Females of *P. spumarius* undergo
52 an ovarian diapause (Witsack 1973) and, even if they can mate soon after emergence (Wiegert 1964,
53 Cornara et al. 2018), they do not mature eggs. At the end of the summer-beginning of autumn, depending on
54 the latitude, adults are back to the herbaceous ground cover and females start maturing and lay eggs,
55 generally on dry leaves or plant material (e.g. straw) on the soil (Weaver and King 1954).

56 *Philaenus spumarius* has been poorly studied during the last 50 years, and research was focused mainly on
57 its polymorphism and its importance in meadow ecosystems. Recently, after the repeated discoveries of the
58 bacterium *Xylella fastidiosa* Wells in Europe, and the associated epidemic disease of olive trees in the
59 Apulian Region of Italy, that already spread to an area of at least 5,000 Km² encompassing one to three
60 million olive trees (Signorile, 2018), interest on spittlebugs has dramatically increased.

61 Indeed, xylem-sap feeder insects (namely sharpshooters in the family Cicadellidae subfamily Cicadellinae
62 and spittlebugs in the family Aphrophoridae) are well-known vectors of the xylem-limited plant pathogenic
63 bacterium *X. fastidiosa* (*Xf*) (Redak et al. 2004). The transmission of *Xf* by insects is peculiar in that it does
64 not require a latent period, yet the bacteria are persistently transmitted. Bacteria are restricted to the foregut
65 (namely the pre-cibarium) and do not infect systemically the insect body (Hill et al. 1995, Almeida et al.
66 2005). The currently available phylogenetic data on *Xf* indicate that the invasive strain in Apulia, belongs to
67 the *X. fastidiosa* subspecies *pauca*, sequence type (ST) 53, and was possibly introduced from Costa Rica
68 (Giampetruzzi et al. 2017). Furthermore, other *Xf* subspecies/STs have been recently discovered in France
69 and Spain (EFSA, 2018). The presence of *Xf* in Mediterranean regions prompted research on the insect
70 vectors of the bacterium in the new infected areas, where a number of potential *X. fastidiosa* vectors are
71 present throughout the Mediterranean basin (EFSA 2015). Preliminary investigations pointed out that,
72 among Aphrophoridae, two species were common in the infected area of Lecce province, *P. spumarius* and
73 *Neophilaenus campestris* (Fallén) (Elbeaino et al. 2014, Ben Moussa et al. 2016). Attempts to identify
74 vectors of the CoDIRO strain of *X. fastidiosa* in Apulia Region were successful and field-collected *P.*
75 *spumarius* were found transmitting *Xf* to periwinkle (Saponari et al. 2014). Cornara, Cavalieri, et al. (2017)
76 confirmed the role of *P. spumarius* and demonstrated that spittlebugs collected in heavily infected olive
77 groves transmitted *Xf* to olive, oleander and periwinkle plants. Finally, the olive-to-olive transmission by *P.*
78 *spumarius* was achieved under fully controlled transmissions, although *N. campestris* failed to transmit under
79 the same experimental conditions (Cornara, Saponari, et al. 2017). Very recently, the *Xf* transmission
80 competence of *N. campestris* and of *Philaenus italosignus* Drosopoulos & Remane have been proved under
81 experimental conditions (Cavalieri et al. 2018).

82 The spread of *X. fastidiosa* diseases is the outcome of complex biotic and abiotic interactions and it is hard to
83 predict; however, the speed of spread depends, among other factors, on the population level of competent
84 vectors. In the olive groves, the main factor regulating vector population level is the availability of a ground
85 cover and its species composition that can be more or less favourable/attractive to spittlebugs. In spite of a
86 rich literature reporting host plants of *P. spumarius* nymphs, e.g. Weaver and King (1954) provided a list of
87 more than 200 plant species, no information is available on host plant preference of this species in
88 Mediterranean region. Similarly, for *Neophilaenus* spp., data from literature indicate that nymphs are

89 associated with gramineous plants (Whittaker and Tribe 1998), but information on host plant preference
90 among these latter is not available. Therefore, the aim of the present work was to describe host plant
91 selection of spittlebug nymphs under field conditions in Apulian olive groves located both inside and outside
92 the *Xf*-infected area, thus identifying those plants that, both inside and nearby olive groves, can act as
93 reservoirs of the vectors.

94

95 **Materials and Methods**

96 Monitoring of spittlebug nymphs was carried in Apulian olive groves during Spring 2015 and 2016. Three
97 survey campaigns were carried out using two different sampling methods: 1) randomized plant sampling,
98 consisting in the examination of about 100 individual plants per each of the most common plant genera
99 found in the different olive orchards (range 8 – 24 plant genera per olive grove), looking for spittle masses of
100 *P. spumarius* nymph; 2) quadrats sampling, consisting in visual counting of spittlebug nymphs, both *P.*
101 *spumarius* and *Neophilaenus campestris*, in 12 samples (1 m² each) randomly distributed along the two
102 diagonals of olive orchards. During spring 2015, six olive groves (provinces of Bari, Brindisi, Lecce and
103 Taranto) were inspected following method 1, and three (province of Lecce) with method 2; in all the nine
104 olive groves surveys were carried out 3-4 times during spring, from late March to early May. In Spring 2016,
105 42 olive groves located in Bari, Brindisi and Lecce provinces were inspected employing method 1 and all
106 olive orchards were sampled only once during March-April. All the sampling sites are reported in Figure 1.
107 During each survey, plants were identified at the genus level according to Pignatti (1982) and checked for
108 presence of spittles and all plants carrying at least one spittle were considered infested. Identification of
109 Poaceae genera was not always possible (e.g. in the pre-flowering stage), and therefore host plants were
110 classified as Poaceae spp.. During visual countings, the nymphal instars of *Philaenus* were morphologically
111 determined according to (Weaver and King 1954). Analyses of host plant selection for *P. spumarius* nymphs
112 were carried out separately for each survey and data from different sampling dates in 2015 surveys were
113 pooled. Pre-imaginal population dynamics were analysed using only the 2015 quadrat samplings data.

114 Data analysis

115 Host plant selection by *P. spumarius* and *Neophilaenus* spp. nymphs was estimated using infestation
116 percentage, both total and mean (\pm SE), and Manly's selection index for a constant prey population (Manly et
117 al. 1994), calculated for each plant genus. In order to allow a clear comparison of the results, the number and
118 percentage of infested plants were pooled by olive grove for all the three surveys, thus the effect of date on
119 plant selection was not investigated. Manly's selection index links the proportion of infested individual
120 plants (positive individual plants) with the plant food supply (number of plants surveyed). An index value
121 above or below the "1/m-threshold" (m, number of available plant genera) indicates a positive or negative
122 selection, respectively. Therefore, a value significantly above the 1/m means that the plant genus is selected
123 disproportionately high compared with its abundance and thus is preferred; on the contrary, if it is below 1/m
124 the plant genus tend to be avoided. However, it is noteworthy that the values for the selection index are
125 normalized, so that their sum is constant ($\Sigma = 1$), this means that if one plant genus is preferred, another one
126 has to be avoided. To test if the mean value of Manly's index was significantly different from 1/m threshold,
127 a percentile bootstrapped (n = 9999), 20% trimmed means, one sample *t*-test was performed (function
128 *trimpb*, *WRS* package, R Core Team 2017).

129 Differences in population density over season between *P. spumarius* and *Neophilaenus* spp. during 2015
130 quadrats sampling were analysed using a mixed generalized linear model (GLMM) (function *glmer*, package
131 *lme4*, R Core Team 2017). Data were modelled using Poisson distribution with log link function, with
132 spittlebug species and olive grove as fixed factors, whereas Date was considered as a random effect factor.
133 Differences within groups were tested using a Holm–Sidak test for pairwise comparisons. The proportion of
134 overall infested plant per olive orchard in 2016 plant samplings was analysed for differences between olive
135 groves located in Bari or Lecce province, through generalized linear model (GLM), assuming binomial
136 distribution; model estimates were corrected for overdispersion (*glm* link function = quasi binomial).

137 Results

138 Host plant selection

139 The surveys carried out in 2015 and 2016 included 90 unique genera of herbaceous plants, for a total of
140 145,821 examined plants and 8,619 infested plants (overall infestation rate 5.9%), belonging to 72 different

141 genera (Suppl. Table S1). The botanic families accounting for the majority of sampled plants were
142 Asteraceae, Poaceae, Fabaceae and Rubiaceae. The botanic families presenting the highest number of plants
143 infested by *P. spumarius* nymphs were Asteraceae (3319 infested plants; 38.51% of total infested plants),
144 Fabaceae (2423; 28.11%), Apiaceae (760; 8.82%) and Poaceae (383; 4.44%).

145 To avoid biases in plant selection given by rare plant taxa with high infestation rates, but little ecological
146 value, only the 25 most common plant genera (i.e. with more individual plants sampled) were used for host
147 plant selection analyses. The 25 most common plant genera represented 67.8% of total plants sampled and
148 were ranked based on total infested plants sampled across the three surveys (Table 1) (the complete list of
149 sampled plant genera, together with the percentage of infested plants, is reported in Suppl. Table S1).

150 *Sonchus* was the plant genus presenting the highest number of infested plants by *P. spumarius* nymphs in all
151 the three surveys; in the 2015 quadrats sampling, *Sonchus* was the prevalent host plant of meadow spittlebug,
152 with an average infestation rate of 44% and representing almost 21% of the total infested plants. Also during
153 the 2015 plants sampling, *Sonchus* was the plant genus with the highest mean percentage of total infested
154 plants (14.3%), followed by *Knautia* (11.4%). The 2016 plants samplings involved a much higher number of
155 olive groves, with different plant composition and environmental conditions and therefore showed a greater
156 variety in the most infested plant genera. Actually, over the 42 olive groves, *Vicia*, *Medicago* and *Knautia*
157 presented mean infestation rates similar to the one registered for *Sonchus* (Table 1).

158 Taking into consideration all the plant genera sampled across the three surveys (Suppl. Table S1), some
159 relatively uncommon plants (i.e. not included in the 25 most common plant taxa) showed very high rates of
160 infestation, sometimes higher than *Sonchus*, e.g. *Foeniculum* (23%), *Lathyrus* (23%), *Galactites* (21%) and
161 *Rosmarinus* (15%).

162 The Manly's selectivity index results concerning the 25 most common plant genera supported the positive
163 selection of *Sonchus* by pre-imaginal instars of *P. spumarius* in all the three surveys (Fig. 2), but also showed
164 other common plant genera preferentially selected during the different surveys, like *Knautia*, *Glebionis* and
165 *Daucus*. However, the host plant selection results were not always similar between the different surveys,
166 given also the differences in sampling methodology and number of olive groves sampled (see M&M). In the
167 2016 survey, that included the highest number of olive orchards (42), the Fabaceae *Medicago*, *Vicia* and
168 *Melilotus*, the Asteraceae *Glebionis* and *Urospermum*, Apiaceae *Daucus* and Poaceae presented mean index

169 values significantly higher than the threshold $1/m$, meaning that they were preferentially selected (Fig. 2c).
170 *Crepis* was among the plant genera selected positively during 2015 quadrats samplings (Fig. 2a), whereas
171 *Lathyrus*, *Picris*, *Melilotus*, *Lotus* and *Plantago* were also selected preferentially during 2015 plant
172 samplings (Fig. 2b).

173 Some common plant genera appeared to be negatively selected, or avoided, by spittlebugs. Several Poaceae,
174 *Lysimachia*, *Raphanus*, *Papaver*, *Fumaria*, *Geranium* and *Sherardia* presented significantly lower values of
175 the Manly's index compared to the $1/m$ threshold (Fig. 2); these results were confirmed by the low mean
176 infestation rates registered for these plant taxa (Table 1). Poaceae, considered as whole, presented a
177 relatively high value of the Manly's index (0.072) only during 2016 plants samplings (Fig. 2c).

178 *Neophilaenus* spp. nymphs were sampled and identified only during the 2015 quadrats survey, with a total of
179 267 nymphs sampled that accounted for 9.97% of the total spittlebug population. Poaceae were by far the
180 most selected host plants, with 94.01% of total *Neophilaenus* spp. nymphs located on plants belonging to this
181 family. In detail, *Avena* was the plant genera on which most of the nymphs were found (52.81% of the total
182 nymphs), followed by *Hordeum* (16.1%), *Lolium* (15.36%), and *Dactylis* (5.99%). *Avena* and *Lolium* were
183 the only plant genera with Manly's selectivity index values significantly above the threshold $1/m$ (0.015)
184 [*Avena*: mean = 0.47 (CI 0.222 – 0.844); *Lolium*: mean = 0.07 (CI 0.029 – 0.126)]. Host plants belonging to
185 other families were seldom selected, with only seven *Neophilaenus* spp. nymphs sampled on forbs
186 throughout the season.

187 Population abundance of spittlebug nymphs

188 During the 2015 quadrats survey, *P. spumarius* and *Neophilaenus* spp. nymphs showed different populations
189 abundance throughout the season. In total, 2409 *P. spumarius* and 267 *Neophilaenus* spp. immatures were
190 sampled, with an overall *Philaenus/Neophilaenus* ratio of 9.02. Densities of *P. spumarius* nymphs were
191 higher than *Neophilaenus* spp. throughout the season in all the three olive groves surveyed (GLMM: $F =$
192 885.63, d.f. = 1, $p < 0.001$). The difference between the two spittlebug species was particularly high in the
193 olive grove located in Surbo, where only 31 grass spittlebugs were sampled and the ratio was 35.2 (Fig. 3c).
194 Excluding the last sampling date (when spittlebug abundances were really low in all the olive groves, as
195 most of insects were already emerged as adults) *Philaenus spumarius* densities throughout the season were
196 significantly different among olive groves, with population in Ruffano orchard significantly lower than the

197 populations observed in the other two olive groves (GLMM: $F = 13.31$, d.f. = 2, $p = 0.001$). However,
198 including all sampling dates, densities were not significantly different among olive groves (GLMM: $F =$
199 2.05 , d.f. = 2, $p = 0.358$). The first sampling dates, around 20-25th March, were carried out when 2nd nymphal
200 instars were prevalent (Fig. 4). The overall seasonal abundance trend of *Philaenus spumarius* nymphs
201 peaked in early-mid April, whereas during the last samplings in late April-early May the nymphal
202 populations were very low (Fig. 3). In the three sites of the Lecce province, nymphs disappeared by the end
203 of April-beginning of May in 2015 (Fig. 3). Populations of *Neophilaenus* spp. seemed to follow a similar
204 trend, although the very low population levels did not allow an accurate description of the populational
205 dynamics.

206 The phenological progression of nymphal stages occurred as a series of overlapping distributions, except for
207 the last sampling in late April-early May, when only 5th instar nymphs were collected. First and 2nd instars
208 nymphs were found until the first week of April, whereas 3rd instar nymphs were present until mid-April. 4th
209 instar nymphs were collected during all the sampling span, with a peak in the first half of April; 5th instar
210 represented most of the nymphs in late April-early May. The high degree of overlapping of the different
211 nymphal stages is well described by the coexistence of all the five stages during the first half of April in all
212 the three olive groves (Fig. 4).

213 Plant infestation rate by spittlebug nymphs in 2016 was significantly higher in olive groves located in Lecce
214 province (6.85 ± 1.18 %) than those situated in Bari province (2.08 ± 0.51 %) (GLM: $\chi^2 = 14.63$ d.f. = 1, $P <$
215 0.001)

216

217 Discussion

218 The host plant selection and nymph population abundance of the vectors *P. spumarius* and *N. campestris* in
219 the herbaceous ground cover of olive groves have been described in the Apulia Region, including the area
220 where *X. fastidiosa* subsp. *pauca* ST53 is epidemic on olive.

221 Host plant selection has been investigated using two different sampling methods, randomized plant sampling
222 and quadrats sampling on a large number of sites over two consecutive years. The results of the different
223 surveys are quite consistent, although ranking of preferred host plants slightly differ because of the different
224 plant composition of herbaceous covers in the different olive groves. Some genera of the families Asteraceae

225 (mainly *Sonchus*, *Crepis*, *Picris*), Fabaceae (mainly *Medicago*, *Vicia*, *Lathyrus*) and Apiaceae (*Daucus*,
226 *Foeniculum*) are preferentially selected by *P. spumarius*, while Poaceae (mainly *Avena*, *Hordeum* and
227 *Lolium*) are preferentially selected by *N. campestris*. Due to the very high polyphagy of the meadow
228 spittlebug, it is interesting to identify, besides the preferred plants, those species that are negatively selected.
229 Among these latter, some Poaceae, *Oxalis* (Oxalidaceae), *Lysimachia* (Myrsinaceae), *Sherardia* (Rubiaceae),
230 *Geranium* (Geraniaceae), *Papaver* (Papaveraceae), *Fumaria* (Fumariaceae) and *Raphanus* (Brassicaceae)
231 were avoided by *P. spumarius* nymphs (i.e. significantly less infested compared to their abundance in the
232 sample area). Our results confirm that pre-imaginal instars of the meadow spittlebug tend to prefer forbs
233 (herbs other than grasses), as often reported in literature (e.g. Cornara et al. 2018; Halkka et al. 1967; Weaver
234 and King, 1954), but also show, only during the large scale survey of 2016, a positive selection for grasses
235 (Poaceae). This outcome can have different explanations: a) some common gramineous species can be
236 relatively attractive for later instar nymphs, such as *Sorghum* and *Avena*, possibly because of their structure,
237 providing wide leaf axils and protected feeding sites (McEvoy 1986); b) seasonality (e.g. premature drying
238 of dicots and unavailability of preferred host plants); c) uneven sprouting of plants following grass cuttings;
239 d) impossibility to separate the effect of site and date of inspection, given that only one sample was carried
240 out per each olive grove. On the contrary, *N. campestris* nymphs appear strictly associated to Poaceae, as
241 reported in the literature (Halkka et al. 1967, Whittaker 1973, Nickel and Hildebrandt 2003).

242 Host plant association of *P. spumarius* nymphs is not fully static, as nymphs, especially later instars, show
243 some dispersal capability, not only within but also among plants (author's observation). This mobility is
244 limited and estimated to a maximum of 60 cm by Halkka et al. (1967), but results of host plant association
245 can be partly biased by the age of the nymph population as early instars nymphs tend to prefer plants with
246 basal rosettes (Bodino et al. 2017) and later instar can probably feed on a wider range of plants (Hoffman
247 and McEvoy 1985). However, the present study describes the host plant selection by *P. spumarius* nymphs
248 on a relative large geographical scale, and therefore could not be focused on plant association of age-
249 structured populations of *P. spumarius*. Interestingly, with the exception of *Erigeron* spp. and *Chenopodium*
250 spp., found infected in late autumn, none of the other host plants in the Apulia Region have been found
251 infected by *X. fastidiosa* ST53 so far. It is worth noting that, even if nymphs acquire the pathogen, they will

252 lose pathogen and infectivity through moulting and therefore newly emerged adults are *Xylella*-free and must
253 feed on an infected plant to become infectious (Almeida et al. 2005).

254 The wide polyphagy of *P. spumarius* is well known (Weaver and King 1954, Ossiannilsson 1981, Cornara et
255 al. 2018) but host plant selection and host plant preference in open field conditions have been rarely
256 investigated using a rational approach (see Halkka et al. 1967). The present study investigated host plant
257 selection under real field conditions in the olive groves rather than host plant preference, as determined under
258 controlled conditions using choice tests. Host plant selection was driven by host plant compositions in the
259 different olive groves we inspected, and thus our results reflected the plant taxa actually exploited by
260 spittlebug nymphs under the peculiar conditions of the investigated areas. This could explain the strong
261 differences in host plant selection between our study and the results reported by Halkka et al. (1967).

262 Host plant selection by *P. spumarius* and other spittlebug species is still unclear, probably being influenced
263 by multiple factors, for example internal factors in the plants (e.g. amino acids concentration, availability of
264 water) (Weaver and King 1954, Horsfield 1978, Thompson 1994), mechanical or ecological barriers
265 (presence of trichomes or lignified tissues) (Hoffman and McEvoy 1985; McEvoy 1986). *Philaenus*
266 *spumarius* nymphs seem indeed to prefer tender shoots, possibly not distant from the apical buds, and their
267 number appear to be correlated with high biomass of green plant material (Weaver and King 1954, Wiegert
268 1964). However, spatial conformation of the plant is also crucial, being leaf axils preferred over the stems,
269 providing better shelter and permitting the formation of bigger foams by nymphs, thus increasing the
270 protection from both natural enemies and desiccation (McEvoy 1986). It is out of the scope of our study to
271 investigate on these determinants, nonetheless our results, highlighting some clear host plant selection and
272 avoidance by *P. spumarius* nymphs, suggest the need of further research on this topic.

273 The maximum population level of spittlebug nymphs measured in the three olive groves located inside the
274 infected area was estimated in a range of 10 – 40 nymphs of *P. spumarius* per square meter, whereas the
275 populations of *N. campestris* were much lower, with a peak of 1 – 7 nymphs per square meter. Indeed, the
276 meadow spittlebug can be present in high densities inside olive groves and, if we consider its role as a vector
277 of *X. fastidiosa*, its abundance can explain why the disease has spread so fast in the area. In this context, it is
278 interesting to note the higher plant infestation rate recorded in olive groves located in Lecce province
279 compared to the ones located in Bari province. Lower populations of the vector north of the infected area

280 may contribute to slow down the *X. fastidiosa* spread. However, these are preliminary data based only on
281 spittle counts, and they should be confirmed by *ad hoc* estimation of vectors' population abundances.
282 Our study shows the high polyphagy and population levels of the principal vector of *X. fastidiosa* in Apulia,
283 *P. spumarius*, pointing out the urgent need of control measures, like the ones that are mandatory to suppress
284 nymph population by soil tilling
285 (http://www.emergenzaXylella.it/portal/portale_gestione_agricoltura/Documenti/lineeGuida). If such a
286 nymph population is left undisturbed, a high number of adults will emerge and move to the olive canopies,
287 where they can acquire and transmit the pathogen (Cornara, Cavalieri, et al. 2017, Cornara, Saponari, et al.
288 2017). A correct timing of soil tilling to prevent the emergence of adults is of key importance and our data
289 suggest that this measure should be applied in correspondence to the peak of nymphal populations (i.e. mid-
290 April) and before the emergence of adults, to achieve the maximum efficacy.
291 A better knowledge of the mechanisms influencing plant choice by the vectors of *X. fastidiosa* could help in
292 developing effective management strategies, such as modifications in plant communities present inside and
293 around olive groves to limit the vectors' population abundance.

294

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298 POnTE".

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- 397

398 Figures and tables legends

399 **Fig. 1:** Locations of Apulian olive groves surveyed for spittlebugs during the 2015-2016 samplings. ■ =
400 2015 quadrat sampling; ▲ = 2015 plants sampling; × = 2016 plants samplings.

401 **Fig. 2:** Manly's selection indexes (mean ± SE) for the top 25 plant genera for abundance in the three surveys,
402 arranged for decreasing mean values of the index (a, 2015 quadrats sampling; b, 2015 plants sampling; c,
403 2016 plants samplings). The dashed lines display the $1/m$ thresholds, where m is the number of available
404 plant genera; values exceeding this threshold indicate positive selection, whereas the values below indicate
405 negative selection for the respective plant genera.

406 **Fig. 3:** Population abundance of spittlebugs nymphs (mean ± SE) in 2015 quadrat samplings in three olive
407 groves located in Ruffano (a), Gallipoli (b) and Surbo (c). Continuous line, *P. spumarius*; dashed line,
408 *Neophilaenus campestris*.

409 **Fig. 4:** Nymphal stages structure of *P. spumarius* over the season in 2015 quadrat samplings in three olive
410 groves located in Ruffano (a), Surbo (b) and Gallipoli (c).

411 **Table. 1:** No. of sampled individual plants, no. of plants infested by *P. spumarius* and percentage (mean ±
412 SE) of plants infested of top 25 plant genera sampled during 2015-2016 spittlebugs surveys in Apulian olive

413 orchards. Plant genera are ranked in descending order based on total infested plants sampled across the three
414 surveys.



Fig. 1: Locations of Apulian olive groves surveyed for spittlebugs during the 2015-2016 samplings. ' = 2015 quadrat sampling; π = 2015 plants sampling; € = 2016 plants samplings.

127x105mm (300 x 300 DPI)

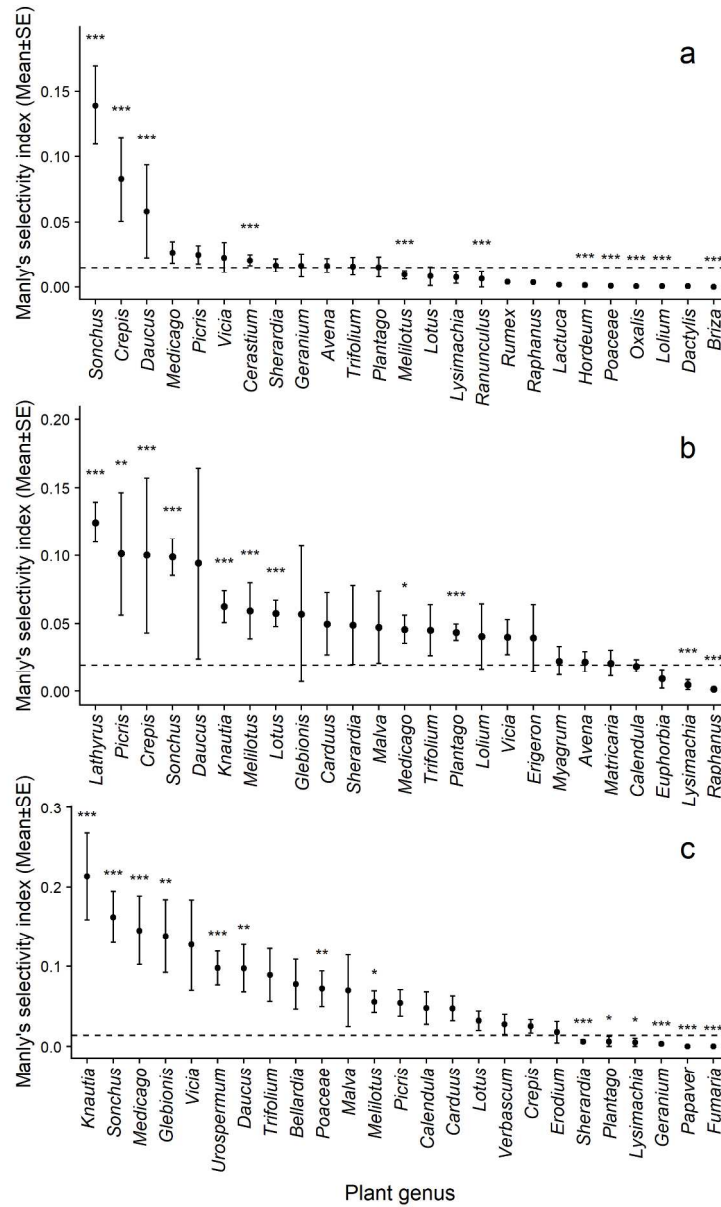


Fig. 2: Manly’s selection indexes (mean ± SE) for the top 25 plant genera for abundance in the three surveys, arranged for decreasing mean values of the index (a, 2015 quadrats sampling; b, 2015 plants sampling; c, 2016 plants samplings). The dashed lines display the 1/m thresholds, where m is the number of available plant genera; values exceeding this threshold indicate positive selection, whereas the values below indicate negative selection for the respective plant genera.

177x279mm (300 x 300 DPI)

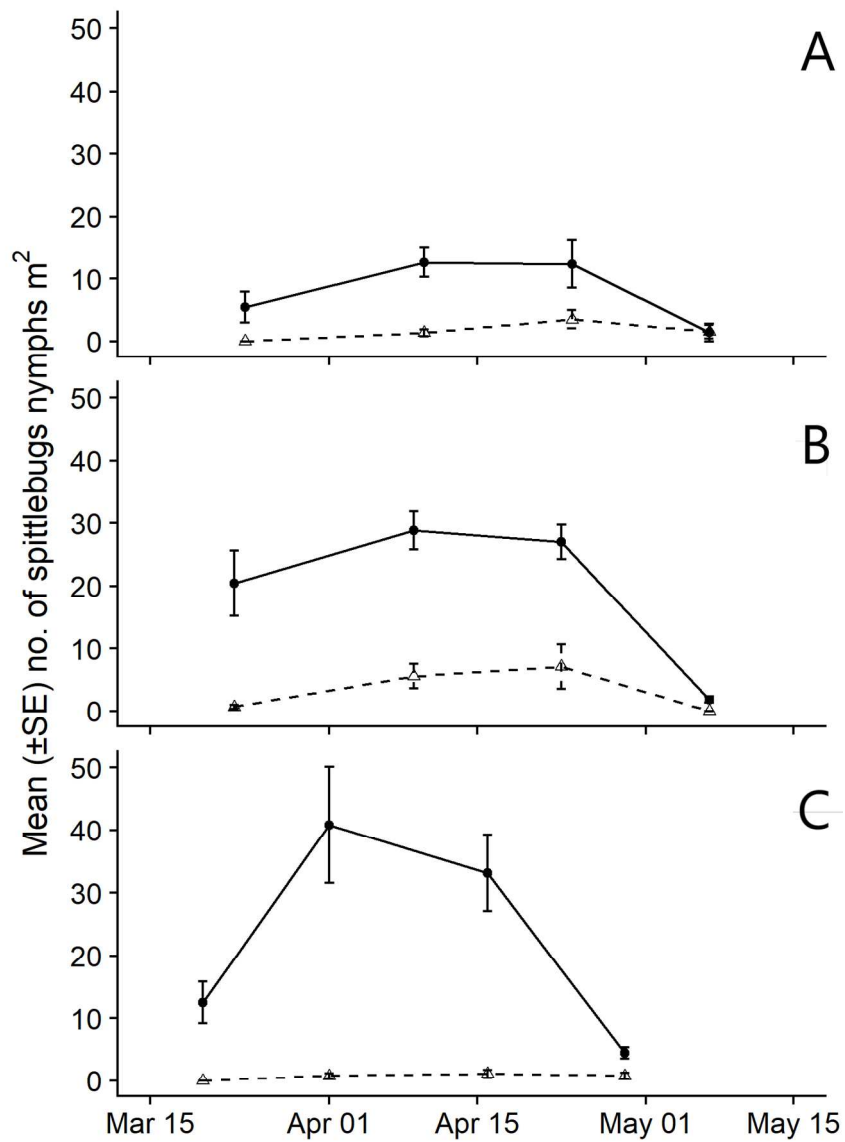


Fig. 3: Population abundance of spittlebugs nymphs (mean \pm SE) in 2015 quadrat samplings in three olive groves located in Ruffano (a), Gallipoli (b) and Surbo (c). Continuous line, *Philaenus spumarius*; dashed line, *Neophilaenus campestris*

396x555mm (96 x 96 DPI)

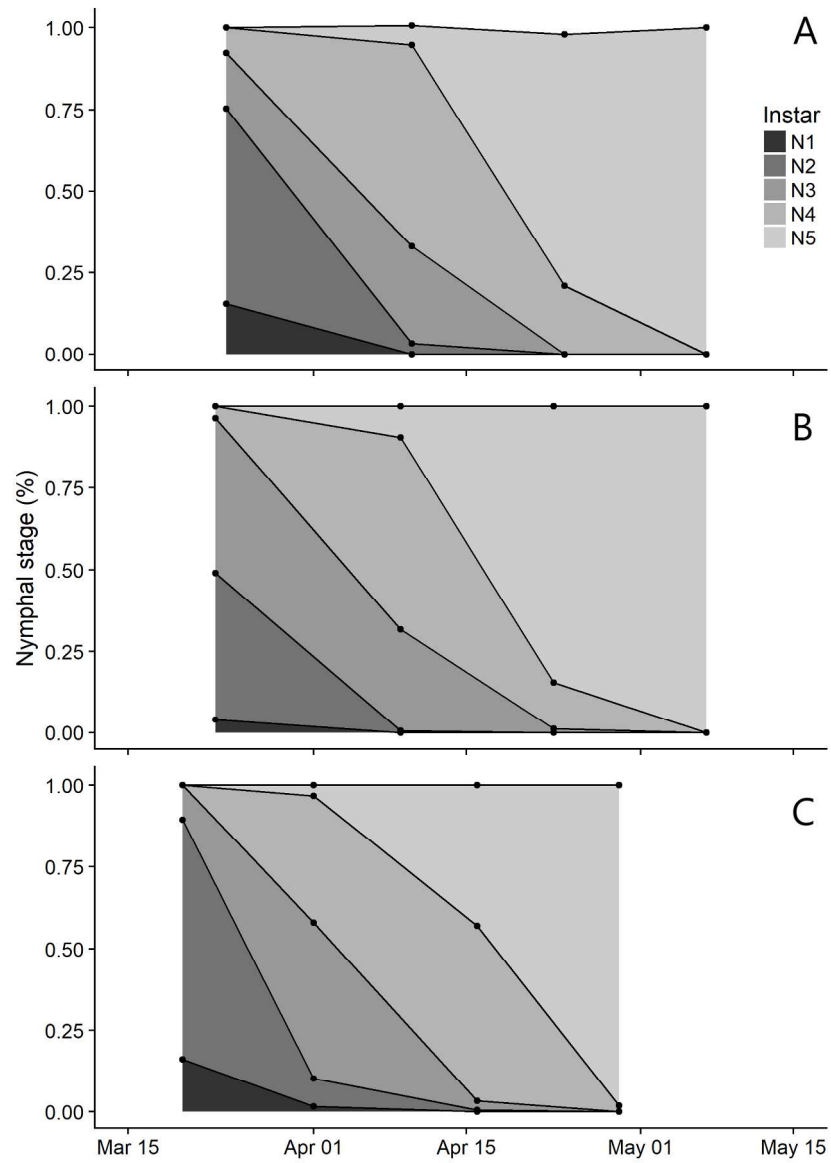


Fig. 4: Nymphal stages structure of *P. spumarius* over the season in 2015 quadrat samplings in three olive groves located in Ruffano (a), Surbo (b) and Gallipoli (c).

555x793mm (96 x 96 DPI)

Tab. 1: No. of sampled individual plants, no. of plants infested by *P. spumarius* and percentage (mean \pm SE) of plants infested of top 25 plant genera sampled during 2015-2016 spittlebugs surveys in Apulian olive orchards. Plant genera are ranked in descending order based on total infested plants sampled across the three surveys.

Genus/taxon	Plant family	Quadrats sampling 2015			Plants sampling 2015			Plants sampling 2016		
		Sampled plants (olive groves)	Infested plants	% infested plants (Mean \pm SE)	Sampled plants (olive groves)	Infested plants	% infested plants (Mean \pm SE)	Sampled plants (olive groves)	Infested plants	% infested plants (Mean \pm SE)
<i>Sonchus</i>	Asteraceae	629 (3)	345	44.3 \pm 17.5	1885 (5)	456	24.3 \pm 1.5	3278 (34)	404	11.9 \pm 3.4
<i>Medicago</i>	Fabaceae	1250 (3)	69	8.8 \pm 3.9	1608 (5)	167	10.3 \pm 3.8	2659 (27)	346	12.7 \pm 4.1
<i>Daucus</i>	Apiaceae	246 (2)	25	9.7 \pm 1.5	2048 (6)	289	12.0 \pm 4.9	1749 (18)	184	10.2 \pm 4.6
<i>Vicia</i>	Fabaceae	465 (3)	23	5.3 \pm 3.3	987 (5)	124	11.5 \pm 4.0	1483 (16)	343	21.7 \pm 9.7
<i>Glebionis</i>	Asteraceae	47 (2)	16	18.2 \pm 18.2	745 (2)	103	10.2 \pm 9.7	2376 (24)	270	10.9 \pm 4.2
<i>Crepis</i>	Asteraceae	1283 (3)	185	18.5 \pm 4.2	763 (2)	122	20.9 \pm 13.9	1724 (18)	79	4.0 \pm 1.9
<i>Knautia</i>	Caprifoliaceae	48 (1)	14	29.2 \pm 0.0	633 (2)	154	24.6 \pm 0.4	1441 (13)	210	13.8 \pm 4.4
<i>Melilotus</i>	Fabaceae	583 (2)	12	1.9 \pm 0.3	1573 (5)	173	11.5 \pm 4.6	2136 (21)	169	7.9 \pm 3.0
<i>Trifolium</i>	Fabaceae	397 (3)	17	4.3 \pm 2.7	2011 (6)	160	8.9 \pm 3.6	2775 (28)	142	5.2 \pm 1.4
<i>Picris</i>	Asteraceae	739 (3)	51	7.9 \pm 3.5	1175 (4)	134	18.8 \pm 7.6	1626 (17)	114	7.1 \pm 3.2
<i>Lotus</i>	Fabaceae	1526 (2)	73	3.0 \pm 2.6	920 (4)	148	13.6 \pm 4.4	2152 (23)	56	2.6 \pm 1.1
<i>Sherardia</i>	Rubiaceae	5777 (3)	186	5.4 \pm 2.5	678 (4)	48	20.0 \pm 15.5	1641 (16)	15	0.8 \pm 0.4
<i>Carduus</i>	Asteraceae	–	–	–	1230 (5)	142	10.3 \pm 3.3	1775 (23)	93	5.5 \pm 2.2
<i>Avena</i>	Poaceae	3529 (3)	83	4.5 \pm 2.3	1817 (5)	98	5.7 \pm 1.6	–	–	–
<i>Malva</i>	Malvaceae	25 (2)	6	23.6 \pm 1.4	936 (3)	76	7.9 \pm 3.9	2071 (22)	81	4.9 \pm 2.5
<i>Calendula</i>	Asteraceae	21 (2)	2	10.1 \pm 2.4	807 (4)	27	4.4 \pm 0.9	1776 (18)	84	5.2 \pm 2.3
Poaceae spp.	Poaceae	2480 (2)	10	0.3 \pm 0.3	–	–	–	1460 (15)	82	5.5 \pm 1.7
<i>Lolium</i>	Poaceae	8370 (3)	16	0.2 \pm 0.1	1342 (4)	70	10.0 \pm 8.2	–	–	–
<i>Plantago</i>	Plantaginaceae	245 (3)	8	3.6 \pm 2.2	658 (2)	54	11.6 \pm 4.6	1100 (12)	10	0.8 \pm 0.8
<i>Geranium</i>	Geraniaceae	592 (3)	16	3.4 \pm 1.6	427 (3)	12	3.7 \pm 3.1	1480 (15)	8	0.5 \pm 0.3
<i>Myagrum</i>	Brassicaceae	–	–	–	775 (3)	30	3.6 \pm 1.2	1208 (12)	3	0.2 \pm 0.2
<i>Hordeum</i>	Poaceae	1830 (3)	7	0.1 \pm 0.1	629 (3)	15	3.7 \pm 3.4	–	–	–
<i>Lysimachia</i>	Primulaceae	342 (3)	3	1.4 \pm 0.7	920 (4)	5	0.4 \pm 0.2	1100 (11)	2	0.2 \pm 0.2
<i>Dactylis</i>	Poaceae	4264 (1)	2	0.0 \pm 0.0	–	–	–	–	–	–
<i>Papaver</i>	Papaveraceae	182 (2)	0	0.0 \pm 0.0	2445 (25)	1	0.0 \pm 0.0	–	–	–

Supplementary table 1: list of plant taxa sampled during the three surveys carried out during 2015-2016

Genus/taxon	Plant family	Quadrats sampling 2015		
		No. sampled plants	No. olive groves	No. infested plants
<i>Adonis</i>	Ranunculaceae			
<i>Allium</i>	Amaryllidaceae	1	1	0
<i>Anthemis</i>	Asteraceae	125	1	6
<i>Astragalus</i>	Fabaceae			
<i>Avena</i>	Poaceae	3529	3	83
<i>Bellardia</i>	Orobanchaceae			
<i>Bellis</i>	Asteraceae	5	1	0
<i>Borago</i>	Boraginaceae			
<i>Brassica</i>	Brassicaceae	2	1	1
<i>Briza</i>	Poaceae	251	2	0
<i>Bromus</i>	Poaceae	166	1	0
<i>Calendula</i>	Asteraceae	21	2	2
<i>Capsella</i>	Brassicaceae			
<i>Carduus</i>	Asteraceae			
<i>Centaurea</i>	Asteraceae	2	1	0
<i>Cerastium</i>	Caryophyllaceae	213	2	5
<i>Cerinthe</i>	Boraginaceae	15	1	0
<i>Chenopodium</i>	Chenopodiaceae			
<i>Cichorium</i>	Asteraceae	9	1	0
<i>Cirsium</i>	Asteraceae			
<i>Convolvulus</i>	Convolvulaceae	156	2	2
<i>Coronilla</i>	Fabaceae			
<i>Crepis</i>	Asteraceae	1283	3	185
<i>Dactylis</i>	Poaceae	4264	1	2
<i>Daucus</i>	Apiaceae	246	2	25
<i>Diplotaxis</i>	Brassicaceae	2	1	0
<i>Ecballium</i>	Cucurbitaceae			
<i>Echium</i>	Boraginaceae	1	1	0
<i>Erigeron</i>	Asteraceae	67	3	13
<i>Erodium</i>	Geraniaceae	200	3	26
<i>Euphorbia</i>	Euphorbiaceae	90	2	8
<i>Foeniculum</i>	Apiaceae	25	1	1
<i>Fumaria</i>	Fumariaceae			
<i>Galactites</i>	Asteraceae	98	2	49
<i>Galium</i>	Rubiaceae	209	2	1
<i>Geranium</i>	Geraniaceae	592	3	16
<i>Glebionis</i>	Asteraceae	47	2	16
<i>Hordeum</i>	Poaceae	1830	3	7
<i>Isatis</i>	Brassicaceae			
<i>Knautia</i>	Caprifoliaceae	48	1	14
<i>Lactuca</i>	Asteraceae	368	1	2
<i>Lamium</i>	Lamiaceae	30	2	0
<i>Lathyrus</i>	Fabaceae			
<i>Legousia</i>	Campanulaceae			
<i>Lolium</i>	Poaceae	8370	3	16

<i>Lotus</i>	Fabaceae	1526	2	73
<i>Lysimachia</i>	Primulaceae	342	3	3
<i>Malva</i>	Malvaceae	25	2	6
<i>Matricaria</i>	Asteraceae	21	1	1
<i>Medicago</i>	Fabaceae	1250	3	69
<i>Melilotus</i>	Fabaceae	583	2	12
<i>Mercurialis</i>	Euphorbiaceae	140	2	0
<i>Muscari</i>	Asparagaceae	7	1	0
<i>Myagrum</i>	Brassicaceae			
<i>Myosotis</i>	Boraginaceae	71	1	0
<i>Nigella</i>	Ranunculaceae	2	1	0
<i>Oxalis</i>	Oxalidaceae	773	3	2
<i>Papaver</i>	Papaveraceae			
<i>Phalaris</i>	Poaceae	192	2	0
<i>Phleum</i>	Poaceae	1	1	0
<i>Phlomis</i>	Lamiaceae			
<i>Picris</i>	Asteraceae	739	3	51
<i>Pisum</i>	Fabaceae	5	1	0
<i>Plantago</i>	Plantaginaceae	245	3	8
Poaceae spp.	Poaceae	2480	2	10
<i>Ranunculus</i>	Ranunculaceae	1075	2	16
<i>Raphanus</i>	Brassicaceae	722	1	3
<i>Rapistrum</i>	Brassicaceae			
<i>Reichardia</i>	Asteraceae			
<i>Reseda</i>	Resedaceae	1	1	0
<i>Rosmarinus</i>	Lamiaceae			
<i>Rumex</i>	Polygonaceae	689	1	3
<i>Sanguisorba</i>	Rosaceae	5	1	0
<i>Scandix</i>	Apiaceae	3	1	0
<i>Scorpiurus</i>	Fabaceae	26	1	6
<i>Senecio</i>	Asteraceae	14	2	0
<i>Sherardia</i>	Rubiaceae	5777	3	186
<i>Silene</i>	Caryophyllaceae			
<i>Solanum</i>	Solanaceae			
<i>Sonchus</i>	Asteraceae	629	3	345
<i>Sorghum</i>	Poaceae	100	1	0
<i>Stellaria</i>	Caryophyllaceae	46	1	2
<i>Tordylium</i>	Apiaceae	38	1	4
<i>Torilis</i>	Apiaceae			
<i>Tragopogon</i>	Asteraceae	1	1	0
<i>Trifolium</i>	Fabaceae	397	3	17
<i>Urospermum</i>	Asteraceae			
<i>Verbascum</i>	Scrophulariaceae	1	1	0
<i>Veronica</i>	Scrophulariaceae	98	2	0
<i>Vicia</i>	Fabaceae	465	3	23

016. Total number of sampled plants, number of olive groves in which they have been s

% infested plants (Mean±SE)	Plants sampling 2015		
	No. sampled plants	No. olive groves	No. infested plants
0 ± 0			
4.8 ± 0	257	1	28
–			
4.52 ± 2.33	1817	5	98
–			
0 ± 0	74	1	0
–			
50 ± 0			
0 ± 0			
0 ± 0			
10.1 ± 2.4	807	4	27
–	339	2	0
–	1230	5	142
0 ± 0			
5.54 ± 3.56	407	2	2
0 ± 0			
–			
0 ± 0			
–			
3.69 ± 2.98	297	4	9
–			
18.52 ± 4.15	763	2	122
0.05 ± 0			
9.71 ± 1.47	2048	6	289
0 ± 0			
–			
0 ± 0			
19.37 ± 6.24	997	4	117
20.28 ± 8.42	500	2	37
8.83 ± 0.13	708	3	24
4 ± 0	370	3	64
–	141	2	1
47.18 ± 5.52			
5.56 ± 5.56	417	4	37
3.4 ± 1.59	427	3	12
18.18 ± 18.18	745	2	103
0.14 ± 0.14	629	3	15
–			
29.17 ± 0	633	2	154
0.54 ± 0	264	1	118
0 ± 0			
–	1091	3	326
–			
0.17 ± 0.1	1342	4	70

3.03 ± 2.63	920	4	148
1.41 ± 0.71	920	4	5
23.61 ± 1.39	936	3	76
4.76 ± 0	1228	4	37
8.82 ± 3.86	1608	5	167
1.87 ± 0.34	1573	5	173
0 ± 0	430	2	0
0 ± 0	65	1	0
–	775	3	30
0 ± 0			
0 ± 0			
0.18 ± 0.09	600	2	0
–	182	2	0
0 ± 0	220	2	0
0 ± 0			
–			
7.94 ± 3.51	1175	4	134
0 ± 0			
3.58 ± 2.24	658	2	54
0.27 ± 0.27			
0.74 ± 0.74	88	1	4
0.42 ± 0	830	3	1
–	300	1	25
–			
0 ± 0			
–			
0.44 ± 0	200	1	0
0 ± 0			
0 ± 0	63	1	0
23.08 ± 0	564	2	10
0 ± 0	591	3	29
5.36 ± 2.47	678	4	48
–			
–			
44.34 ± 17.47	1885	5	456
0 ± 0			
4.35 ± 0	146	1	6
10.53 ± 0	200	1	6
–			
0 ± 0			
4.35 ± 2.72	2011	6	160
–			
0 ± 0	610	2	207
0 ± 0			
5.29 ± 3.33	987	5	124

sampled, number of infested individual plants and mean (+SE) percentage of infested pl

% infested plants (Mean±SE)	Plants sampling 2016		
	No. sampled plants	No. olive groves	No. infested plants
	300	3	10
–	300	3	0
10.89 ± 0	1100	11	13
–	750	8	6
5.67 ± 1.57			
–	1474	16	112
0 ± 0			
–	550	6	22
–			
–			
4.4 ± 0.92	1776	18	84
0 ± 0	910	10	0
10.25 ± 3.33	1775	23	93
–			
0.52 ± 0.52	320	4	1
–			
–	300	3	0
–	300	3	0
–	455	5	10
9.19 ± 8.06	1200	12	1
–	152	2	6
20.9 ± 13.92	1724	18	79
–			
11.95 ± 4.87	1749	18	184
–	803	8	8
–	49	1	1
–	370	6	1
9.54 ± 8.3	258	3	54
7.16 ± 4.2	1281	14	89
2.41 ± 1.45	1092	16	14
23.2 ± 16.18	647	7	173
1.61 ± 1.61	1645	17	0
–	160	2	6
17.28 ± 11.12	902	10	17
3.69 ± 3.11	1480	15	8
10.16 ± 9.73	2376	24	270
3.74 ± 3.42			
–	70	3	0
24.63 ± 0.37	1441	13	210
44.7 ± 0	619	7	21
–	300	3	0
31.77 ± 9.25	400	4	15
–	500	5	1
10 ± 8.21			

13.64 ± 4.42	2152	23	56
0.43 ± 0.2	1100	11	2
7.88 ± 3.89	2071	22	81
3.45 ± 1.13	581	6	21
10.27 ± 3.76	2659	27	346
11.45 ± 4.61	2136	21	169
0 ± 0	1160	12	2
0 ± 0	330	5	0
3.61 ± 1.2	1208	12	3
–			
–	105	2	0
0 ± 0	100	1	0
0 ± 0	2445	25	1
0 ± 0			
–			
–	195	4	0
18.77 ± 7.61	1626	17	114
–	400	4	21
11.64 ± 4.64	1100	12	10
–	1460	15	82
4.55 ± 0	100	1	0
0.09 ± 0.09	200	2	0
8.33 ± 0			
–	600	6	10
–	300	3	1
–	120	1	18
0 ± 0	200	2	0
–			
0 ± 0	800	8	8
1.85 ± 1.18	351	4	11
6.54 ± 4.17	360	4	0
20.03 ± 15.55	1641	16	15
–	178	2	6
–	300	3	17
24.31 ± 1.49	3278	34	404
–			
4.11 ± 0	400	4	0
3 ± 0	1000	10	2
–	200	2	4
–	263	6	5
8.91 ± 3.56	2775	28	142
–	1801	19	152
25.43 ± 24.93	1265	16	49
–	350	4	0
11.49 ± 4.04	1483	16	343

plants are reported for each plant taxa. Plant taxa are in alphabetical order.

% infested plants
(Mean±SE)

3.33 ± 3.33
 0 ± 0
 1.18 ± 0.99
 0.75 ± 0.62
 –
 7.28 ± 3.7
 –
 5.5 ± 3.58
 –
 –
 –
 5.16 ± 2.32
 0 ± 0
 5.48 ± 2.17
 –
 1.25 ± 1.25
 –
 0 ± 0
 0 ± 0
 2.49 ± 1.34
 0.08 ± 0.08
 4.38 ± 1.38
 3.98 ± 1.93
 –
 10.19 ± 4.58
 0.99 ± 0.68
 2.04 ± 0
 0.42 ± 0.42
 22.08 ± 19.51
 6.6 ± 5.72
 1.63 ± 1.44
 27.66 ± 11.24
 0 ± 0
 4 ± 1
 2.19 ± 1.27
 0.53 ± 0.29
 10.91 ± 4.18
 –
 0 ± 0
 13.82 ± 4.45
 3.89 ± 2.47
 0 ± 0
 3.75 ± 2.17
 0.2 ± 0.2
 –

2.56 ± 1.09
0.18 ± 0.18
4.92 ± 2.48
3.59 ± 1.78
12.73 ± 4.13
7.89 ± 3.01
0.17 ± 0.17
0 ± 0
0.23 ± 0.23
–
0 ± 0
0 ± 0
0.04 ± 0.04
–
–
0 ± 0
7.12 ± 3.16
5.25 ± 2.25
0.83 ± 0.83
5.47 ± 1.71
0 ± 0
0 ± 0
–
1.67 ± 1.48
0.33 ± 0.33
15 ± 0
0 ± 0
–
1 ± 0.73
4.67 ± 3.69
0 ± 0
0.84 ± 0.35
3.85 ± 3.85
5.67 ± 5.67
11.9 ± 3.42
–
0 ± 0
0.2 ± 0.13
2 ± 0
1.38 ± 0.66
5.17 ± 1.39
7.32 ± 2.91
3.84 ± 1.59
0 ± 0
21.74 ± 9.67

