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Xavier Mesmin, Marguerite Chartois, Sabrina Borgomano, Jean-Yves Rasplus, Jean-Pierre Rossi, et al.. Interaction networks between spittlebugs and vegetation types in and around olive and clementine groves of Corsica; implications for the spread of Xylella fastidiosa. Agriculture, Ecosystems & Environment, 2022, 334, pp.107979. 10.1016/j.agee.2022.107979 . hal-04003011

HAL Id: hal-04003011
https://hal.inrae.fr/hal-04003011v1

Submitted on 22 Jul 2024

Interaction networks between spittlebugs and vegetation types in and around olive and clementine groves of Corsica; implications for the spread of *Xylella fastidiosa*

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Abstract

The bacterium *Xylella fastidiosa* (*Xf*) is a major threat to European agriculture and notably to the olive and *Citrus* industry. It is transmitted by xylem-feeding insects, whose plant-feeding preferences still require investigation in European agroecosystems. Here we studied olive and clementine groves of the oriental plain of Corsica. Insect-vegetation type interaction networks for nymphs and adults of xylem-feeding insects were investigated three times a year during two years in and around crops. Networks were dominated by the *Philaenus spumarius* – *Cistus monspeliensis* interaction and were similar for olive and clementine groves, despite differences in plant communities of the ground vegetation and agricultural practices. To a lesser extent, *Dittrichia viscosa* was also a suitable feeding plant for *P. spumarius,* the main vector of *Xf* in Europe. *Neophilaenus campestris* was associated with grove ground vegetation, whereas *Lepyronia coleoptrata* and *Aphrophora alni* exhibited no or weak association with any of the target vegetation types. All species occurred on olive and clementine foliage in similar low abundance. Our results suggest that soil tillage in spring would be less efficient than in Italy to control *P. spumarius*. Instead, removing *C. monspeliensis* bushes from the close vicinity of groves could reduce risk of spread of *Xf* to crops. Finally, conserving *D. viscosa* in olive groves as a biological control strategy against the olive fruit fly is rather counter-productive as it maintains populations of *P. spumarius* under susceptible crops. Overall, our study shows that management strategies should be designed in relation to local insect-plant interaction networks that should be investigated in both cultivated areas and their immediate environment.

Keywords

Vector-borne disease, Community ecology, Meadow spittlebug, Phytopathogen

1 Introduction

Xylella fastidiosa (Wells, 1987) (*Xf*) (Xanthomonadales, Xanthomonadaceae) is transmitted between plants by xylem-sap feeding hemipterans (Cornara et al., 2019; Krugner et al., 2019). Biofilm-like colonies (Alves et al., 2004) and/or tyloses and pectin gels (De Benedictis et al., 2017) are formed that can completely occlude vessels of the xylem, thereby blocking water transport, which can lead to plant death (Chatterjee et al., 2008). Since decades and every year, the bacterium causes more than US$100 millions losses to the US grape industry (Pierce's disease) and to the Brazilian citrus industry (Citrus Variegated Chlorosis; Bové and Ayres, 2007; Tumber et al., 2014). Since 2013, the presence of *Xf* has been confirmed in different Mediterranean regions of Europe (EPPO, 2021) and research has intensified to better understand and control its spread.

As other insect-microbial-plant pathosystems (*e.g.* Irwin and Thresh, 1990), the *Xf* pathosystem is complex and gaps of knowledge remain although the bacterium has been extensively studied in the Americas, where it originated (Sicard et al., 2018). *Xf* can infect 595 wild or cultivated plant species from over 85 families (EFSA, 2020). In addition, most insect vectors are polyphagous (Cornara et al., 2019; Redak et al., 2004), which increases chances of transmission between semi-natural and cultivated habitats. Thus, connexions between agroecosystems and their immediate environment created by insect vectors need to be investigated to anticipate and limit outbreaks (Almeida et al., 2005; Coletta-Filho et al., 2011).

Insect vectors found in the New World are almost completely different from those found in Europe, making knowledge transfer difficult. Although networks of interactions between plant and vector communities are complex, all interactions do not equally contribute to disease spread. Understanding what are the main plant reservoirs of *Xf* as well as what are the main vectors and their preferred feeding plants is crucial to identify routes leading to transmission to susceptible crops (Farigoule et al., 2020; Rasplus et al., 2016). In addition, identifying key entities to plant-*Xf*-vector networks integrity should help design agro-ecological management strategies to control them and, consequently, to reduce the spread of *Xf* (Fontenille et al., 2020).

So far, a few studies have investigated vector feeding preferences in european agro-ecosystems (Antonatos et al., 2021; Bodino et al., 2021, 2020a; Cornara et al., 2017; Dongiovanni et al., 2019a; Villa et al., 2020). Most of them focused on olive groves of Southern Italy, a region that suffered from the dramatic economic and socio-cultural consequences of *Xf* introduction (Saponari et al., 2019). Nevertheless, there are other important crops threatened by *Xf*. For example, the Mediterranean basin produces almost 20% of the citruses worldwide (FAO, 2017) and to date only Thanou et al. (2020) reported samples of Auchenorrhyncha species in Greek *Citrus* groves. Given the impact of the Citrus Variegated Chlorosis (Bové and Ayres, 2007), other studies are urgently needed to anticipate possible outbreak.

In addition, although vectors are polyphagous, they seem to locally aggregate on preferred host plants. Thus, nymphs of *Philaenus spumarius* (L.), the most significant vector of *Xf* in Europe so far (Cornara et al., 2019) were reported to aggregate on Asteraceae, Apiaceae and Fabaceae in most large scale studies performed in Southern Italy (Bodino et al., 2020a; Dongiovanni et al., 2019a), Spain or Portugal (Morente et al., 2018; Villa et al., 2020). They were reported preferentially on Apiaceae and Rubiaceae, especially *Foeniculum vulgare* L. and *Galium album* Mill on a specific research center of central Italy (Latini et al., 2019). In Coastal California, where *P. spumarius* has been introduced from Europe, nymphs are particularly abundant on the seaside daisy *Erigeron glaucus* Ker Gawl (Karban and Strauss, 2004). In Corsica, *P. spumarius* seems to aggreate on *Cistus monspeliensis* L., at least locally

(Albre et al., 2021; Cruaud et al., 2018). These local associations and possible regional specificities question the generalization of sustainable management plans.

Finally, the role of surrounding semi-natural habitats is rarely investigated (but see Bodino et al., 2020a), even though, for example, riparian vegetation has been shown to be key in the primary transmission of *Xf* to grapevines in California (Coletta-Filho et al., 2011).

In this work, we analyzed the relative abundance of known and potential vectors of *Xf* (nymphs and adults) on four vegetation types in and around two economically important crops of Corsica (Agreste, 2021): clementine (*Citrus clementina* hort. ex Tanaka) and olive (*Olea europaea* L.) with statistical approaches and interaction network metrics. In addition to crop foliage and grove ground vegetation, we chose to focus on *C. monspeliensis* bushes and *D. viscosa* covers in the immediate grove environment. Indeed, based on literature and preliminary observations, substantial populations of *P. spumarius* were expected on these two plants. We investigated whether vectors shifted between vegetation types in the course of the year and we were particularly interested in detecting potential transfers to crop foliage as observed in previous studies in a similar climatic context (Cornara et al., 2017).

2 Materials and Methods

2.1 Study sites and sampling design

We monitored 8 and 6 organically-managed clementine and olive groves respectively. Their general features as well as the farming practices applied to these groves are presented in Table 1. All groves were located in a climatically homogeneous region of Corsica, France (Fig. 1) in which, during the two years of the study, minimum day temperature ranged from 0.1 to 4.6 °C (mean = 3.0 °C), maximum day temperature ranged from 26.5 to 30.4 °C (mean = 28.7 °C) and annual precipitation ranged from 637 to 1066 mm (mean = 809 mm) (source Météo France). On-field map of the groves and their vicinity were drawn prior to the first sampling session. Circular zones centered on the groves, thereafter called “microlandscapes” were defined so that their diameter (1 km) did not exceed the average dispersal capacity of the target insects (Bodino et al., 2020b; Lago et al., 2021). Depending on the size of the grove, either one or two microlandscapes were defined and a total of 17 microlandscapes were sampled (9 in clementine and 8 in olive groves; Table 2; Supplementary maps).

Three times a year during two years (2019 and 2020), known and potential vectors of *Xf* were counted on four vegetation types in each microlandscape: 1. on the tree crop foliage, 2. on the grove ground vegetation, 3. on *C. monspeliensis* bushes and 4. on *D. viscosa* covers. These two last vegetation types were chosen because *C. monspeliensis* (Albre et al., 2021; Cruaud et al., 2018) and *D. viscosa* (pers. obs.) are suspected to host significant populations of *P. spumarius* in Corsica. Other vegetation types covering large areas such as forests (Table 3) were left unsampled because Chartois et al. (2021) showed that they host low abundances of *Xf* vectors.

A sampling event on each vegetation type consisted in a 10 minutes count of nymphs or adults (see Insect Collection).

For tree foliage, peripheral branches up to 2.5m were targeted. The grove ground vegetation as a whole was included in the survey. A botanical inventory of the grove ground vegetation was carried out in October 2019, June 2020 and October 2020 using one square meter quadrats randomly positioned in two inter-rows with four repetitions per row (*i.e.*, 8 quadrats per site). Each species recorded (or genus if the phenological stage did not allow for a more precise identification) was associated with an “abundance-dominance” coefficient derived from Braun-Blanquet (1964) (1: <1% cover of the quadrat; 2: 10 to 25% cover; 3, 4 and 5: 25 to 50, 50 to 75 and 75 to 100% cover of the quadrat). For *C. monspeliensis* and *D. viscosa,* when several patches were present in the microlandscape, patches (young seedlings and old shrubs) closest to the grove were sampled first. Then, collectors progressively moved away from the grove to sample more distant patches until the 10 min time limit was reached. The same patches were visited in each sampling session. Table 3 shows the areas available/actually sampled for each vegetation type as well as the distance among sampled vegetation types (for a comprehensive description of spatial size and location of sites, see the Supplementary maps).

2.2 Insect collection

Cercopoidea populations were monitored in mid April when spittle abundance was the highest as well as in June and October, when populations of adults of *P. spumarius* before and after aestivation were the largest (pers. obs.). Therefore, our sampling shedule was primarly designed to get the best focus possible on *P. spumarius*, the main vector of *Xf*, but was also relevant for other spittlebugs. Indeed, Bodino et al. (2021, 2019) suggested that the phenologies of *P. spumarius*, *N. campestris* and *A. alni* are similar in Italian olive groves. Monitoring was not possible in April 2020 due to restrictions relative to the Covid-19 pandemic.

Insect monitoring (nymphs and adults) was based on an equal sampling duration of 10 minutes on each of the four target vegetation types. For nymphs, a preliminary test was performed to assess an on-sight sampling method. Four hundred forty individuals were randomly collected from various spittles, assigned to species based on literature and identified in the lab under a binocular microscope (Appendix 1 in Supplementary Materials). Precisely, spittle masses found at the crown of grass plants were assigned to *Neophilaenus campestris* (Fallén); those found at the crown of dicotyledonous plants species were assigned to *Aphrophora alni* (Fallén) and those found on the upper part of graminaceous or dicotyledonous plants were assigned to *P. spumarius* (Halkka et al., 1977; Fig. 2). Nymphs of *Lepyronia coleoptrata* (L.) appeared later in our climatic context (Barro and Pavan, 1999), and no spittle could be attributed to this species. In our context, on sight identification by our trained eye was validated in over 99 % of cases (Appendix 1). Spittle masses were therefore counted and identified directly in the field (upper and lower surfaces of the leaves were inspected when relevant). In the rare cases where identification was troublesome, we dispersed the spittle with a fine paintbrush and identified nymphs to species with morphological characters (Fig. 2). Because the number of nymphs per spittle was close to one for all species (1.45 for *P. spumarius*, 1.24 for *N. campestris* and 1.39 for *A. alni*; Bodino et al., 2020a), we considered the number of spittles as a good proxy of the number of nymphs.

For adults, the 10 minutes sampling were fragmented in periods of 30 seconds of vegetation sweeping with alternate backhand and forehand strokes of sweeping nets followed by 10-30 seconds of collection of spittlebugs with mouth aspirators. Sweep netting is indeed recognized as the best method to collect the target insects (Morente et al., 2018). Sweeping the vegetation over a longer period would have increased risks of missing target insects in the net among the many plant debris and non-target arthropods. When the 10 min time limit was up, insects collected in the mouth aspirators were stored in 75° alcohol and brought to the laboratory for identification under a binocular microscope using Biedermann & Niedringhaus (2009) identification key.

2.3 Data analysis

Analyses of i) networks between insects and target vegetation types; ii) insect abundances per vegetation type; iii) insect shifts between vegetation types; iv) insect occurrences on crop foliage and v) grove ground vegetation were performed in R (R core team, 2019) using generalized linear mixed models (GLMMs; Bolker et al., 2009; Table 4).

Details on each model adjustment (error distributions, link functions, observation-level random effects) are available in Appendix 2. Random effects on microlanscape or site locations were used to account for spatial or temporal dependence resulting from our sampling design (Faraway, 2006; Appendix 2). GLMM validity hypotheses of correct distribution, dispersion, frequency of outliers and homoscedasticity were checked with the R package ‘DHARMa’ (Hartig, 2020). The structure of each model was simplified by successive backward elimination of non-significant fixed effects based on analysis of deviance (R package ‘car’, Fox and Weisberg, 2019). Post-hoc pairwise comparisons of estimated marginal means were performed on the final model (R package ‘emmeans’, Lenth, 2020) to assess differences among factor levels.

2.3.1 Interaction networks

We built an interaction network (insect vs. vegetation type) for each microlandscape and each sampling session. To compare the diversity and evenness of interactions, we computed the connectance (*i.e.* the ratio between the number of observed interactions and the potential number of interactions with the R package ‘bipartite’; Dormann et al., 2008), the interaction evenness (*i.e.* the observed Shannon’s diversity of interactions divided by the maximum Shannon’s diversity attainable, with the same package) and the proportion of interactions represented by the bipartite *P. spumarius – C. monspeliensis* interaction (that was highligted as predominant). We assessed the correlation between each of these metrics and tree crop, sampling month and their interaction (Table 4A). For network visualization, we computed one summed network per tree crop and sampling month (R package ‘bipartite’) using weights to take the uneven sampling efforts into account (Table 2, Appendix 3).

2.3.2 Association with vegetation types

We analyzed insect association with vegetation types by assessing the correlation between the number of sampled individuals and species, sampling month, vegetation type and tree crop. As we expected varying effects of tree crop, vegetation type and sampling month with respect to insect species, we introduced interactions between insect species and these three factors (Table 4B).

In order to test whether host associations varied in the course of the year, we used one GLMM per insect species, testing the interaction between sampling month and vegetation type, while controlling for the effects of sampling month, vegetation type and tree crop (Table 4C).

Finally, we tested the hypothesis that *P. spumarius* was the most frequent Cercopoidea, including on crop foliage. Abundance was coded as a dummy variable (0 for absence, 1 for presence) and only sampling months for which at least one individual was found on crop foliage were kept. We assessed the correlation between insect occurrence and insect species; tree crop, and sampling month (Table 4D).

2.3.3 Differences in ground vegetation between crops

Divergence between plant communities found in inter-rows of clementine and olive groves was assessed using a correspondence analysis (Chessel et al., 2004) performed on species presence/absence. To minimize the sensitivity of this analysis to rare plant species, only species found on at least 5% of the quadrats were kept.

To get a functional view of vegetation communities, we retrieved Ellenberg's indicator values (EIVs) established in Italy (Pignatti et al., 2005) for moistness and nutrient availability of all plant species found in this study (R package 'TR8'; Bocci, 2015). EIVs give a general view of plant species requirements based on experts' knowledge (Ellenberg et al., 2001), are unitless, and range from 1 to 12 (for moistness) or from 1 to 9 (for nutrients). Plant species requirements for the abiotic factor increase with the EIV value. A community weighted mean ("CWM"; Violle et al., 2007, see Appendix 4 for details) was computed for each EIV on each quadrat, giving the average level of moistness ("CWM_moistness") and nutrient availability ("CWM_nutrients") on each quadrat as reflected by the vegetation. We assessed the correlation between these two CWMs and the tree crop plus the sampling month (Table 4E).

3 Results

Overall, we counted 6,647 nymphs and 1,714 adults (Fig. 3). Four species of Aphrophoridae were found in the sampled sites: *P. spumarius*, *N. campestris*, *L. coleoptrata* and *A. alni*.

3.1 Interaction networks

The connectance and evenness of the interaction networks were higher in October than in April (nymphs) or June (Figs. 3-4, Table 4A). The connectance did not differ significantly between olive and clementine groves, whatever the sampling month, and evenness of interactions was higher in olive groves (Figs. 3-4, Table 4A). The *P. spumarius*-*C. monspeliensis* interaction was predominant. This interaction was the strongest in April (nymphs), and was globally stronger in clementine groves (Figs. 3-4, Table 4A).

3.2 Association with vegetation types

Philaenus spumarius was more abundant than any other species in April (nymphs) and October. *Lepyronia coleoptrata* was the least abundant in October (Fig. 3, Table 4B & S5.1). Insect abundance was generally low in June and did not differ significantly among species, except that *L. coleoptrata* was more abundant than *N. campestris* (Table S5.1).

The association with the vegetation type differed for the four species but only *P. spumarius* and *N. campestris* exhibited marked associations (Fig. 3, Table 4B). For all sampling months combined, *C. monspeliensis* bushes hosted the largest abundance of *P. spumarius*. Populations of *P. spumarius* were smaller on *D. viscosa* covers, even smaller on grove ground vegetation and the smallest on crop foliage (Fig. 3, Table S5.2). For *N. campestris* and *L. coleoptrata*, the largest populations were recorded on grove ground vegetation and populations were smaller on *D. viscosa* covers, *C. monspeliensis* bushes and on crop foliage (Fig. 3, Table S5.2). Finally, *A. alni* population sizes did not differ significantly among vegetation types (Fig. 3, Table 4B). All vegetation types combined, whatever the species considered, Cercopoidea populations were larger in olive groves (Table 4B).

The association of *P. spumarius* with *C. monspeliensis* bushes, followed by *D. viscosa* covers, grove ground vegetation and, lastly, crop foliage, did not change substantially depending on sampling month, even though a significant interaction between vegetation type and sampling month was found (Table 4C, S5.3). The association with the vegetation types (or lack of it) described above for the three other species did not vary with the sampling month (Table 4C).

In June and October, all tree crops combined, *P. spumarius*, *N. campestris*, *L. coleoptrata* and *A. alni* were respectively found on 7.0 (± 3.4, standard deviation), 3.5 (± 2.4), 3.5 (± 2.4) and 14.0 (± 4.6) percent of the samples made on crop foliage. The difference in frequency between species was not significant and neither was the difference between crops (Table 4D). Contrastingly, the probability to find cercopoids on crop foliage was higher in October (0.11 ± 0.03) than in June (0.03 ± 0.01, Table 4D) and no nymph was found on crop foliage in April.

3.3 *Differences in ground vegetation between crops*

Plant communities of the ground vegetation were different in olive and clementine groves (Fig. 5A), even if axes 1 and 2 of the correspondance analysis only captured 15.9% of the inertia in the data. The moisture and nutrient availability in ground vegetation, as reflected by plant communities, did not significantly vary with the sampling month but were higher in clementine groves (Table 4E, Fig. 5B).

4 Discussion

4.1 *Spittlebug association with vegetation types*

As expected from their ability to fly, adults have connection with more vegetation types than nymphs that hardly move from their native plant. Our sampling showed that populations of *P. spumarius* were significantly larger on *C. monspeliensis* patches located in the vicinity of olive and clementine groves than on any other of the target vegetation types. Thus, so far, Corsica appears to be the only place where *P. spumarius* is preferentially associated with *C. monspeliensis* although this plant is common over the whole Mediterraneean basin (Fernández-Mazuecos and Vargas, 2010). While *D. viscosa* was never reported as one of its preferred host plants, it also hosted substantial populations of *P. spumarius* (both nymphs and adults), which is not surprising since *P. spumarius* frequently aggregates on Asteraceae (Cornara et al., 2018).

Expectations regarding other species were globally confirmed. *Neophilaenus campestris* was mostly found on grove ground vegetation, in accordance with its expected association with Poaceae (Bodino et al., 2020a; Dongiovanni et al., 2019a; Villa et al., 2020). *Dittrichia viscosa* also appeared a suitable host for adults of *N. campestris*, mostly during autumn, which adds another shift in host plant family to those previously documented (*e.g.* in Spain where it has been recorded on *Pinus halepensis*; Lago et al., 2021; Morente et al., 2018). *Aphrophora alni* and *L. coleoptrata* were not, or only weakly associated with a specific vegetation type. However, it should be noted that our sampling design focused on insect-vegetation associations that were the most noticeable to us in preliminary experiments. We especially focused on two plants of the grove vicinity (*C. monspeliensis* bushes and *D. viscosa* covers) that appeared to be significant reservoirs of *P. spumarius*. Several vegetation types representing large areas were left unsampled in our microlandscapes (*e.g.* oak forests or riparian forests, Table 3) and insect-vegetation type associations were probably overlooked based on our sampling design. We probably missed few significant interactions in oak forests since Chartois et al. (2021) showed that they host low abundances of *Xf* vectors. Still, *L. coleoptrata* nymphs were found on *Quercus suber*, *Arbutus unedo*, *Myrtus communis* or *Pistacia lentiscus* in forest borders (this study, pers. obs.) and may require further attention. Substantial populations of *A. alni* were also found in riparian forests during previous field work (Chauvel et al., 2015). Such associations should be investigated to get a more comprehensive view of the distribution of *Xf* vectors in ecosystems, but this was beyond the scope of this study.

Finally, it is important to note that, although assignation of spittles to species could have been, in our specific case, accurately derived from plant host class, spittle position and spittle aspect, this can be misleading to non-trained eye and unreliable when associations with vegetation type are weaker. Therefore, we would not advise this method for untrained experimenters and/or studies performed in habitats where several species of spittlebugs are mixed on the same vegetation types. In such cases, the collection and identification of all nymphs is advisable.

4.2 Interaction networks and epidemiology of Xf *in Corsica*

Plant communities found in olive and clementine crops reflected different conditions in terms of moisture and nutrient richness. Moreover, the number of mowing operations in olive groves was about two times lower, meaning that the insects were generally less disturbed. Contrastingly, we found only minor differences on the interaction networks between spittlebugs and vegetation types. Spittlebug populations (especially *N. campestris*) were slightly larger in olive groves, with a more even repartition of interactions in the networks. This is in line with results of Sanna et al. (2021) who found decreasing abundance of *P. spumarius* with increasing mowing frequency. But above all, these results suggest a weak link between plant communities, ecological conditions, and insect populations in the ground vegetation of Corsican clementine and olive groves, at least within the climatic context studied. This suggests that if *Xf* strains to which olive and clementine groves are susceptible were to be introduced in Corsica, the transmission chances to both crop species would be likely similar.

For any of the species studied, no transfer from ground vegetation to crop foliage was observed in June. This contrasts with what was observed in June-July in Italy, where populations of *P. spumarius* occuring on ground vegetation decrease, while populations remain stable or increase on crop foliage (Bodino et al., 2020a, 2019; Cornara et al., 2017). Given this contrast, it would be interesting to complement our sampling with collection in mid-summer, to check whether transfer to crop foliage does not occur later in Corsica. More generally, shifts between the studied vegetation types or with unsampled types may occur in the middle of the summer when even mediterraneous shrubs such as *C. monspeliensis* get dry. This remains an open research avenue because spittlebug preferences in summer are poorly documented (Albre et al., 2021; Chauvel et al., 2015; but see Cornara et al., 2021).

Spittlebug density on ground vegetation and crop foliage were globally much lower than reported in Italy. Indeed, Bodino et al. (2019) reported adult densities of 1-2 individuals per m^2 on average on ground vegetation (in June and October) and Bodino et al. (2020a) reported abundances of *ca.* 1-2 individuals per olive tree (in May, June and July). Contrastingly, in our study, maximum abundances were reached in October and were respectively of *ca.* 3.1×10^{-3} individuals per m^2 (1.2 individuals on 390 m^2, Table 3) and of *ca.*1.9×10^{-2} individuals per olive tree (0.14 individuals for 7.5 trees). Although a rigorous comparison of these densities is difficult due to different sampling methods, data suggest that the density of *P. spumarius* adult is 100 to 1000 times higher in Italian olive groves than in Corsican olive or clementine groves (confirmed by observations in Apulia, Cruaud & Rasplus, pers. com.). Understanding what landscape features (see *e.g.* Santoiemma et al., 2019) and/or farming practices (see *e.g.* Sanna et al., 2021) explain the difference between these two contexts is one of the perspectives opened by our study.

In epidemiological terms, the conclusions drawn from the two previous paragraphs, i.e. low transfer from ground vegetation to crop foliage and smaller populations of *P. spumarius*, suggest that *Xf* propagation to tree crops could be slower in the Corsican context than in the Italian one.

We found that the four spittlebugs occurred at similar frequencies on crop foliage, contrary to Antonatos et al. (2021) or Bodino et al. (2020a), who found a strong predominance of *P. spumarius* on the foliage of olive trees (usually 4-6 times more abundant than *A. alni* or *N. campestris*). In our context, based on relative frequencies, *P. spumarius*, *N. campestris*, *A. alni* and *L. coleoptrata* could contribute similarly to *Xf* epidemics in Corsican groves. However, aside from frequency, species may also have different transmission efficiency. Transmission rate has not been quantified for *L. coleoptrata* and *A. alni* (Cornara et al., 2019), but Cavalieri et al. (2019) showed that *N. campestris* is consistently less efficient than *P. spumarius* in transmitting *Xf* to healthy plants. Further studies are thus needed to understand on what species control measures are most needed.

Finally, spittlebug frequency on crop foliage was higher in October than in June, contrary to Italy, where maximum densities are observed in June-July (Bodino et al., 2020a). This result has two contrasting implications for *Xf* epidemics in Corsica. On the one hand, spittlebugs occur on crop foliage when they are the most infective, because insect infectivity *in natura* globally rises from their emergence in spring to following winter (Beal et al., 2021). On the other hand, several authors found that the probability of *Xf* winter curing is higher when *Xf* inoculation date occurs late (Cao et al., 2011; Feil et al., 2003). Consequently corsican clementine and olive trees would be more likely to recover thanks to winter curing than if they were infected earlier in the season. However, climatic conditions, specific features of plant species and *Xf* subspecies may modulate overwinter recovery and specific studies are also needed on that topic.

4.3 Implications for the agroecological management of Xf *vectors*

Given host plant association for *P. spumarius*, removing *C. monspeliensis* bushes that are close to groves could decrease risk of transfer of *Xf* to crops and the consequences of such practice should be properly evaluated. *Dittrichia viscosa* is occuring naturally and is conserved by some farmers to control the olive fruit fly *Bactrocera oleae* (Diptera: Tephritidae) (Boccaccio and Petacchi, 2009). Indeed, species within the *Eupelmus urozonus* complex (Hymenoptera: Eupelmidae) are thought to parasitize larvae of *B. oleae* in summer and those of another tephritid, *Myopites stylata* that forms gall in flowers of *D. viscosa*, in winter (Michelakis, 1986; Warlop, 2006). Therefore, *D. viscosa* is supposed to maintain substantial population of parasitoid in winter which should improve control of *B. oleae* in the next year. The conservation of *D. viscosa* near and inside olive groves has therefore been encouraged, especially in organic farming (Warlop, 2006; Warlop et al., 2010). However, taxonomic revision of the *E. urozonus* complex by Al Khatib et al. (2014) casts doubts on the identification of parasitoids in earlier works. Uncertainties remain regarding their host specificity and the actual frequency of host shifting between *B. oleae* and *M. stylata* (Al Khatib et al., 2014). As our results show that *D. viscosa* hosts significant populations of *P. spumarius* and in the absence of quantitative studies assessing the effect of *D. viscosa* conservation on *B. oleae* occurrence and damage, removing *D. viscosa* from olive groves is recommended.

Finally, soil tillage has been advocated in Italy to kill *P. spumarius* nymphs (Dongiovanni et al., 2019b) that develop on ground vegetation. Recent work has shown that soil tillage indeed limits *P. spumarius* density on ground vegetation (Sanna et al., 2021), but only in the short term (differences disappeared within *ca.* 2 months). Here, we found that the predominance of the *P. spumarius*-*C. monspeliensis* interaction was the strongest in April, with very few nymphs developing on the ground vegetation. This result suggests that soil tillage in the spring would likely be inefficient to limit spittlebug populations in Corsican olive and clementine groves.

Instead, release of *Ooctonus vulgatus* (Hymenoptera: Mymaridae) in autumn (Mesmin et al., 2020), of *Verrallia aucta* (Diptera: Pipunculidae) in late spring/early summer (Molinatto et al., 2020), and/or of *Zelus renardii* (Hemiptera: Reduviidae) in autumn (Liccardo et al., 2020) in the close vicinity of groves, could be efficient to reduce *P. spumarius* pressure. However, while these three natural enemies naturally occur in mainland France (Garrouste, 2019; Mesmin et al., 2020; MNHN and OFB, 2021), information are still missing regarding the occurrence of the last two in Corsica. Complementary studies are needed to avoid releasing allochthonous species and reduce risk of non-target effects (Van Driesche and Hoddle, 2016).

5 Conclusion

We showed that *P. spumarius* displays an unusual association with *C. monspeliensis* in the studied agro-ecosystems and their immediate environment. The relative frequency of four common spittlebugs on olive or clementine foliage suggest that species others than *P. spumarius* may have a significant role in *Xf* spread in Corsican groves, should they be proven efficient vectors. Finally, as insect association with vegetation types changes inside a common geographic and climatic context, our results and those obtained in Italy emphasize that management methods to decrease risk associated with *Xf* should be designed in relation to local insect-plant interaction networks.

6 Acknowledgements

We thank the farmers who participated in the survey as well as Olivier Audibert (Inter Bio Corse), Laurent Julhia (INRAE) and Marina Girard (Terre d'Agrumes) for their help in building this farmers' network. We are also grateful to François Casabianca (INRAE, Corte, France) and Laetitia Hugot (CBNC, Corte, France) for their collaboration in the setup of the research project.

Funding: this work was supported by the Collectivité Territoriale de Corse and the European Union Horizon 2020 research and innovation program [Grant Agreement No. 727987 XF-ACTORS].

7 Data statement

Data used to perform all statistics and graphics shown in the article are freely available at https://doi.org/10.15454/8QJI30.

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Table 1 Characteristics and agricultural practices of the studied groves. Mean values and standard deviations (in brackets) are provided, except for the proportion of irrigated groves that is shown in percents.

Table 2 Sampling events on vegetation types targeted in the study. Changes in agricultural practices through time led to the inclusion/suppression of groves. Changes in the number of *C. monspeliensis* bushes and *D. viscosa* covers are due to their unavailability in some groves.

Table 3 Area of each sampled vegetation type, distance among sampled vegetation types and area of available vegetation types in the microlandscapes. Median values are provided. Variation in sampled areas for adults (larger) and nymphs was due to the difference in sampling methods (sweeping net versus on sight count). Available areas were assessed based on aerial photographs, field knowledge and photographs made in the field, but not on a comprehensive on-field cartography. They are therefore accurate for most vegetation types but should be seen as an order of magnitude for *C. monspeliensis* bushes and *D. viscosa* covers. “Forests” are mainly oak forests in our meso-mediterranean context (Reymann et al., 2016, p. 9). Riparian forests were defined as 5 m buffers around stream banks (Sawtschuk et al., 2014). An interactive and comprehensive description of the spatial ditribution of sampling sites can be found in the Supplementary maps.

Table 4 Description and results of analyses using GLMMs. Fixed effects and sample sizes (“#obs”, missing values removed) used to analyze insect-vegetation type networks (A), insect abundances per vegetation type (B), vegetation type shifts per species (C), insect occurrence frequency on crop foliage (D) and ground vegetation (E). “x : y” stands for “interaction between x and y”. Vegetation type refers to olive or clementine foliage, grove ground vegetation, *C. monspeliensis bushes* and *D. viscosa* covers located within a 500 m-radius to the crop. For each GLMM and each fixed effect, values and significance of Type-II

Wald chi square tests are shown. Non significant fixed effects were dropped in model selection and are depicted with a “-“ in χ^2, df and P columns. For all significant interactions, text in exponent refers to tables of Appendix 5 that detail pairwise comparisons of factor levels. CWM : community weighted mean (see text).

Figure 1 Sampling sites. A and B, studied area (white circles and triangles for clementine and olive groves, respectively); C, details of one olive grove (see Supplementary maps for a comprehensive description of the spatial distribution of sampling sites). Elevations and orthophotographs are from BD ALTI® 25M (© IGN – 2022) and ORTHO HR® (© IGN – 2022), respectively.

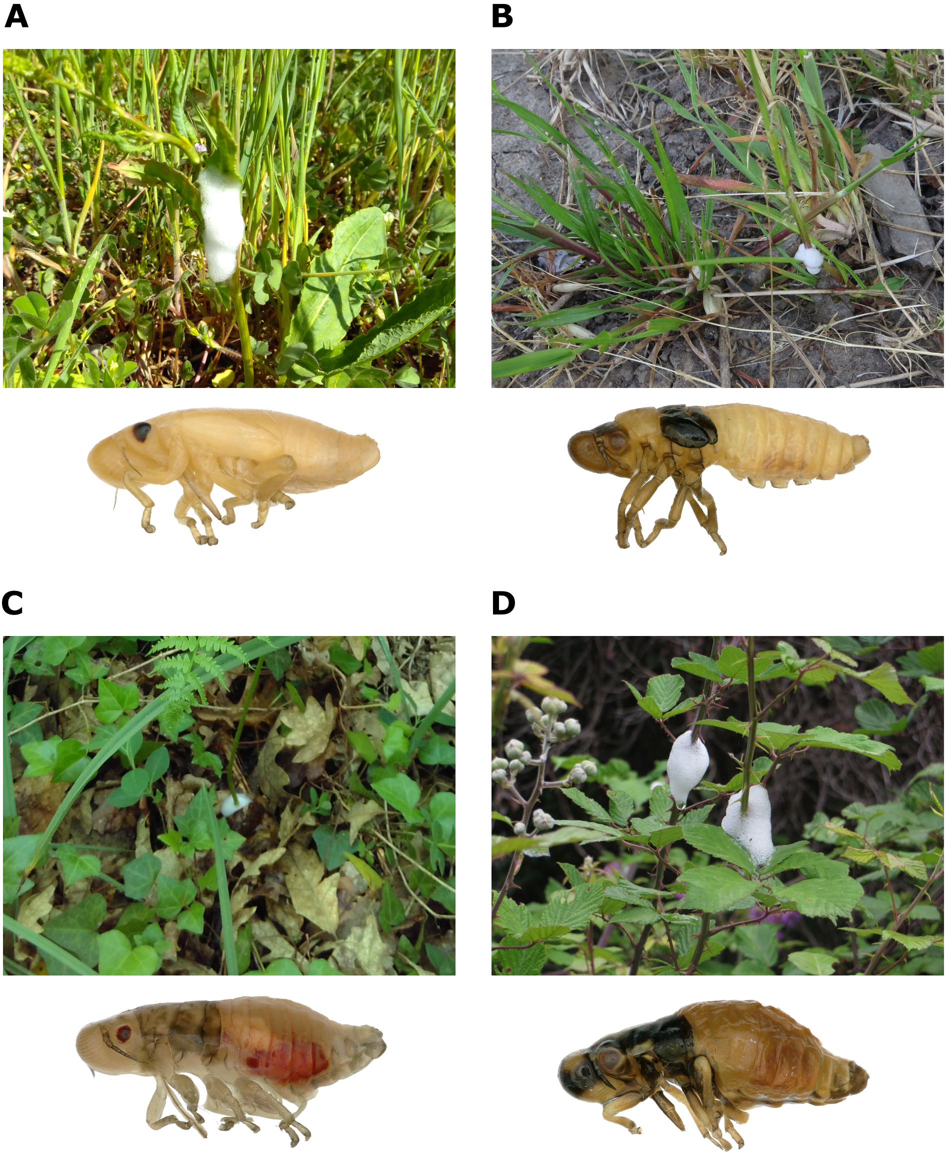
Figure 2 Typical positions and aspects of spittles produced by nymphs and lateral views of nymphs. *Philaenus spumarius* (A), *N. campestris* (B), *A. alni* (C) and *L. coleoptrata* (D). Nymphs of comparable sizes were selected for illustration purpose, and nymphal stage differs between species.

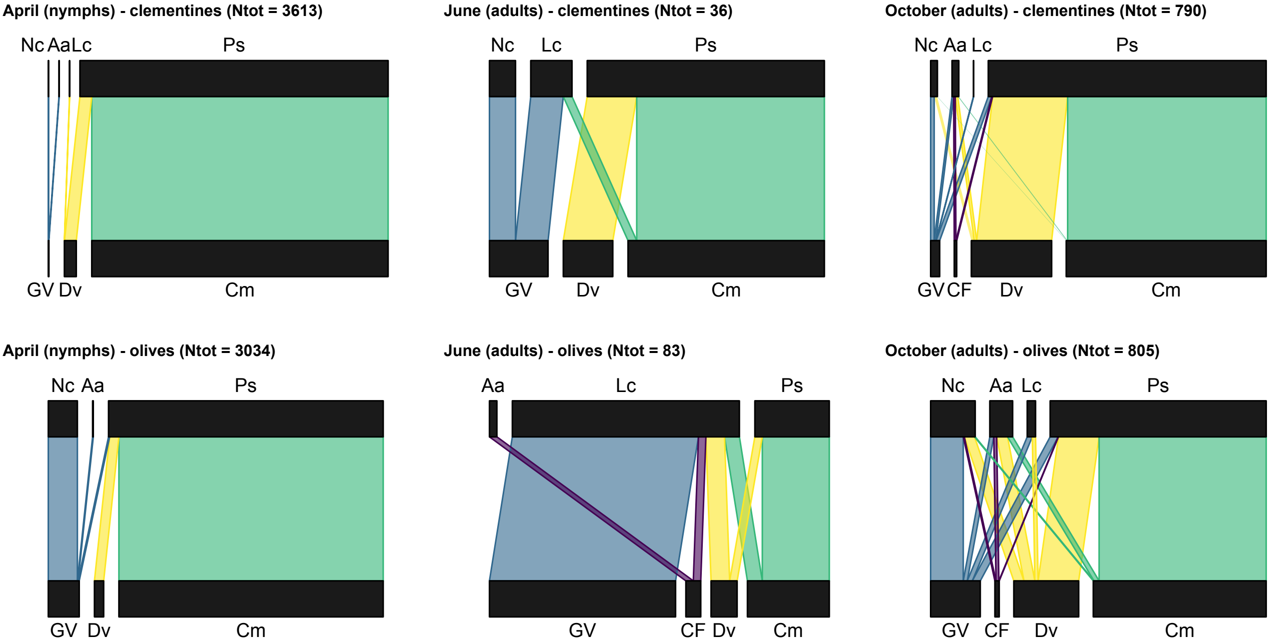
Figure 3 Insect-vegetation type interaction networks for each sampling month and each crop. Numbers of nymphs (April) or adults (June, October) on which networks are based are displayed as "Ntot". Abbreviations of insect names (upper part of each network) are as follows: Nc: *Neophilaenus campestris*, Aa: *Aphrophora alni*, Lc: *Lepyronia coleoptrata*, Ps: *Philaenus spumarius*. Abbreviations of vegetation type (lower part of each network) are as follows: GV: grove ground vegetation, CF: crop foliage, Dv: *Dittrichia viscosa* cover, Cm: *Cistus monspeliensis* bushes.

Figure 4 Values of connectance, interaction evenness and *P. spumarius*-*C. monspeliensis* predominance depending on sampling month and crop. Each point represents a network established on a given microlandscape for a given sampling session (circles and triangles for clementine and olive groves, respectively). Estimated marginal means of the model fitted on the data are displayed as black squares together with their 95% confidence levels and letters depict the significance of the effect of sampling month on network metrics (pairwise comparisons of estimated marginal means). For each panel taken independently, sampling months sharing a letter do not differ significantly.

Figure 5 Comparaison of ground vegetation between olive and clementine crops. Correspondance analysis performed on the botanical composition of the quadrats (A) and functional characterization of the vegetation based on the Ellenberg indicator values for moistness and nutrients (CWM; community weighted means). In A, each point is a vegetation quadrat (circles and triangles for clementine and olive groves, respectively); each abbreviation depicts a plant species (initials of the genus and species names; see Table S6.1 for complete names) and ellipses show 75% confidence enveloppes of quadrats (computed with the R package 'FactoMineR'; Lê et al., 2008). In A, only species found on at least 5% of the quadrats are shown. In B, data are shown as density traces ("violin plots"; Hintze and Nelson, 1998) highlighting the distribution of the data. The significance of correlation between each variable and crop is shown with asterisks (***<p=0.001<**<p=0.01<*<p=0.05<NS).


A
43.0°N
42.5°N
42.0°N
41.5°N
Bastia
Calvi
Corte
Ajaccio
Sartène
8.4°E
8.6°E
8.8°E
9.0°E
9.2°E
9.4°E
B
Elevation
2500
2000
1500
1000
500
0
Tree crop
○ Clementines
△ Olives
C
Grove
Vegetation types sampled (adults)
Crop foliage
Grove ground vegetation
C. monspeliensis bushes
D. viscosa covers
N
0
100
200
300
400
500 m


A
B
C
D



April (nymphs) - clementines (Ntot = 3613)

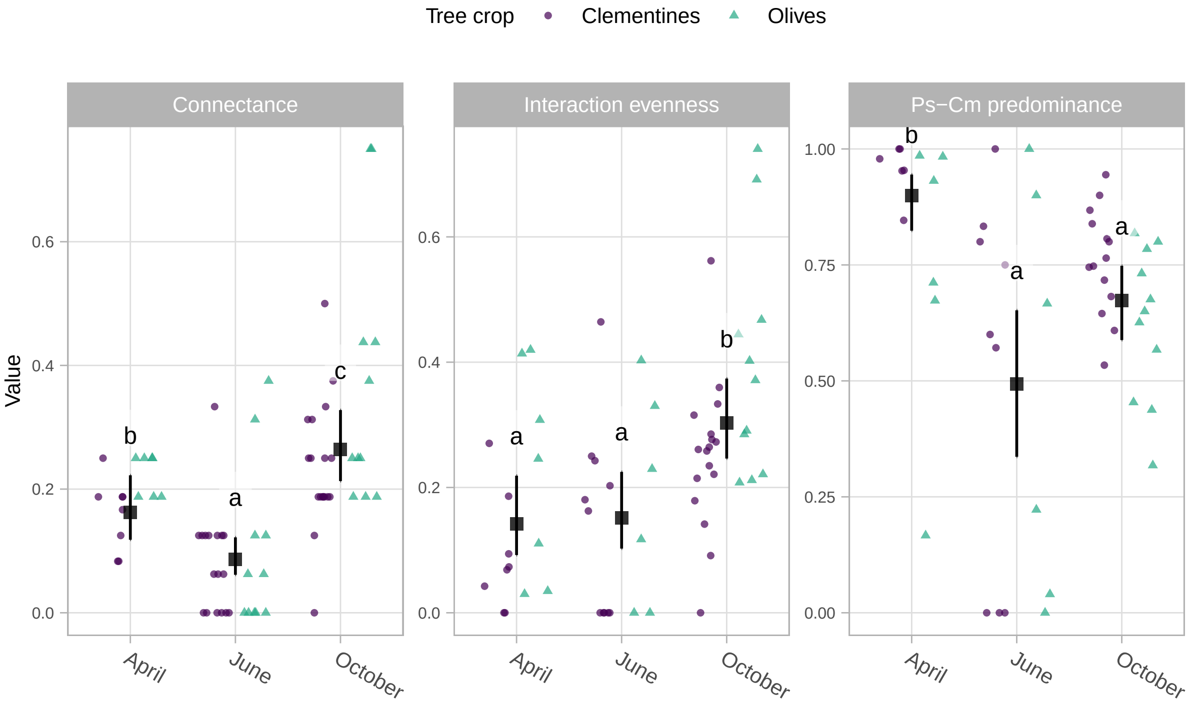
June (adults) - clementines (Ntot = 36)

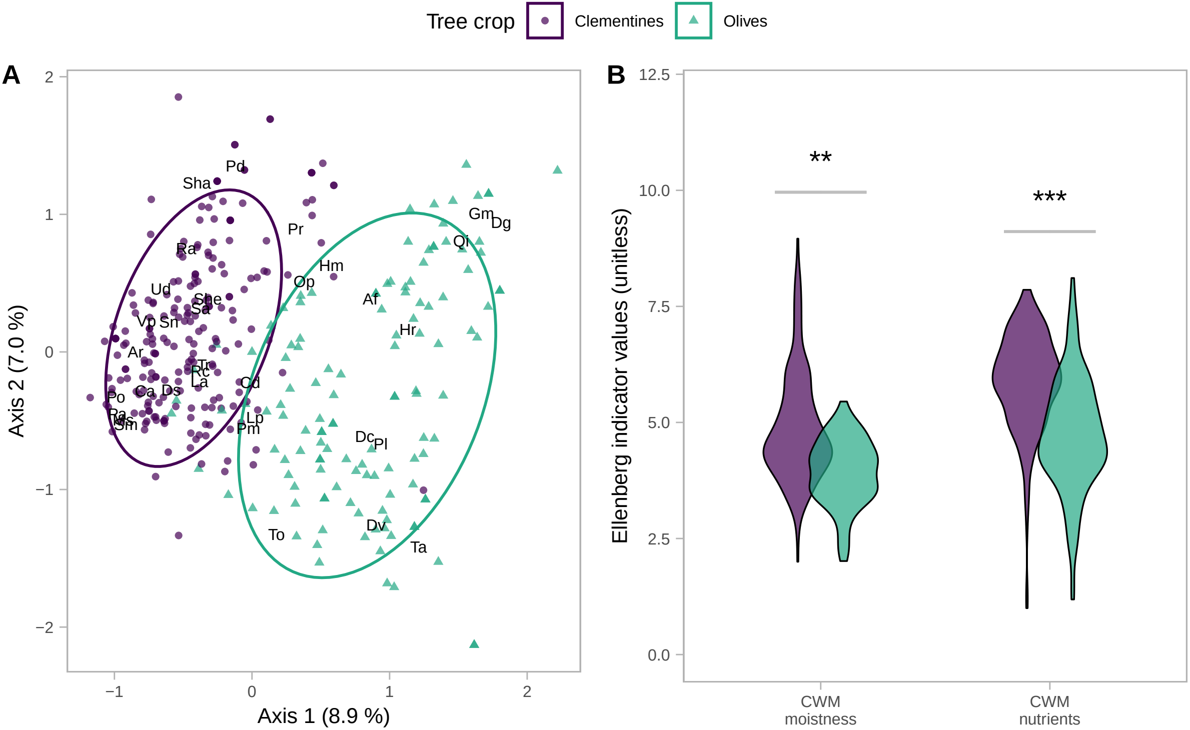
October (adults) - clementines (Ntot = 790)

April (nymphs) - olives (Ntot = 3034)

June (adults) - olives (Ntot = 83)

October (adults) - olives (Ntot = 805)


Tree crop
Clementines
Olives
Connectance
Interaction evenness
Ps−Cm predominance
Value
0.0
0.2
0.4
0.6
0.00
0.25
0.50
0.75
1.00
a
b
c
April
June
October


Tree crop
Clementines
Olives
A
Axis 2 (7.0 %)
Axis 1 (8.9 %)
2
1
0
−1
−2
−1
0
1
2
Pd
Sha
Pr
Ra
Hm
Op
Ud
She
Sa
Af
Vp
Sn
Hr
Ar
Tr
Rc
La
Cd
Ca
Ds
Po
Ra
Ms
Sm
Lp
Pm
Dc
Pl
Gm
Dg
Qi
To
Dv
Ta
B
Ellenberg indicator values (unitless)
12.5
10.0
7.5
5.0
2.5
0.0
**
***
CWM moistness
CWM nutrients

Tree crop		**Olives**		**Clementines**	
Year		2019	2020	2019	2020
Grove age (years)		16.6 (15.1)	21 (16.9)	26.9 (9.5)	27.9 (9.5)
Irrigated		86%	80%	100%	100%
Mowing operations		4.3 (1.8)	4 (1.2)	10.2 (3.7)	9.6 (2.7)
Tillage operations		0.3 (0.5)	0 (0)	0.4 (0.9)	1.4 (3)
Treatments against insects	Physical	2 (1.4)	0 (0)	2 (1.4)	0 (0)
	Biological	0 (0)	3.8 (2.3)	0 (0)	3.8 (2.3)

Tree crop	**Olives**					**Clementines**				
Year	2019			2020		2019			2020	
Month	Apr	Jun	Oct	Jun	Oct	Apr	Jun	Oct	Jun	Oct
Crop foliage	7	6	6	5	5	8	8	9	9	9
Ground vegetation	7	6	6	5	5	8	8	9	9	9
C. monspeliensis bushes	6	6	6	5	5	6	6	7	7	7
D. viscosa covers	7	6	6	5	5	5	4	6	5	5
Total	**27**	**24**	**24**	**20**	**20**	**27**	**26**	**31**	**30**	**30**

	Sampled					**Available**
	Areas (m^2)		Distance among habitats (m)			Areas (percent of microlandscape area)
	Nymphs	Adults	Ground vegetation	*C. monspeliensis* bushes	*D. viscosa* covers	
Crop foliage	64	76	0	74	53	14.5 %
Ground vegetation	72	390	-	62	51	14.5 %
C. monspeliensis bushes	210	232	-	-	26	0.3 %
D. viscosa covers	33	36	-	-	-	0.1 %
Forest	Not sampled					17.9 %
Riparian forest	Not sampled					1.8 %

	Response	#obs	Fixed effects	χ^2	df	P
A	Connectance	72	Sampling month	54	2	< 0.001
			Tree crop	-	-	-
			Sampling month: Tree crop	-	-	-
	Interaction evenness	60	Sampling month	23.2	2	< 0.001
			Tree crop	6.4	1	0.012
			Sampling month: Tree crop	-	-	-
	Ps-Cm predominance	52	Sampling month	26.5	2	< 0.001
			Tree crop	8.5	1	0.004
			Sampling month: Tree crop	-	-	-
B	Insect abundance	1036	Insect species	72.8	3	< 0.001
			Sampling month	87.1	2	< 0.001
			Vegetation type	91.5	3	< 0.001
			Tree crop	12.0	1	< 0.001
			Insect species : Sampling month $^{S5.1}$	69.4	6	< 0.001
			Insect species : Vegetation type $^{S5.2}$	222.4	9	< 0.001
			Insect species : Tree crop	-	-	-
C	*P. spumarius* abundance	259	Sampling month	-	-	-
			Vegetation type	155.2	3	< 0.001
			Tree crop	-	-	-
			Vegetation type : Sampling month $^{S5.3}$	313.6	8	< 0.001
	N. campestris abundance	259	Sampling month	23.8	2	< 0.001
			Vegetation type	37.5	3	< 0.001
			Tree crop	12.5	1	< 0.001
			Vegetation type : Sampling month	-	-	-
	A. alni abundance	259	Sampling month	-	-	-
			Vegetation type	-	-	-
			Tree crop	-	-	-
			Vegetation type : Sampling month	-	-	-
	L. coleoptrata abundance	259	Sampling month	-	-	-
			Vegetation type	40	3	< 0.001
			Tree crop	-	-	-
			Vegetation type : Sampling month	-	-	-
D	Insect presence / absence on crop foliage	228	Insect species	-	-	-
			Sampling month	8.5	1	0.004
			Tree crop	-	-	-
E	CWM_moistness	344	Sampling month	-	-	-
			Tree crop	9.3	1	0.002
	CWM_nutrients	343	Sampling month	-	-	-
			Tree crop	33.4	1	< 0.001