Plant Selection and Population Trend of Spittlebug Immatures (Hemiptera: Aphrophoridae) in Olive Groves of the Apulia Region of Italy

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

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Abstract. The xylem-limited bacterium *Xylella fastidiosa* Wells is the causal agent of severe diseases of several cultivated and wild plants. It is transmitted by xylem-sap feeder insects, such as spittlebugs (Hemiptera: Cercopoidea) and sharpshooters (Hemiptera: Cicadellinae). A dramatic epidemic of *X. fastidiosa* subspecies pauca Sequence Type 53 is currently affecting a large area of the Apulia Region of Italy, where it is spread by *Philaenus spumarius* L. adults within olives. In 2015 and 2016, field surveys were carried out in Apulian olive groves to investigate host plant selection of spittlebug nymphs, in order to identify the main plant species that can act as reservoirs of the vectors. Two different sampling methods were used: randomized plant sampling and quadrats sampling. Host plant selection by *P. spumarius* and *Neophilaenus campestris* (Fallen) nymphs was estimated using Manly's selection index. The botanic families presenting the highest number of plants infested by *P. spumarius* nymphs were Asteraceae, Fabaceae, and Apiaceae. Nymphs of *P. spumarius* were sampled on 72 plant genera, and, among the most common 25 genera, *Sonchus*, *Knautia*, *Glebionis*, *Urospermum* (Asteraceae), *Medicago*, *Vicia*, *Melilotus* (Fabaceae) and *Daucus* (Apiaceae) were the ones selected preferentially, according to Manly's index results. Populations of *P. spumarius* nymphs peak in early April, with densities ranging between 10-40 nymph m^{-2}, and were about 10-fold those of *N. campestris*. Plant infestation rate by spittlebug nymphs in 2016 was significantly higher in olive groves located in Lecce province (infected area) than those situated in Bari province (non-infected area).

Keywords: insect vectors, Cercopoidea, host plant, olive

Introduction

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

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

Philaenus spumarius has been poorly studied during the last 50 years, and research was focused mainly on its polymorphism and its importance in meadow ecosystems. Recently, after the repeated discoveries of the bacterium *Xylella fastidiosa* Wells in Europe, and the associated epidemic disease of olive trees in the Apulian Region of Italy, that already spread to an area of at least 5,000 Km^2 encompassing one to three million olive trees (Signorile, 2018), interest on spittlebugs has dramatically increased.

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

The spread of *X. fastidiosa* diseases is the outcome of complex biotic and abiotic interactions and it is hard to predict; however, the speed of spread depends, among other factors, on the population level of competent vectors. In the olive groves, the main factor regulating vector population level is the availability of a ground cover and its species composition that can be more or less favourable/attractive to spittlebugs. In spite of a rich literature reporting host plants of *P. spumarius* nymphs, e.g. Weaver and King (1954) provided a list of more than 200 plant species, no information is available on host plant preference of this species in Mediterranean region. Similarly, for *Neophilaenus* spp., data from literature indicate that nymphs are associated with gramineous plants (Whittaker and Tribe 1998), but information on host plant preference among these latter is not available. Therefore, the aim of the present work was to describe host plant selection of spittlebug nymphs under field conditions in Apulian olive groves located both inside and outside the *Xf*-infected area, thus identifying those plants that, both inside and nearby olive groves, can act as reservoirs of the vectors.

Materials and Methods

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

Data analysis

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

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

Results

Host plant selection

The surveys carried out in 2015 and 2016 included 90 unique genera of herbaceous plants, for a total of 145,821 examined plants and 8,619 infested plants (overall infestation rate 5.9%), belonging to 72 different genera (Suppl. Table S1). The botanic families accounting for the majority of sampled plants were Asteraceae, Poaceae, Fabaceae and Rubiaceae. The botanic families presenting the highest number of plants infested by *P. spumarius* nymphs were Asteraceae (3319 infested plants; 38.51% of total infested plants), Fabaceae (2423; 28.11%), Apiaceae (760; 8.82%) and Poaceae (383; 4.44%).

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

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

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

The Manly's selectivity index results concerning the 25 most common plant genera supported the positive selection of *Sonchus* by pre-imaginal instars of *P. spumarius* in all the three surveys (Fig. 2), but also showed other common plant genera preferentially selected during the different surveys, like *Knautia*, *Glebionis* and *Daucus*. However, the host plant selection results were not always similar between the different surveys, given also the differences in sampling methodology and number of olive groves sampled (see M&M). In the 2016 survey, that included the highest number of olive orchards (42), the Fabaceae *Medicago*, *Vicia* and *Melilotus*, the Asteraceae *Glebionis* and *Urospermum*, Apiaceae *Daucus* and Poaceae presented mean index values significantly higher than the threshold 1/m, meaning that they were preferentially selected (Fig. 2c). *Crepis* was among the plant genera selected positively during 2015 quadrats samplings (Fig. 2a), whereas *Lathyrus*, *Picris*, *Melilotus*, *Lotus* and *Plantago* were also selected preferentially during 2015 plant samplings (Fig. 2b).

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

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

Population abundance of spittlebug nymphs

During the 2015 quadrats survey, *P. spumarius* and *Neophilaenus* spp. nymphs showed different populations abundance throughout the season. In total, 2409 *P. spumarius* and 267 *Neophilaenus* spp. immatures were sampled, with an overall *Philaenus*/*Neophilaenus* ratio of 9.02. Densities of *P. spumarius* nymphs were higher than *Neophilaenus* spp. throughout the season in all the three olive groves surveyed (GLMM: F = 885.63, d.f. = 1, $p < 0.001$). The difference between the two spittlebug species was particularly high in the olive grove located in Surbo, were only 31 grass spittlebugs were sampled and the ratio was 35.2 (Fig. 3c). Excluding the last sampling date (when spittlebug abundances were really low in all the olive groves, as most of insects were already emerged as adults) *Philaenus spumarius* densities throughout the season were significantly different among olive groves, with population in Ruffano orchard significantly lower than the populations observed in the other two olive groves (GLMM: $F = 13.31$, d.f. = 2, $p = 0.001$). However, including all sampling dates, densitites were not significantly different among olive groves (GLMM: $F = 2.05$, d.f. = 2, $p = 0.358$. The first sampling dates, around 20-25th March, were carried out when 2nd nymphal instars were prevalent (Fig. 4). The overall seasonal abundance trend of *Philaenus spumarius* nymphs peaked in early-mid April, whereas during the last samplings in late April-early May the nymphal populations were very low (Fig. 3). In the three sites of the Lecce province, nymphs disappeared by the end of April-beginning of May in 2015 (Fig. 3). Populations of *Neophilaenus* spp. seemed to follow a similar trend, although the very low population levels did not allow an accurate description of the populational dynamics.

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

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

Discussion

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

Host plant selection has been investigated using two different sampling methods, randomized plant sampling and quadrats sampling on a large number of sites over two consecutive years. The results of the different surveys are quite consistent, although ranking of preferred host plants slightly differ because of the different plant composition of herbaceous covers in the different olive groves. Some genera of the families Asteraceae (mainly *Sonchus, Crepis, Picris*), Fabaceae (mainly *Medicago*, *Vicia*, *Lathyrus*) and Apiaceae (*Daucus*, *Foeniculum*) are preferentially selected by *P. spumarius*, while Poaceae (mainly *Avena, Hordeum and Lolium*) are preferentially selected by *N. campestris*. Due to the very high polyphagy of the meadow spittlebug, it is interesting to identify, besides the preferred plants, those species that are negatively selected. Among these latter, some Poaceae, *Oxalis* (Oxalidaceae), *Lysimachia* (Myrsinaceae), *Sherardia* (Rubiaceae), *Geranium* (Geraniaceae), *Papaver* (Papaveraceae), *Fumaria* (Fumariaceae) and *Raphanus* (Brassicaceae) were avoided by *P. spumarius* nymphs (i.e. significantly less infested compared to their abundance in the sample area). Our results confirm that pre-imaginal instars of the meadow spittlebug tend to prefer forbs (herbs other than grasses), as often reported in literature (e.g. Cornara et al. 2018; Halkka et al. 1967; Weaver and King, 1954), but also show, only during the large scale survey of 2016, a positive selection for grasses (Poaceae). This outcome can have different explanations: a) some common gramineous species can be relatively attractive for later instar nymphs, such as *Sorghum* and *Avena*, possibly because of their structure, providing wide leaf axils and protected feeding sites (McEvoy 1986); b) seasonality (e.g. premature drying of dicots and unavailability of preferred host plants); c) uneven sprouting of plants following grass cuttings; d) impossibility to separate the effect of site and date of inspection, given that only one sample was carried out per each olive grove. On the contrary, *N. campestris* nymphs appear strictly associated to Poaceae, as reported in the literature (Halkka et al. 1967, Whittaker 1973, Nickel and Hildebrandt 2003).

Host plant association of *P. spumarius* nymphs is not fully static, as nymphs, especially later instars, show some dispersal capability, not only within but also among plants (author's observation). This mobility is limited and estimated to a maximum of 60 cm by Halkka et al. (1967), but results of host plant association can be partly biased by the age of the nymph population as early instars nymphs tend to prefer plants with basal rosettes (Bodino et al. 2017) and later instar can probably feed on a wider range of plants (Hoffman and McEvoy 1985). However, the present study describes the host plant selection by *P. spumarius* nymphs on a relative large geographical scale, and therefore could not be focused on plant association of age-structured populations of *P. spumarius.* Interestingly, with the exception of *Erigeron* spp. and *Chenopodium spp.*, found infected in late autumn, none of the other host plants in the Apulia Region have been found infected by *X. fastidiosa* ST53 so far. It is worth noting that, even if nymphs acquire the pathogen, they will lose pathogen and infectivity through moulting and therefore newly emerged adults are *Xylella*-free and must feed on an infected plant to become infectious (Almeida et al. 2005).

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

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

The maximum population level of spittlebug nymphs measured in the three olive groves located inside the infected area was estimated in a range of 10 – 40 nymphs of *P. spumarius* per square meter, whereas the populations of *N. campestris* were much lower, with a peak of 1 – 7 nymphs per square meter. Indeed, the meadow spittlebug can be present in high densities inside olive groves and, if we consider its role as a vector of *X. fastidiosa*, its abundance can explain why the disease has spread so fast in the area. In this context, it is interesting to note the higher plant infestation rate recorded in olive groves located in Lecce province compared to the ones located in Bari province. Lower populations of the vector north of the infected area may contribute to slow down the *X. fastidiosa* spread. However, these are preliminary data based only on spittle counts, and they should be confirmed by *ad hoc* estimation of vectors' population abundances.

Our study shows the high polyphagy and population levels of the principal vector of *X. fastidiosa* in Apulia, *P. spumarius*, pointing out the urgent need of control measures, like the ones that are mandatory to suppress nymph population by soil tilling (http://www.emergenza*Xylella*.it/portal/portale_gestione_agricoltura/Documenti/lineeGuida). If such a nymph population is left undisturbed, a high number of adults will emerge and move to the olive canopies, where they can acquire and transmit the pathogen (Cornara, Cavalieri, et al. 2017, Cornara, Saponari, et al. 2017). A correct timing of soil tilling to prevent the emergence of adults is of key importance and our data suggest that this measure should be applied in correspondence to the peak of nymphal populations (i.e. mid-April) and before the emergence of adults, to achieve the maximum efficacy.

A better knowledge of the mechanisms influencing plant choice by the vectors of *X. fastidiosa* could help in developing effective management strategies, such as modifications in plant communities present inside and around olive groves to limit the vectors' population abundance.

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Figures and tables legends

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

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.

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

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).

Table. 1: No. of sampled individual plants, no. of plants infested by *P. spumarius* and percentage (mean ± 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.

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.

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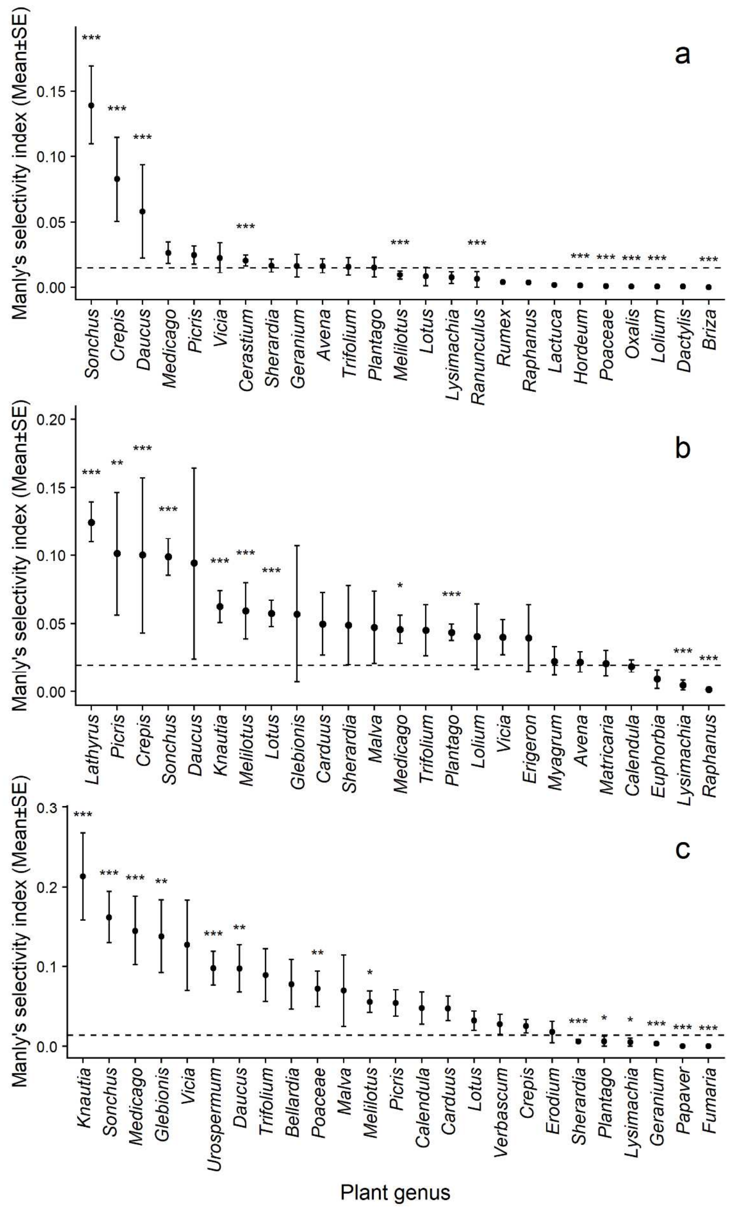

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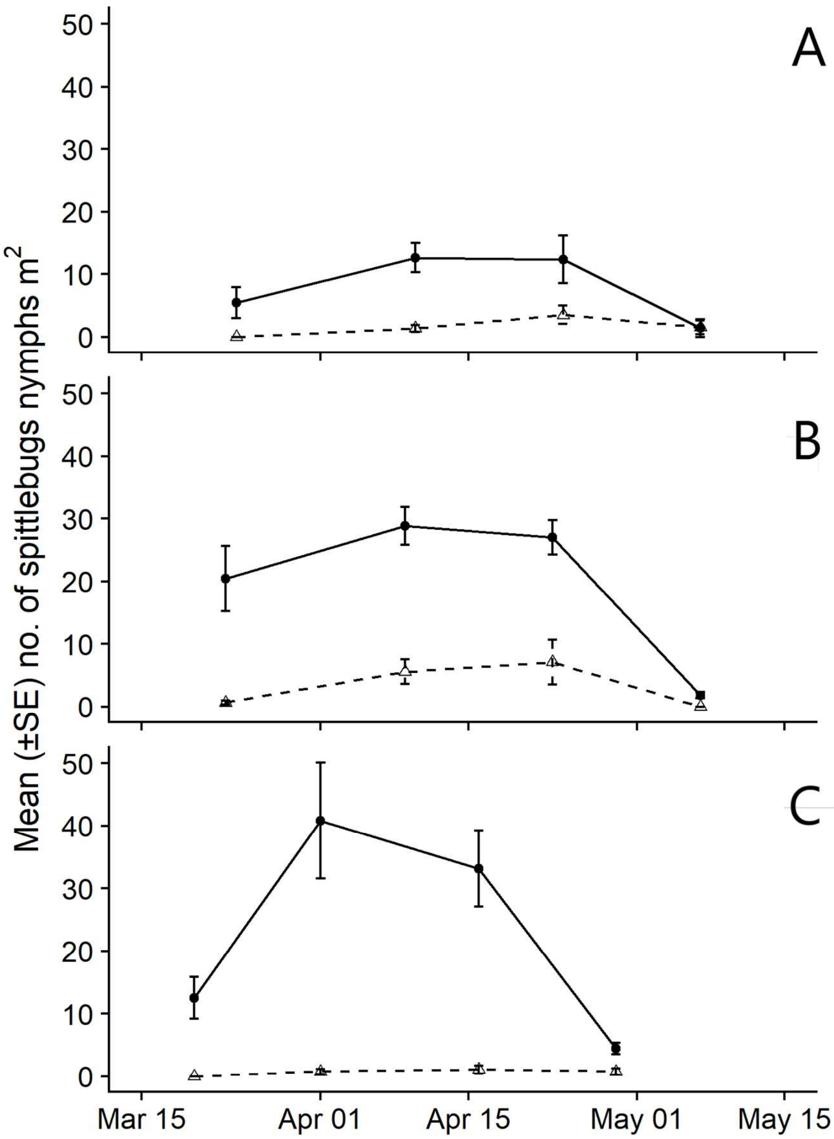

Fig. 3: Population abundance of spittlebugs nymphs (mean ± SE) in 2015 quadrat samplings in three olive groves located in Ruffano (a), Gallipoli (b) and Surbo (c). Continuous line, Philaenus spumarius; dashed line, Neophilaenus campestris

396x555mm (96 x 96 DPI)

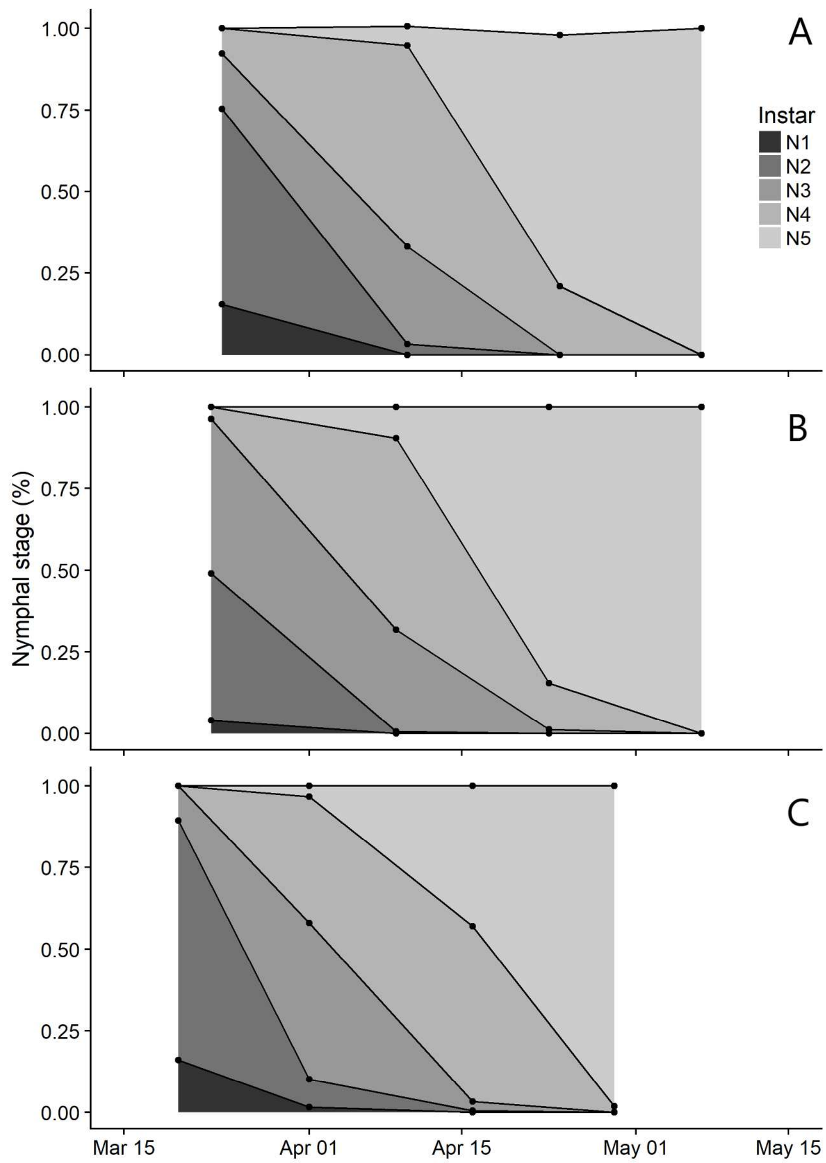

Fig. 4: Nymphal stages structure of P. spumarius over the season in 2015 quadrat samplings in three olive groves located in Ruffano (a), Surbo (b) and Gallipoli (c).

555x793mm (96 x 96 DPI)

Tab. 1: No. of sampled individual plants, no. of plants infested by *P. spumarius* and percentage (mean ± 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.

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

Supplementary table 1: list of plant taxa sampled during the three surveys carried out during 2015-2

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

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

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

	Plants sampling 2015		
% infested plants (Mean±SE)	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

	Plants sampling 2016		
% infested plants (Mean±SE)	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

lants 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