Spatio-temporal dynamics of vectors of *Xylella fastidiosa* subsp. *pauca* across heterogeneous landscapes

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With 3 figures and 2 tables

Abstract: *Xylella fastidiosa* subsp. *pauca* is a plant pathogen that causes the Olive Quick Decline Syndrome, the spread of which is linked to insect vectors. Since these vectors can use and move across multiple managed and natural habitats, understanding their occurrence in different habitat types at the landscape scale is particularly challenging. Here, we applied a bipartite network approach to explore the spatio-temporal distribution of confirmed and potential vectors of *X. fastidiosa* in olive groves. We sampled sharpshooters and spittlebugs in 10 heterogeneous landscapes in southern Italy during spring, summer, and autumn. In each landscape, we sampled insects in the main habitat types, i.e., arable land, grassland, olive grove, vineyard, and woodland. We then built and analyzed the resulting bipartite species–habitat networks. The abundance of vectors in different habitat types throughout the seasons varied from species to species, with *Philaenus spumarius*, the main vector of *X. fastidiosa*, being mostly collected in olive groves. However, the analysis of habitat specialization showed that *P. spumarius* acted as a super-generalist species, occupying all the habitats. Insect vectors in olive grove patches were strongly influenced by other olive grove patches in the landscape and also by grasslands, particularly in spring, therefore highlighting the focal role of non-crop habitats on potential pathogen spread. Landscapes dominated by olive orchards and grasslands seemed to provide the most suitable conditions to support large vector populations. Network analyses helped untangle the complex interactions between vectors of *X. fastidiosa* and the landscapes and habitats they use.

Keywords: Aphrophoridae, Cicadellidae, habitat specialization, *Neophilaenus campestris*, pest management, *Philaenus spumarius*

1 Introduction

Plant pathogenic viruses, bacteria, and phytoplasma transmitted by insect vectors constitute emerging threats to agriculture worldwide (Krishnareddy 2013). Habitat type, presence of food resources, and habitat disturbances across heterogeneous landscapes can affect vector populations, influencing the spread of pathogens (e.g., Overgaard et al. 2003). Investigating the spatio-temporal distribution of vectors across the whole landscape is therefore essential for improving our understanding of plant pathogen dynamics. An illustrative case study is represented by the recent arrival in Europe of the gram-negative bacterium *Xylella fastidiosa* subsp. *pauca*, responsible for the Olive Quick Decline Syndrome, a disease that causes severe damage to

olive trees. The spread of the bacterium has mainly been associated with the spittlebug vector *Philaenus spumarius* L. (1758) (Hemiptera: Aphrophoridae) (Saponari et al. 2014; Cornara et al. 2017; Bodino et al. 2021a), although other xylem-sap feeders might also be potential vectors of the pathogen (EFSA PLH Panel 2015). Until now, the study of the vector distribution has adopted a classical landscape approach by sampling a focal habitat such as olive groves or grasslands and relating vector abundance to the landscape by using the proportion of surrounding suitable or unsuitable habitats (Santoiemma et al. 2019).

Depending on their degree of ecological specialization, however, vector species can use a diversified range of resources across multiple habitats. In order to capture the complexity of these spatial interactions, the whole land-

scape should be sampled, observing the species presence in all habitat types. A key tool to analyze community response to landscape processes could be the use of spatial bipartite networks (Marini et al. 2019). In particular, habitat types and species (i.e., vectors) occurring within each habitat in the landscape constitute the two types of nodes of a bipartite species-habitat network. This approach is particularly suitable for modelling the response of habitat generalists that use a wide array of resources and habitats across heterogeneous landscapes.

To fill this gap, we sampled confirmed and potential vectors of *X. fastidiosa* across 10 landscapes in southern Italy. First, we built species–habitat networks and evaluated the role of vector species within each network across the seasons. Second, we evaluated the level of habitat selectivity of the most abundant vector species. Third, we assessed the influence of the different habitat types on vectors occurring in olive groves providing data on potential insect spillover. We expected that different species would use habitats across heterogeneous landscapes differently throughout the seasons, but that most species would shift to cool habitats such as olive groves and woodlands during the warmest months. Moreover, we expected that vector populations in olive groves would be strongly influenced by other olive groves within the landscapes, while more disturbed habitats such as vineyards or arable fields should not contribute to an increase in vector population in olive groves (Santoiemma et al. 2019).

2 Materials and methods

2.1 Study area
The study was conducted in the Abruzzo region, in southern Italy, in the provinces of Pescara (42.43 N, 14.13 E) and Chieti (42.39 N, 14.21 E). The agricultural landscapes in the area are generally dominated by olive groves (25%), grasslands (20%, which include both pastures and mown meadows), arable land (20%), vineyards (15%), and broadleaved woodlands (15%). Climate is transitional between continental and Mediterranean, with hot dry summers and mild winters. Although the Apulian outbreak is approximately 300 km away and *X. fastidiosa* has not yet been established in the study area, the region is predicted to be invaded soon (Kottelenberg et al. 2021).

2.2 Sampling design
Sampling took place in 10 agricultural landscapes of about 50 ha each. In each landscape, we selected 12 points (13 in one case), for a total of 121 sampling points (Table S1). Landscapes were selected after a preliminary screening realized by using GEarthView plugin in QGIS 2.18 (QGIS Development Team 2014). To ensure an even spatial distribution, an 800 × 600 m grid (200 m on cell side) was used

on each landscape. Each point in each cell was assigned to either cropland or semi-natural habitats, depending on which macro-habitat type covered more than 50% of the cell according to 2018 Google Satellite images. Arable land, grassland, olive grove, vineyard, and woodland patches were manually digitized in Google Earth Pro Google Inc. ©. The inter-row vegetation of all selected vineyards and olive groves was a permanent grass cover.

2.3 Insect sampling and identification
Adult spittlebugs (Hemiptera: Aphrophoridae and Cercopidae) and sharpshooters (Hemiptera: Cicadellidae, tribe Cicadellini) were sampled using yellow sticky traps, one per sampling point, from the end of April to mid-October of 2018, for a total of six monitoring periods covering 175 days. The use of yellow sticky traps guaranteed a standardized sampling technique across different habitats. While the use of sweep net is usually considered more appropriate to quantify vector abundance within olive groves (Cornara et al. 2020; Bodino et al. 2021b), this method is not suitable for comparing habitats with very different vegetation physiognomy and degree of disturbance (e.g., mowing, tillage). Sampling was continuous and took place c. every three weeks in spring and autumn, while in summer the exposition period was extended to six weeks due to the low insect abundance. Based on Biedermann & Niedringhaus (2004), all confirmed and potential vectors of *X. fastidiosa* present in the study area were identified to the species level, i.e., *Aphrophora alni* (Fallén), *Cercopis sanguinolenta* (Scopoli), *Cicadella viridis* (Linnaeus), *Lepyronia coleoptrata* (Linnaeus), *Neophilaenus campestris* (Fallén), and *Philaenus spumarius*, the latter two being the only confirmed vectors of *X. fastidiosa* in southern Italy along with *P. italosignus* Drosopoulos & Remane, which was not found in the study area (Purcell 1990; Cornara et al. 2017; 2020; EFSA PLH Panel 2015). However, while *P. spumarius* was confirmed as a vector in the field, *N. campestris* was only confirmed under laboratory conditions so far.

2.4 Species–habitat networks
Species–habitat networks were built from bipartite interaction matrices between habitat patches (rows) and confirmed and potential vector species (columns). In these networks, habitat patches and vector species act as nodes, while vector abundance in each patch acts as link (Marini et al. 2019). Bipartite interaction matrices were computed per season, i.e., spring (two sampling periods, from the end of April to the end of May), summer (two sampling periods, from mid-June to the end of August), and autumn (two sampling periods, from the end of August to mid-October), for a total of 30 interaction matrices, i.e., species–habitat networks (10 landscapes × 3 seasons).

We focused on node-level metrics. First, to investigate the vector habitat specialization, we computed the Resource

Range index and the Paired Difference Index (Poisot et al. 2012). The Resource Range is a specialization index based on presence-absence data, and it is calculated as the fraction of habitats visited by each species out of the total number of habitats within the network. The Paired Difference Index is the quantitative version of the Resource Range, as it contrasts a species strongest link with one habitat with those over all remaining habitats. Both index values range from 0, for habitat-generalist species, to 1, for habitat-specialist species.

Second, using habitat patches, we calculated the Potential for Apparent Competition (PAC), which is usually employed to study host-parasitoid interactions (Müller et al. 1999). This index is based on the idea that host species can negatively influence each other depending on the number of parasitoids that hatch from them and then attack other hosts (Müller et al. 1999). In analogy with this scenario, habitat patches can influence the biotic assemblages of other patches depending on the species and the number of individuals that they host, and that can potentially disperse to other patches (Fig. S1), (e.g., Nardi & Marini 2021). By calculating the PAC, we were therefore able to determine the potential influence of all habitat patches on olive grove patches in terms of vector spillover. Hereafter, PAC will be referred to as a measure of potential spillover between habitats. The index value ranges from 0, if one patch cannot influence another one, to 1, i.e., maximum influence.

2.5 Statistical analyses

To explore the effects of season, habitat, and species identity on confirmed and potential vector abundance and node-level metrics, we used generalized linear mixed models. All the network and statistical analyses were performed using the R software (R Core Team 2019; see the additional references appendix in Supplementary Materials for the list of packages).

First, we tested the effect of habitat type and season on confirmed and potential vector abundance. We only considered the most abundant species, i.e., those for which we collected at least 100 individuals (*C. viridis, N. campestris*, and *P. spumarius*). We therefore built three models, in which the response variables were the abundances of single species, while the explanatory variables were habitat type, season, and their interaction. To account for spatial dependence in the design, we included landscape identity and sampling point identity within each landscape as random factors. Moreover, we added the number of sampling days for each season as an offset. For this model, which included count data, we used a Poisson distribution.

Second, we tested whether vector specialization varied between species and season. Again, we only considered the most abundant species, as specialization of rare species is often overestimated (Dorado et al. 2011). The response variables of the two models were the Resource Range and the Paired Difference Index, respectively. In both models, the

explanatory variables were season, species, and their interaction, while the random factor was landscape identity. For these models, we used a Gaussian distribution.

Third, we tested whether the influence in terms of vector spillover to olive groves, our target habitat, varied with habitat type and season. The response variable was the PAC index (cubic-root transformed) and the explanatory variables were habitat type, season, and their interaction. Since we tested the influence of multiple patches within the same network, we included landscape identity and olive grove identity within each landscape as random factors. Again, we used a Gaussian distribution.

3 Results

We checked a total of 726 traps during the six sampling periods and collected 4344 confirmed and potential vectors of *X. fastidiosa* (Table S2). The most abundant species, which was found in all sampling points and seasons, was *P. spumarius* with 3334 individuals (Fig. S2), while the rarest species was *L. coleoptrata* with 29 individuals. Most individuals were collected in olive groves (N = 2200). According to their biology, *C. sanguinolenta* was found only in spring, while all other species were found throughout the seasons. The number of individuals collected in the three seasons was comparable, as 36% of insects were collected in spring (N = 1570), 35% in summer (N = 1519), and 29% in autumn (N = 1255).

The three most abundant confirmed and potential vector species were found in all habitat types, but showed different habitat preferences throughout the seasons (Fig. 1; Table 1). *Cicadella viridis* and *P. spumarius* responded to the interaction between habitat type and season, as opposite to *N. campestris*. *Cicadella viridis* was mostly found in arable lands during all seasons, and in grasslands and woodlands especially in spring (Fig. 1a; Table 1a). *Philaenus spumarius* abundance was high in olive groves during all seasons, but its abundance peaked in spring, especially in grasslands (Fig. 1b; Table 1b). *Neophilaenus campestris* was mostly found during spring, in higher density in grasslands (Fig. 1c; Table 1c).

Specialization for habitats differed among the most abundant vector species (Fig. 2; Table 2a, b). *Philaenus spumarius* was the most generalist species, having the lowest values of both Resource Range and the Paired Difference Index, while the other species showed a medium-high level of specialization for certain habitats.

Vector spillover from olive groves to other olive groves was high in all seasons (Fig. 3, S3; Table 2c). Grasslands held a high vector spillover value in spring, which slightly decreased in summer and increased again in autumn. Conversely, woodlands showed the lowest value in spring, but it increased in summer and autumn.
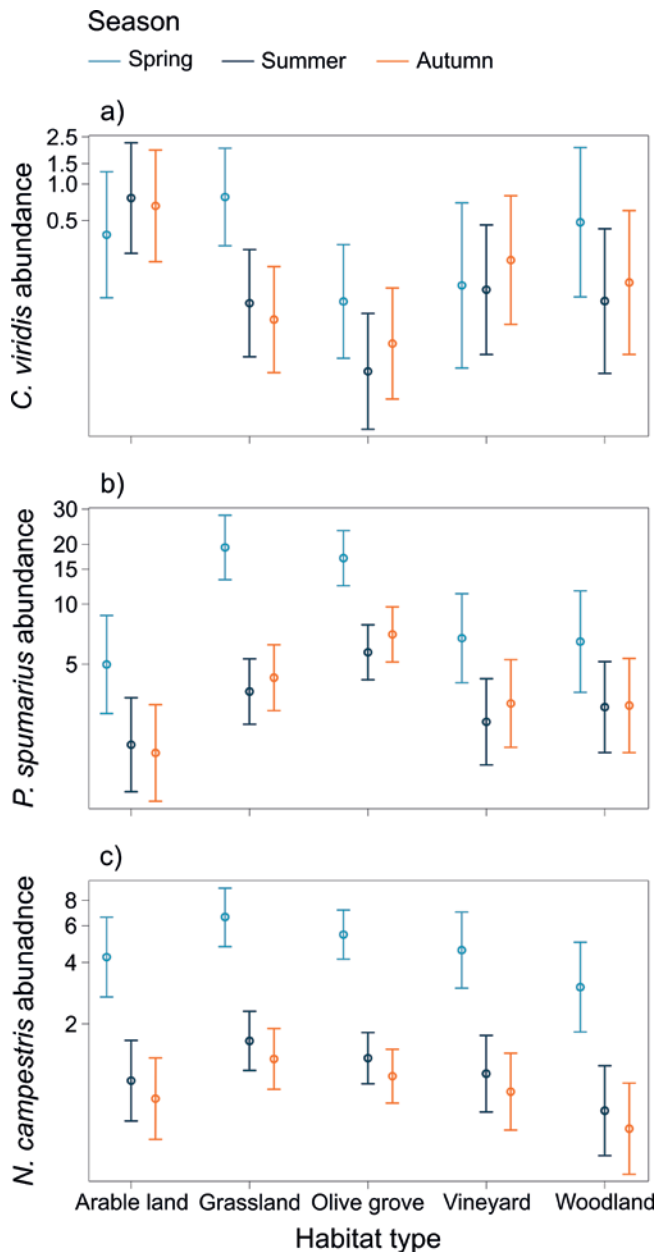
Fig. 1. Abundance of the most abundant (total abundance > 100) confirmed and potential vectors of *Xylella fastidiosa*, i.e., a) *Cicadella viridis* (potential vector), b) *Philaenus spumarius* (confirmed vector), and c) *Neophilaenus campestris* (confirmed vector), in response to habitat type over the three sampling seasons. Plots include model estimates (points) and 95% confidence intervals (bars).

Table 1. Results of the generalized linear mixed models (Poisson distribution) fitted by restricted maximum likelihood testing the response of abundance of the most abundant (total abundance > 100) confirmed and potential vectors of *Xylella fastidiosa*, i.e., a) *Cicadella viridis* (potential vector), b) *Philaenus spumarius* (confirmed vector), and c) *Neophilaenus campestris* (confirmed vector) to habitat and season.

	χ^2	DF	*p*-value
a) *C. viridis* abundance			
Habitat type	12.172	4	0.016
Season	4.173	2	0.124
Habitat type × Season	62.204	8	< 0.001
b) *P. spumarius* abundance			
Habitat type	37.572	4	< 0.001
Season	29.431	2	< 0.001
Habitat type × Season	61.299	8	< 0.001
c) *N. campestris* abundance			
Habitat type	6.387	4	0.172
Season	24.263	2	< 0.001
Habitat type × Season	10.832	8	0.211

4   Discussion

Network analyses helped to improve our understanding of the spatio-temporal dynamics of *X. fastidiosa* vectors across heterogeneous agricultural landscapes. The network approach proved to be a promising tool for informing the management of generalist pests, highlighting the role of single habitat types and habitat preferences of vectors on the epidemiology of *X. fastidiosa*.

Philaenus spumarius, the main vector of *X. fastidiosa*, was the most common species in the study area. During spring, *P. spumarius* was particularly abundant in grasslands, but as temperature increased its abundance decreased. During the hottest months, when the vegetation started to dry out, *P. spumarius* tended to move to sheltered and cooler habitats, avoiding open areas (Cornara et al. 2021). In olive groves, however, its abundance was high irrespective of the sampling season, suggesting that olive trees provided suitable thermal conditions and trophic resources for the adults. Bodino et al. (2020) also found high vector density in olive orchards during summer in regions with a cooler climate. This situation could be particularly challenging with the potential arrival of *X. fastidiosa* in the Abruzzo, as the high abundance and continuous presence of *P. spumarius* in olive groves could favour the bacterium spread. Interestingly, vineyards were among the less visited habitats, although Markheiser et al. (2020) reported a strong preference of *P. spumarius* for grapevines and other cultivated plant species. *Philaenus spumarius* also emerged as the most generalist species. Habitat generalist vectors are usually difficult to manage, and they have a greater ability to colonize new areas. They can therefore potentially spread the pathogen faster than other, more specialized vectors. *Philaenus spumarius* is one of the most polyphagous insects currently known (Weaver & King 1954; Cornara et al. 2019), therefore being easily adaptable to many habitat types across heterogeneous landscapes. The ability of this species to switch from
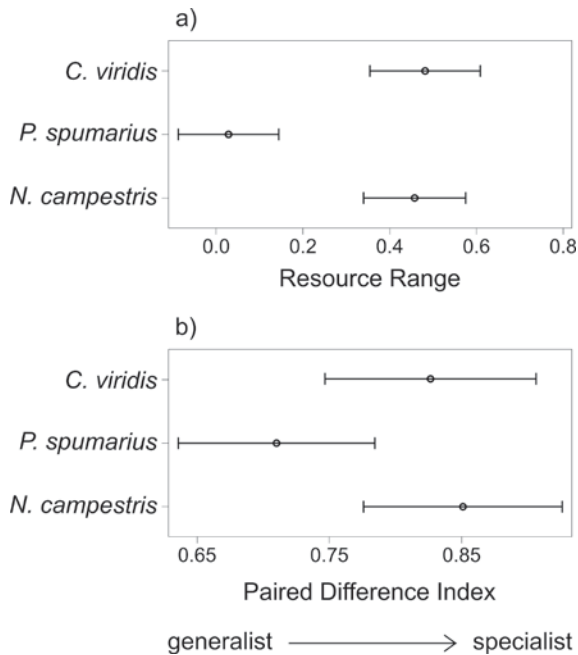
	χ^2	**DF**	*p*-value
a) Resource Range			
Species	47.661	2	< 0.001
Season	2.499	2	0.287
b) Paired Difference Index			
Species	15.399	2	< 0.001
Season	2.226	2	0.329
c) PAC ($\sqrt[3]{\ }$)			
Habitat type	111.161	4	< 0.001
Season	2.768	2	0.251
Habitat type × Season	39.792	8	< 0.001

Fig. 2. Habitat specialization of the most abundant (total abundance > 100) confirmed and potential vectors of *Xylella fastidiosa*, i.e., *Cicadella viridis, Philaenus spumarius*, and *Neophilaenus campestris*, in terms of a) Resource Range and b) Paired Difference Index. Both index values increase with increasing species specialization. Plots include model estimates (points) and 95% confidence intervals (bars).

one habitat type to another and its seasonal plasticity make it extremely challenging to manage.

Neophilaenus campestris, the other confirmed vector of *X. fastidiosa*, was mostly collected in spring and showed a certain level of specialization and preference for grasslands, as it mostly feeds on monocots (Biedermann & Niedringhaus 2004; Bodino et al. 2021b). Pesticide-free habitats such as grasslands therefore seemed to support populations of vector species. On the contrary, *C. viridis* was especially abundant in arable lands, vineyards, and woodlands. As there is still no evidence of its vector competence, it is not considered a key species in the spread of *X. fastidiosa* subsp. *pauca*. However, it is equally fundamental to investigate its biology, since the possible introduction of other strains of *X. fastidiosa*, potentially able to affect grapevine, almonds, and other cultivated plants (Hopkins & Purcell 2002; Moralejo et al. 2020), could make it a focal vector.

Landscapes in the study area were a mosaic of arable land, grasslands, olive groves, vineyards, and woodlands. Vector spillover showed which habitat patches could influence the confirmed and potential vector species assemblages in olive groves. Vector spillover to olive groves from other olive patches was always high. Instead, vector spillover from grasslands was high in spring and decreased in summer, when vector spillover from woodlands increased. Spillover

from arable lands and vineyards was limited. Landscapes with a high proportion of olive trees can strongly favour vector movements, therefore increasing the possibility of pathogen spread (Santoiemma et al. 2019). On the contrary, intensively managed arable lands and vineyards, which in the area are usually conventionally managed with one or two applications of pesticides a year, can probably reduce vector community populations (Santoiemma et al. 2019). Recent studies on *N. campestris* demonstrated that this species is able to disperse for distances longer than 2 km in 5 weeks (Lago et al. 2021), while *P. spumarius* can travel up to 200 m in just a few days (Bodino et al. 2021c) and possibly, for both species, even farther by passive dispersal. The dispersal ability of other spittlebug species is probably similar (Waloff 1973). Confirmed and potential vectors can therefore effectively move for relatively long distances from one habitat patch to another, reaching new olive groves.

The network analysis helped to understand which habitats were ideal for confirmed and potential vectors of *X. fastidiosa*, how these species could potentially spread from these habitats to olive groves, and how different species were affected by landscape composition. Landscapes dominated by adjacent olive groves revealed to be ideal for the spread of *X. fastidiosa*, and we highlighted the potential key role of non-managed grasslands in the spread of the plant pathogen. Although the management of plant pathogens across heterogeneous landscapes is particularly challenging (Daugherty et al. 2015), some actions could be useful to contrast the movement of confirmed and potential vectors of *X. fastidiosa*. In particular, local management practices such as early spring grassland mowing could therefore be integrated with landscape management, i.e., fragmentation of olive groves
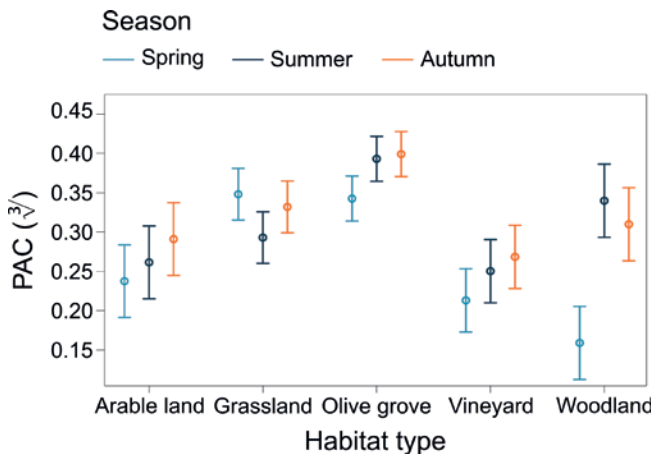
Fig. 3. Vector spillover, calculated using the PAC index, from all habitat types to olive grove patches over the three sampling seasons. Plot includes model estimates (points) and 95% confidence intervals (bars).

in order to intersperse olive orchards with open, dry spaces (Strona et al. 2017). Since olive groves emerged as the most suitable habitats to support vector populations, more research should be done to test alternative local management practices to reduce the vector populations within the agroecosystems (e.g., Sanna et al. 2021), which could lead to a lower probability of disease transmission in conjunction with other interventions.

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Figure S1–S3, Table S1–S2, additional references