



Landscape composition predicts the distribution of *Philaenus spumarius*, vector of *Xylella fastidiosa*, in olive groves

Giacomo Santoiemma¹ · Giovanni Tamburini² · Francesco Sanna¹ · Nicola Mori¹ · Lorenzo Marini¹

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Abstract

The meadow spittlebug, *Philaenus spumarius* (Hemiptera: Aphrophoridae; Linnaeus, 1758), is considered the main vector in the ongoing *Xylella fastidiosa* outbreak in the olive groves of southern Italy. Identifying the factors driving the spatial distribution of *P. spumarius* is of primary importance to determine *X. fastidiosa* infection risk in healthy olive groves. Here, we investigated the local and landscape factors shaping the occurrence and abundance of *P. spumarius* by sampling 182 olive groves over 2 years in the Abruzzo region. We found the occurrence and abundance of the vector to be positively associated with the proportion of olive groves in the landscape and negatively with the cover of vineyards. *Philaenus spumarius* best responded to landscape processes at small spatial scale (125–250 m) confirming the available information regarding its dispersal ability. At the local scale, soil management and pesticide application did not affect the vector probably because both interventions were not timed according to the vector biology and ecology. Our findings suggest that the management of agricultural landscape mosaics can drive the spatial distribution of *P. spumarius*. In particular, the landscape composition of the close surrounding of the olive groves may potentially influence the emergence probability of local *X. fastidiosa* epidemics through its effects on the vector spatial distribution and activity.

Keywords Landscape epidemiology · Meadow spittlebug · Pathogen · Vineyard

Key message

- The meadow spittlebug, *Philaenus spumarius*, is considered the main vector in the ongoing *Xylella fastidiosa* outbreak in the olive groves of southern Italy.

- Occurrence and abundance of *P. spumarius* were measured in 182 healthy olive groves at risk of *X. fastidiosa* infection.
- Vector occurrence and abundance were positively associated with the proportion of olive groves in the landscape and negatively with the cover of vineyards (125–250-m scale).
- Local management effects on *P. spumarius* control need further investigation.

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Giacomo Santoiemma and Giovanni Tamburini have equally contributed to the study.

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✉ Giovanni Tamburini
giovanni.tamburini@slu.se

¹ DAFNAE, University of Padova, Viale dell'Università 16, 35020 Legnaro, Paduva, Italy

² Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 75007 Uppsala, Sweden

Introduction

Xylella fastidiosa is a xylem-limited gram-negative bacterium, known to be the causal agent of a variety of economically important diseases in commercial crops and ornamental plants in North and South America (Purcell 2013; Sicard et al. 2018). In Europe, *X. fastidiosa* was first recorded on olive trees in southern Italy (Puglia region, province of Lecce) where it has been recognized to be the main cause of the so-called olive quick decline syndrome (Saponari et al. 2013, 2017; Loconsole et al. 2014). The detrimental impact

of this pathogen on yield production and its high infectivity have imposed dramatic control measures in an attempt to halt the spreading pathogen, i.e., the destruction of infected plants and healthy ones around them (EFSA Panel on Plant Health 2015; European Union 2015). *Xylella fastidiosa* represents a serious threat for many important agricultural industries (e.g., olive, grapevine, stone fruits, citrus) among several Mediterranean countries. Nevertheless, the chances of eradicating *X. fastidiosa* from the region have been showed to be extremely low (Strona et al. 2017) and new introductions of infected plants from outside Europe have already been recorded in southern France and in the island of Mallorca (Denancé et al. 2017; EPPO 2016). There is, therefore, an urgent need to better understand the cryptic epidemiology of the outbreak, in order to define new management strategies to contain the epidemic (Strona et al. 2017; Sicard et al. 2018).

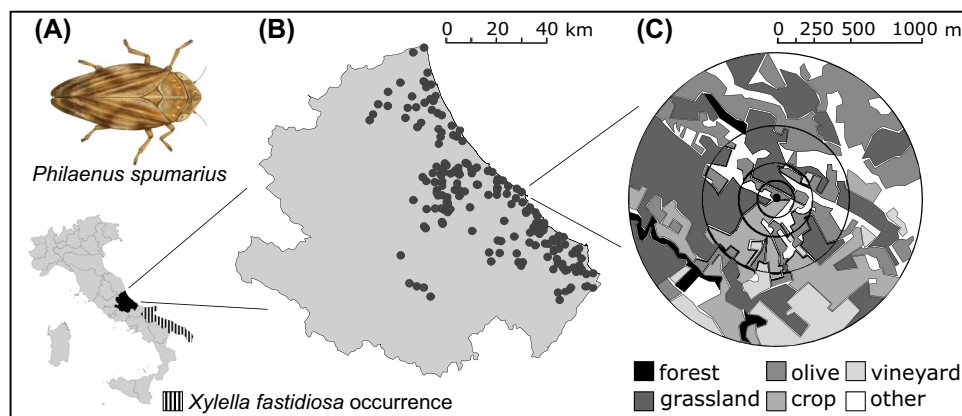
Xylella fastidiosa is transmitted to host plants by a wide range of xylem fluid-feeding sharpshooters and spittlebugs worldwide (Almeida et al. 2005). The bacterium is persistent in the vector and can multiply in the foregut (Hill and Purcell 1995; Baldi and La Porta 2017). The meadow spittlebug, *Philaenus spumarius* (Hemiptera: Aphrophoridae; Linnaeus 1758; Fig. 1a), is considered the main vector in the ongoing *X. fastidiosa* outbreak in the olive groves of southern Italy (Saponari et al. 2014; EFSA Panel on Plant Health 2015; Cornara et al. 2017b; White et al. 2017). It is in fact the most abundant xylem fluid-feeding hemipteran in the area (Cornara et al. 2014), commonly present in grasslands and field edges, and it has been found to be the only species that consistently tested positive for the presence of the pathogen (Cornara et al. 2017a, b). *Philaenus spumarius* completes one generation per year, and it develops as a low mobility nymph on weeds during the spring (Morente et al. 2018), moving beneath olive trees and then to olive canopy during the dry period (Cornara et al. 2017b). *Philaenus spumarius* has the potential to live under different environmental conditions as long as the host plants are actively growing and not

subjected to severe water stress (Cornara et al. 2018). Adults, being able to both jump and fly, can travel for only hundreds of meters during their lifetime (4–6 months. Weaver and King 1954; EFSA Panel on Plant Health 2015). Identifying the factors driving the spatial distribution of *P. spumarius* is of primary importance to determine *X. fastidiosa* infection risk in healthy olive groves (Cornara et al. 2018).

Vector biology dictates the transmission dynamics of vector-borne pathogens in a given environment where the host is present (Reisen 2010). However, the characteristics of that environment (e.g., habitat type, presence of food resources, disturbances) can strongly affect vector population growth and dispersal ability, ultimately influencing infection risk (e.g., Overgaard et al. 2003). Locally, crop management can influence the infection risk depending on whether it favors or limits the presence of the vector in the immediate host surroundings (see Plantegenest et al. 2007). The removal of vegetation cover (e.g., mowing, soil tillage) and the application of pesticides within and surrounding olive orchards are expected to reduce *P. spumarius* populations because of their impact on nymphs (Cornara et al. 2018). At the landscape scale, the presence of suitable habitats surrounding the orchards can enhance the potential infection pressure on the focal field. Moreover, the presence of *Xylella* host in the landscape (e.g., olive orchards), besides supporting vector populations, can prolong the persistence of the disease in the area (Cornara et al. 2018).

Here, we investigate the local and landscape factors shaping the occurrence and abundance of *P. spumarius* in healthy olive groves at risk of *X. fastidiosa* infection. We sampled 182 olive groves across 2 years in Abruzzo region. According to available spread models, the region is considered at risk of infection for its proximity to *X. fastidiosa* outbreak (Strona et al. 2017; White et al. 2017). To develop effective and timely management strategies to contain *X. fastidiosa*, it is therefore crucial to start investigating vector ecology before the arrival of the disease (EFSA Panel on Plant Health 2015). We hypothesized that: (1) Intensive local

Fig. 1 Study organism *Philaenus spumarius* (a), location of experimental groves (b) and example of landscape buffer from 125- to 1000-m scale (c)



management (i.e., vegetation removal through tillage and pesticide application) would negatively affect *P. spumarius*; (2) landscapes characterized by a high proportion of grasslands and olive groves would favor the vector occurrence in olive groves, whereas (3) a high proportion of cropland would limit it. We also explored *P. spumarius* response to elevation, expecting higher occurrence probability in relatively cool sites.

Materials and methods

Study area

The study was conducted in Abruzzo region, southern Italy (Fig. 1b). The agricultural landscapes in the area are generally dominated by olive groves (25%), grasslands (20%) and vineyards (15%). Semi-natural habitats (25%) are mainly represented by grasslands and mixed broadleaf forests. Grasslands include both pastures and intensive mown meadows (see Table S1 in supplementary materials). Climate is transitional between continental and Mediterranean and is strongly influenced by elevation and distance from the sea. The mean annual temperature is 15 C, and the annual precipitation is 850 mm.

Experimental setup

Sampling took place in 182 olive groves mainly located in the eastern part of the region (Fig. 1b). The survey was carried out in 2 years, 2016 and 2017, and included, respectively, 70 and 127 groves (15 sites were monitored in both years). The elevation of the groves ranged from 6 to 636 m a.s.l., covering the whole elevational range of olive tree in the region. The insect monitoring and the local management information collection were performed by the phytosanitary services of the Abruzzo region.

For each experimental grove, local inspectors collected information regarding soil and pest management. Twenty-seven olive groves out of 70 in 2016 and 10 out of 127 in 2017 were treated against the olive fly in summer mostly using dimethoate. Sixty-four groves out of 70 in 2016 and 73 out of 127 in 2017 were characterized by a permanent grass cover that was mown several times during the growing season, whereas the rest were superficially tilled once in late spring. After tillage, weeds generally re-colonize the bare soil. Repeated tillage is not applied in the study area due to soil erosion problems. No specific local management is currently in place to control *P. spumarius*. Hence, both pesticide application and soil tillage were not timed according to the vector biology and ecology.

We quantified the landscape characteristics around each olive grove within a 125, 250, 500 and 1000 m radius buffer

(Fig. 1c). Within each buffer, we manually digitized grassland, forest, olive, crop and vineyard patches by visual inspection of high-resolution satellite images in Google Earth Pro (Google Inc.© 2017). We kept separated vineyards and annual crops since their specific management could influence *P. spumarius* occurrence in different ways. In particular, vineyards are frequently tilled and usually treated 1–2 times against several pests such as grape berry moth, scales, thrips and leafhoppers. Repeated tillage is a common practice due to the local vine training system characterized by a dense canopy cover that protects the soil from direct rain impact. We quantified habitat cover (%) at four spatial scales as measure of landscape composition and patch density (number of patches per 100 hectares) at the three largest spatial scales (Table S1; Connors et al. 2013). We did not calculate patch density at 125-m scale because the average patch size in the study area (mean = 6.25 ha, SD = ± 2.94; measured at 1000-m scale) was larger than the buffer area (4.91 ha). All the analyses performed at 125-m scale included therefore patch density measured at the closest appropriate scale, i.e., 250 m. We performed landscape analyses in GIS (Quantum GIS 2.14, QGIS Development Team 2014). We found low correlations among landscape features and local management factors (Table S2, Fig. S1). We did not explicitly incorporate olive grove size in the analyses because fields are usually well connected and the definition of field boundaries can often be arbitrary. We decided to use the cover of olive groves at our smallest spatial scale (125 m) as a better proxy for olive habitat area.

Adult insect sampling

In each year, the regional phytosanitary service performed a mean of 7 (SD = ± 2.1) consecutive sampling rounds in each site. *Philaenus spumarius* adults were sampled using one unbaited yellow sticky trap (20 × 24.5 cm) placed in the center of each grove and hung on an olive tree c. 1 m from the ground. This trap has been proved to effectively attract the meadow spittlebug (Elbeaino et al. 2014). In 2016, the sampling started on the 22nd of July and ended on the 28th of October, while in 2017 it started on the 14th of July and ended on the 30th of November. Sticky traps were exposed on average 13 days (SD = ± 2.0) per sampling round. The traps were checked in the laboratory and the number of *P. spumarius* individuals counted by the staff at the University of Padova.

Statistical analysis

We explored the effects of local and landscape factors on *P. spumarius* occurrence (presence/absence data) and abundance (number of adults per trap, per sampling round) with generalized linear mixed-effects models (GLMMs; binomial

and negative binomial distribution, respectively). We run four models for each response variable to test the effect of landscape factors at different spatial scales (125, 250, 500 and 1000 m radius). Each model included the cover proportion for different habitats (grassland, olive grove, cropland, vineyard) and patch density in the landscape and site elevation as continuous variables, and soil management (grass vs. tilled) and insecticide application (yes vs. no) as categorical variables. We included year and sampling month (categorical) in the model to describe the temporal dynamics of the vector. Since the number of exposure days slightly differed among traps, this continuous variable was included in the models as fixed effect (presence/absence data) or as an offset (abundance data). Site ID was considered as random factor. Forest cover was not included since it was expected to have a much weaker effect on *P. spumarius* compared to the other types of habitat (Cornara et al. 2018). Preliminary analyses confirmed our hypothesis. The variables included in the models as fixed effects presented low collinearity (see Table S2 and Fig. S1 in Supplementary material). The variance inflation factor (VIF) was used to further assess multicollinearity: The highest VIF scores were below 2 (common threshold for VIF is usually > 10 ; Dormann et al. 2013). The best landscape scale was then identified based on AIC (Akaike 2011). We performed the analyses using the “lme4” package (Bates et al. 2017) implemented in R (R Core Team 2018). We checked the models for overdispersion and residual distribution using the “DHARMA” package (Hartig 2017). The DHARMA package uses a simulation-based approach to create readily interpretable scaled residuals from fitted GLMM. There was no evidence of either spatial or temporal autocorrelation of model residuals (analyses performed using “ncf” and “acf” packages, respectively; Bjørnstad 2016). Because of the large amount of zeros in our dataset (60.1% of the observations), we further tested the response of *P. spumarius* to local and landscape factors with zero-inflated GLMMs (eight models: occurrence and abundance data tested at four landscape scales). We used zero-inflated models as true absences could not be distinguished from potential false absences related to sampling incompleteness. Models’ characteristics were the same as described above. Results from zero-inflated models were strongly consistent with those of the GLMMs (see Supplementary materials; Tables S3–S4) suggesting against the presence of frequent false absences in the dataset (Martin et al. 2005).

Results

We checked 1429 traps exposed during the 2 years, and *P. spumarius* was present on 562. We counted a total of 2263 *P. spumarius* individuals (mean per trap = 1.58, SD = ± 4.8).

The model at 125-m scale yielded the lowest AIC for both occurrence and abundance (Tables 1 and 2, respectively). For abundance, the model at 250-m scale was equally supported ($\Delta\text{AIC} < 2$). Despite the worse fit of the models at larger scales, results were qualitatively similar to those at the 125-m scale. The probability of occurrence and the abundance of *P. spumarius* was both positively influenced by olive grove cover in the landscape (Fig. 2a, d) and negatively affected by vineyard cover (Fig. 2b, d). Vector occurrence was also found to increase with elevation (Fig. 2c). Both occurrence and abundance were higher in 2016 than in 2017 and peaked in August (and October for abundance data), while we found no significant effects of patch density, local management and sampling period on vector populations.

Discussion

We found several environmental factors driving the occurrence and abundance of *P. spumarius* in olive groves. At the landscape scale, high proportions of olive groves generally supported a higher occurrence and abundance of *P. spumarius*, whereas high cover of vineyards was found to negatively affect its presence. *P. spumarius* best responded to landscape processes at small spatial scale (125–250 m) confirming the available information in the literature regarding its dispersal ability (Weaver and King 1954). Olive groves situated at higher elevations had higher probability to harbor this spittlebug. Our findings suggest that the composition of agricultural landscapes affects the spatial distribution of *P. spumarius*, potentially influencing the emergence probability of local *X. fastidiosa* epidemics.

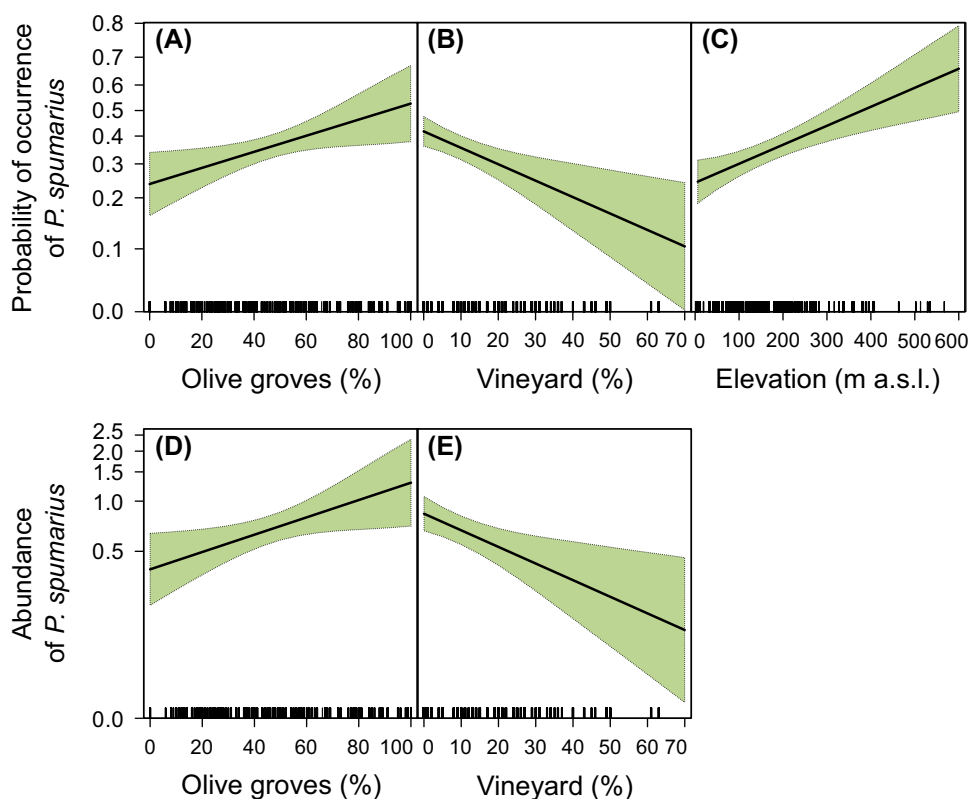
Our study shows that olive groves represent a suitable habitat for the persistence of *P. spumarius* populations in agricultural landscapes. A high proportion of olive groves in the landscape supported higher occurrence probability and abundance of *P. spumarius* in the focal grove. Our findings suggest that olive groves probably sustain *P. spumarius* all along its life cycle: The ground cover vegetation allows nymph development in spring (Morente et al. 2018) while olive trees provide food resources for the adults and a suitable environment for reproduction during summer (EFSA Panel on Plant Health 2015; Cornara et al. 2017b).

We found high proportion of vineyards in the landscape to negatively affect the occurrence and abundance of *P. spumarius* in the focal groves. Vineyards are generally expected to support more diverse and abundant insect communities, including *P. spumarius* populations, in comparison with annual crops (Cornara et al. 2018). Nevertheless, intensively managed vineyards are well known to have detrimental effects on biodiversity at multiple trophic levels (Bruggisser et al. 2010; Nascimbene et al. 2012; Winter et al. 2018). The management of vineyards in the study region is generally

Table 1 Results of the GLMMs (family: binomial) testing the response of *Philaenus spumarius* occurrence to landscape composition, site elevation, patch density, sampling month (July, August, September, October, November), sampling year (2016, 2017), insecticide (no, yes) and soil management (grass, tilled). The model considering landscape variables at 125-m scale includes patch density calculated at 250 m since the average patch size in the landscape was larger than the buffer area at 125-m scale. The number of days of trap exposure was included as covariate. Marginal (mR^2) and conditional (cR^2) pseudo-R-squared, model estimate (Est), standard error (SE), Z and P values are presented for each model

	Scale: 125 m					Scale: 250 m					Scale: 500 m					Scale: 1000 m					
	$\Delta AIC: 0$					$\Delta AIC: 6.4$					$\Delta AIC: 11.8$					$\Delta AIC: 12.8$					
	$mR^2 = 0.15$	$cR^2 = 0.29$	Est	SE	Z	P	Est	SE	Z	P	Est	SE	Z	P	Est	SE	Z	P	Est	SE	Z
Grassland	-0.019	0.121	-0.160	0.8726	0.110	0.116	0.952	0.3409	0.169	0.120	1.415	0.1570	0.047	0.124	0.379	0.7046					
Olive	0.313	0.131	2.394	0.0167	0.355	0.117	3.043	0.0023	0.331	0.111	2.977	0.0029	0.201	0.111	1.817	0.0692					
Crop	0.097	0.112	0.869	0.3850	0.079	0.105	0.751	0.4529	0.129	0.102	1.264	0.2061	0.111	0.101	1.100	0.2711					
Vineyard	-0.374	0.121	-3.097	0.0020	-0.299	0.121	-2.463	0.0138	-0.195	0.127	-1.535	0.1247	-0.302	0.130	-2.317	0.0205					
Elevation	0.343	0.093	3.690	0.0002	0.320	0.093	3.456	0.0005	0.341	0.096	3.569	0.0004	0.352	0.100	3.501	0.0005					
Patch density	0.086	0.093	0.923	0.3558	0.090	0.095	0.944	0.3453	0.085	0.094	0.897	0.3697	0.096	0.097	0.995	0.3197					
Month (vs. July)																					
August	0.468	0.231	2.027	0.0427	0.474	0.231	2.053	0.0400	0.467	0.231	2.022	0.0432	0.457	0.231	1.981	0.0476					
September	0.316	0.227	1.396	0.1629	0.323	0.227	1.427	0.1536	0.312	0.227	1.376	0.1689	0.307	0.227	1.355	0.1753					
October	0.389	0.237	1.642	0.1006	0.407	0.237	1.715	0.0863	0.400	0.237	1.684	0.0922	0.394	0.237	1.659	0.0972					
November	0.004	0.403	0.010	0.9921	0.025	0.404	0.061	0.9513	0.010	0.404	0.025	0.9797	0.002	0.404	0.006	0.9951					
Year (vs. 2016)																					
2017	-0.906	0.214	-4.243	<0.0001	-0.907	0.215	-4.219	<0.0001	-0.918	0.215	-4.262	<0.0001	-0.916	0.218	-4.209	<0.0001					
Insecticide (vs. no)																					
Yes	-0.053	0.243	-0.219	0.8268	-0.050	0.245	-0.202	0.8396	-0.032	0.248	-0.128	0.8978	-0.070	0.252	-0.280	0.7796					
Soil (vs. grass)																					
Tilled	0.244	0.195	1.253	0.2101	0.202	0.197	1.024	0.3060	0.116	0.198	0.584	0.5591	0.104	0.201	0.518	0.6042					
Days	0.066	0.086	0.773	0.4396	0.071	0.087	0.823	0.4105	0.069	0.086	0.797	0.4253	0.065	0.087	0.745	0.4564					

Fig. 2 Probability of occurrence (a–c) and abundance (d–e) of *Philaenus spumarius* (per trap per sampling round) in response to the proportion of olive groves and vineyards in the landscape (125-m scale) and to elevation. Plots include model estimate (black line) and 95% confidence interval (green shading). Plots presenting partial residuals are available in the supplementary materials (Fig. S2). (Color figure online)



conventional, and it often includes bare soil management and one–two applications of pesticides per year. Our results suggest that *P. spumarius* might persist with difficulties in intensively managed vineyards and that a high cover of this crop might limit the insect presence at the landscape scale.

Unexpectedly, we did not find any positive effects of grassland cover in the landscape on *P. spumarius* populations. Although grasslands potentially represent an important habitat for the meadow spittlebug (Cornara et al. 2018), their effects on population abundances are conditioned largely by management intensity (Weaver and King 1954). Pastures and intensive mown meadows might not favor *P. spumarius* development and persistence because of vegetation disturbance due to frequent mowing and grazing (Weaver and King 1954). Moreover, although the number of patches in the landscape is known to potentially affect herbivore populations (e.g., Olson et al. 2018), we did not find patch density to be an important predictor of *P. spumarius* occurrence and abundance. The vector in our study area was most probably limited more by the cover of suitable habitats rather than by the configuration of the landscape that potentially affect its dispersal.

The effects of landscape composition on the occurrence of *P. spumarius* in olive groves were consistent across different spatial scales but stronger at 125 m radius. Our results are consistent with the available information on the ability of the meadow spittlebug to move across habitats (Cornara

et al. 2018) and are in line with the available data regarding its dispersal ability (few hundreds of meters per year; Weaver and King 1954; EFSA Panel on Plant Health 2015).

We found high elevation to increase the meadow spittlebug occurrence probability, although this effect was not significant when exploring vector abundance. Even though *P. spumarius* can tolerate a wide variety of climatic conditions (Cornara et al. 2018), olive groves located at higher elevations might have favored its persistence because of cooler temperatures. The optimal temperature described for the survival and reproduction of *P. spumarius* is in fact 15.6 °C (Karban and Strauss 2004). This result suggests that the northern and cooler regions are highly suitable for the vector establishment and persistence. Moreover, we found *P. spumarius* occurrence and abundance to peak in August, the warmest month of the year in the study area: The meadow spittlebug is in fact known to move to olive canopies during the dry period (Cornara et al. 2017b). Vector abundance peaked again in October, probably because of increased adult activity driven by cooler temperatures (Cornara et al. 2017b).

Pest control measures adopted in olive groves targeting other organisms (e.g., *Prays oleae* B., *Bactrocera oleae* R., *Euphyllura olivina* C., *Saissetia oleae* O.; Paredes et al. 2015) did not affect adults of *P. spumarius*. The timing and the location of insecticide application (ground vs. tree foliage) should be targeted to *P. spumarius* to increase

Table 2 Results of the GLMMs (family: negative binomial) testing the response of *Philaenus spumarius* abundance to landscape composition, site elevation, patch density, sampling month (July, August, September, October, November), sampling year (2016, 2017), insecticide (no, yes) and soil management (grass, tilled). The model considering landscape variables at 125-m scale includes patch density calculated at 250 m since the average patch size in the landscape was larger than the buffer area at 125-m scale. The number of days of trap exposure was included as an offset. Marginal (mR^2) and conditional (cR^2) pseudo-R-squared, model estimate (Est), standard error (SE), Z and P values are presented for each model

	Scale: 125 m					Scale: 250 m					Scale: 500 m					Scale: 1000 m				
	$mR^2 = 0.23$					$mR^2 = 0.22$					$mR^2 = 0.23$					$mR^2 = 0.21$				
	Est	SE	Z	P	$cR^2 = 0.65$	Est	SE	Z	P	$cR^2 = 0.63$	Est	SE	Z	P	$cR^2 = 0.64$	Est	SE	Z	P	$cR^2 = 0.64$
Grassland	0.062	0.122	0.508	0.6113	0.179	0.116	1.541	0.1233	0.0226	0.118	0.270	0.118	2.280	0.0226	0.162	0.122	1.331	0.1830		
Olive	0.300	0.129	2.322	0.0203	0.352	0.114	3.092	0.0020	0.347	0.107	3.229	0.0012	0.209	0.108	1.946	0.0517				
Crop	0.204	0.112	1.816	0.0694	0.164	0.104	1.577	0.1148	0.189	0.100	1.891	0.0586	0.123	0.099	1.239	0.2153				
Vineyard	-0.331	0.122	-2.725	0.0064	-0.273	0.121	-2.255	0.0241	-0.166	0.124	-1.336	0.1815	-0.279	0.129	-2.165	0.0304				
Elevation	0.147	0.093	1.590	0.1119	0.140	0.091	1.534	0.1251	0.150	0.093	1.614	0.1066	0.147	0.098	1.497	0.1345				
Patch density	0.023	0.095	0.244	0.8074	0.037	0.095	0.389	0.6969	-0.011	0.093	-0.114	0.9096	0.044	0.096	0.457	0.6480				
Month (vs. July)																				
August	0.409	0.182	2.249	0.0245	0.418	0.182	2.302	0.0214	0.412	0.182	2.263	0.0237	0.407	0.182	2.241	0.0251				
September	0.272	0.180	1.514	0.1301	0.279	0.179	1.554	0.1203	0.271	0.180	1.508	0.1315	0.269	0.180	1.498	0.1340				
October	0.409	0.190	2.149	0.0316	0.424	0.190	2.227	0.0259	0.422	0.190	2.217	0.0266	0.419	0.190	2.201	0.0277				
November	0.005	0.347	0.015	0.9884	0.010	0.347	0.028	0.9773	-0.015	0.346	-0.045	0.9644	-0.024	0.346	-0.071	0.9437				
Year (vs. 2016)																				
2017	-0.834	0.184	-4.541	<0.0001	-0.827	0.183	-4.514	<0.0001	-0.843	0.183	-4.610	<0.0001	-0.854	0.185	-4.613	<0.0001				
Insecticide (vs. no)																				
Yes	-0.054	0.237	-0.230	0.8181	-0.067	0.235	-0.285	0.7755	-0.046	0.235	-0.196	0.8442	-0.110	0.240	-0.459	0.6462				
Soil (vs. grass)																				
Tilled	0.236	0.191	1.235	0.2167	0.190	0.191	0.996	0.3191	0.105	0.190	0.554	0.5799	0.091	0.194	0.468	0.6399				

pesticide effectiveness. For example, treatments in mid-summer have been previously found to be ineffective in spittlebug control, because of successive migration from surrounding habitats. On the other hand, although removal of vegetation cover through tillage is expected to drastically reduce vector populations (Cornara et al. 2018), one tillage event per year might be insufficient in affecting *P. spumarius*. Weedy vegetation can in fact rapidly re-colonize the bare soil after disturbance, probably allowing an efficient re-establishment of *P. spumarius* population from the surroundings. It is important to stress that no olive grove in the area kept a permanent bare ground cover due to erosion problems. Hence, more studies are urgently needed to identify specific local management strategies to effectively control *P. spumarius* (Cornara et al. 2018).

The probability of spread of *X. fastidiosa* and its establishment in novel areas in Europe is considered to be very high, because of the abundance of suitable host plants and the wide distribution and polyphagy of its vectors (EFSA Panel on Plant Health 2015). Determining the factors driving *X. fastidiosa* disease invasion is pivotal to better forecast future spread patterns (White et al. 2017). Our study shows that olive groves are a key habitat for the presence and abundance of the vector in agroecosystems. Landscapes at higher elevations dominated by a matrix of olive groves are more likely to harbor populations of *P. spumarius* and are therefore more exposed to the risk of emergence of novel *X. fastidiosa* epidemics. More studies are urgently needed to, first, identify efficient local management strategies to control *P. spumarius*, and second, to better understand the role of multiple habitats (e.g., field margins) in affecting vector movements across agricultural landscapes.

Author contributions

LM and NM conceived and designed research. NM supervised data collection. GS and FS identified specimens and compiled landscape dataset. GS, GT and LM performed data analysis and manuscript drafting.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights This article does not contain any studies with human participants or animals (vertebrates) performed by any of the authors.

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