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

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15 **Abstract**

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

36

37 **Keywords**

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

39 **1 Introduction**

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

50 As other insect-microbial-plant pathosystems (*e.g.* Irwin and Thresh, 1990), the *Xf*
51 pathosystem is complex and gaps of knowledge remain although the bacterium has been
52 extensively studied in the Americas, where it originated (Sicard et al., 2018). *Xf* can infect 595
53 wild or cultivated plant species from over 85 families (EFSA, 2020). In addition, most insect
54 vectors are polyphagous (Cornara et al., 2019; Redak et al., 2004), which increases chances of
55 transmission between semi-natural and cultivated habitats. Thus, connexions between
56 agroecosystems and their immediate environment created by insect vectors need to be
57 investigated to anticipate and limit outbreaks (Almeida et al., 2005; Coletta-Filho et al.,
58 2011).

59 Insect vectors found in the New World are almost completely different from those found in
60 Europe, making knowledge transfer difficult. Although networks of interactions between
61 plant and vector communities are complex, all interactions do not equally contribute to
62 disease spread. Understanding what are the main plant reservoirs of *Xf* as well as what are the
63 main vectors and their preferred feeding plants is crucial to identify routes leading to

64 transmission to susceptible crops (Farigoule et al., 2020; Rasplus et al., 2016). In addition,
65 identifying key entities to plant-*Xf*-vector networks integrity should help design agro-
66 ecological management strategies to control them and, consequently, to reduce the spread of
67 *Xf* (Fontenille et al., 2020).

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

78 In addition, although vectors are polyphagous, they seem to locally aggregate on
79 preferred host plants. Thus, nymphs of *Philaenus spumarius* (L.), the most significant vector
80 of *Xf* in Europe so far (Cornara et al., 2019) were reported to aggregate on Asteraceae,
81 Apiaceae and Fabaceae in most large scale studies performed in Southern Italy (Bodino et al.,
82 2020a; Dongiovanni et al., 2019a), Spain or Portugal (Morente et al., 2018; Villa et al., 2020).
83 They were reported preferentially on Apiaceae and Rubiaceae, especially *Foeniculum vulgare*
84 L. and *Galium album* Mill on a specific research center of central Italy (Latini et al., 2019). In
85 Coastal California, where *P. spumarius* has been introduced from Europe, nymphs are
86 particularly abundant on the seaside daisy *Erigeron glaucus* Ker Gawl (Karban and Strauss,
87 2004). In Corsica, *P. spumarius* seems to aggregate on *Cistus monspeliensis* L., at least locally

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

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

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

103

104 **2 Materials and Methods**

105 *2.1 Study sites and sampling design*

106 We monitored 8 and 6 organically-managed clementine and olive groves respectively.
107 Their general features as well as the farming practices applied to these groves are presented in
108 Table 1. All groves were located in a climatically homogeneous region of Corsica, France
109 (Fig. 1) in which, during the two years of the study, minimum day temperature ranged from
110 0.1 to 4.6 °C (mean = 3.0 °C), maximum day temperature ranged from 26.5 to 30.4 °C (mean
111 = 28.7 °C) and annual precipitation ranged from 637 to 1066 mm (mean = 809 mm) (source
112 Météo France). On-field map of the groves and their vicinity were drawn prior to the first

113 sampling session. Circular zones centered on the groves, thereafter called “microlandscapes”
114 were defined so that their diameter (1 km) did not exceed the average dispersal capacity of the
115 target insects (Bodino et al., 2020b; Lago et al., 2021). Depending on the size of the grove,
116 either one or two microlandscapes were defined and a total of 17 microlandscapes were
117 sampled (9 in clementine and 8 in olive groves; Table 2; Supplementary maps).

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

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

128 For tree foliage, peripheral branches up to 2.5m were targeted. The grove ground
129 vegetation as a whole was included in the survey. A botanical inventory of the grove ground
130 vegetation was carried out in October 2019, June 2020 and October 2020 using one square
131 meter quadrats randomly positioned in two inter-rows with four repetitions per row (*i.e.*, 8
132 quadrats per site). Each species recorded (or genus if the phenological stage did not allow for
133 a more precise identification) was associated with an “abundance-dominance” coefficient
134 derived from Braun-Blanquet (1964) (1: <1% cover of the quadrat; 2: 10 to 25% cover; 3, 4
135 and 5: 25 to 50, 50 to 75 and 75 to 100% cover of the quadrat). For *C. monspeliensis* and *D.*
136 *viscosa*, when several patches were present in the microlandscape, patches (young seedlings
137 and old shrubs) closest to the grove were sampled first. Then, collectors progressively moved

138 away from the grove to sample more distant patches until the 10 min time limit was reached.
139 The same patches were visited in each sampling session. Table 3 shows the areas
140 available/actually sampled for each vegetation type as well as the distance among sampled
141 vegetation types (for a comprehensive description of spatial size and location of sites, see the
142 Supplementary maps).

143 2.2 *Insect collection*

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

152 Insect monitoring (nymphs and adults) was based on an equal sampling duration of 10
153 minutes on each of the four target vegetation types. For nymphs, a preliminary test was
154 performed to assess an on-sight sampling method. Four hundred forty individuals were
155 randomly collected from various spittles, assigned to species based on literature and identified
156 in the lab under a binocular microscope (Appendix 1 in Supplementary Materials). Precisely,
157 spittle masses found at the crown of grass plants were assigned to *Neophilaenus campestris*
158 (Fallén); those found at the crown of dicotyledonous plants species were assigned to
159 *Aphrophora alni* (Fallén) and those found on the upper part of graminaceous or
160 dicotyledonous plants were assigned to *P. spumarius* (Halkka et al., 1977; Fig. 2). Nymphs of
161 *Lepyronia coleoptrata* (L.) appeared later in our climatic context (Barro and Pavan, 1999),
162 and no spittle could be attributed to this species. In our context, on sight identification by our

163 trained eye was validated in over 99 % of cases (Appendix 1). Spittle masses were therefore
164 counted and identified directly in the field (upper and lower surfaces of the leaves were
165 inspected when relevant). In the rare cases where identification was troublesome, we
166 dispersed the spittle with a fine paintbrush and identified nymphs to species with
167 morphological characters (Fig. 2). Because the number of nymphs per spittle was close to one
168 for all species (1.45 for *P. spumarius*, 1.24 for *N. campestris* and 1.39 for *A. alni*; Bodino et
169 al., 2020a), we considered the number of spittles as a good proxy of the number of nymphs.

170 For adults, the 10 minutes sampling were fragmented in periods of 30 seconds of
171 vegetation sweeping with alternate backhand and forehand strokes of sweeping nets followed
172 by 10-30 seconds of collection of spittlebugs with mouth aspirators. Sweep netting is indeed
173 recognized as the best method to collect the target insects (Morente et al., 2018). Sweeping
174 the vegetation over a longer period would have increased risks of missing target insects in the
175 net among the many plant debris and non-target arthropods. When the 10 min time limit was
176 up, insects collected in the mouth aspirators were stored in 75° alcohol and brought to the
177 laboratory for identification under a binocular microscope using Biedermann & Niedringhaus
178 (2009) identification key.

179 2.3 Data analysis

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

184 Details on each model adjustment (error distributions, link functions, observation-level
185 random effects) are available in Appendix 2. Random effects on microlandscape or site
186 locations were used to account for spatial or temporal dependence resulting from our
187 sampling design (Faraway, 2006; Appendix 2). GLMM validity hypotheses of correct

188 distribution, dispersion, frequency of outliers and homoscedasticity were checked with the R
189 package ‘DHARMA’ (Hartig, 2020). The structure of each model was simplified by
190 successive backward elimination of non-significant fixed effects based on analysis of
191 deviance (R package ‘car’, Fox and Weisberg, 2019). Post-hoc pairwise comparisons of
192 estimated marginal means were performed on the final model (R package ‘emmeans’, Lenth,
193 2020) to assess differences among factor levels.

194 2.3.1 *Interaction networks*

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

206 2.3.2 *Association with vegetation types*

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

212 In order to test whether host associations varied in the course of the year, we used one
213 GLMM per insect species, testing the interaction between sampling month and vegetation
214 type, while controlling for the effects of sampling month, vegetation type and tree crop (Table
215 4C).

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

221 2.3.3 Differences in ground vegetation between crops

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

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

236

237 3 Results

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

241 3.1 Interaction networks

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

248 3.2 Association with vegetation types

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

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

261 vegetation types (Fig. 3, Table 4B). All vegetation types combined, whatever the species
262 considered, Cercopoidea populations were larger in olive groves (Table 4B).

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

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

276 3.3 Differences in ground vegetation between crops

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

282

283 4 Discussion

284 4.1 Spittlebug association with vegetation types

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

295 Expectations regarding other species were globally confirmed. *Neophilaenus campestris*
296 was mostly found on grove ground vegetation, in accordance with its expected association
297 with Poaceae (Bodino et al., 2020a; Dongiovanni et al., 2019a; Villa et al., 2020). *Dittrichia*
298 *viscosa* also appeared a suitable host for adults of *N. campestris*, mostly during autumn, which
299 adds another shift in host plant family to those previously documented (e.g. in Spain where it
300 has been recorded on *Pinus halepensis*; Lago et al., 2021; Morente et al., 2018). *Aphrophora*
301 *alni* and *L. coleoprata* were not, or only weakly associated with a specific vegetation type.
302 However, it should be noted that our sampling design focused on insect-vegetation
303 associations that were the most noticeable to us in preliminary experiments. We especially
304 focused on two plants of the grove vicinity (*C. monspeliensis* bushes and *D. viscosa* covers)
305 that appeared to be significant reservoirs of *P. spumarius*. Several vegetation types
306 representing large areas were left unsampled in our microlandscapes (e.g. oak forests or
307 riparian forests, Table 3) and insect-vegetation type associations were probably overlooked

308 based on our sampling design. We probably missed few significant interactions in oak forests
309 since Chartois et al. (2021) showed that they host low abundances of *Xf* vectors. Still,
310 *L. coleoptrata* nymphs were found on *Quercus suber*, *Arbutus unedo*, *Myrtus communis* or
311 *Pistacia lentiscus* in forest borders (this study, pers. obs.) and may require further attention.
312 Substantial populations of *A. alni* were also found in riparian forests during previous field
313 work (Chauvel et al., 2015). Such associations should be investigated to get a more
314 comprehensive view of the distribution of *Xf* vectors in ecosystems, but this was beyond the
315 scope of this study.

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

323

324 4.2 Interaction networks and epidemiology of *Xf* in Corsica

325 Plant communities found in olive and clementine crops reflected different conditions in
326 terms of moisture and nutrient richness. Moreover, the number of mowing operations in olive
327 groves was about two times lower, meaning that the insects were generally less disturbed.
328 Contrastingly, we found only minor differences on the interaction networks between
329 spittlebugs and vegetation types. Spittlebug populations (especially *N. campestris*) were
330 slightly larger in olive groves, with a more even repartition of interactions in the networks.
331 This is in line with results of Sanna et al. (2021) who found decreasing abundance of
332 *P. spumarius* with increasing mowing frequency. But above all, these results suggest a weak

333 link between plant communities, ecological conditions, and insect populations in the ground
334 vegetation of Corsican clementine and olive groves, at least within the climatic context
335 studied. This suggests that if *Xf* strains to which olive and clementine groves are susceptible
336 were to be introduced in Corsica, the transmission chances to both crop species would be
337 likely similar.

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

348 Spittlebug density on ground vegetation and crop foliage were globally much lower than
349 reported in Italy. Indeed, Bodino et al. (2019) reported adult densities of 1-2 individuals per
350 m² on average on ground vegetation (in June and October) and Bodino et al. (2020a) reported
351 abundances of *ca.* 1-2 individuals per olive tree (in May, June and July). Contrastingly, in our
352 study, maximum abundances were reached in October and were respectively of *ca.* 3.1×10^{-3}
353 individuals per m² (1.2 individuals on 390 m², Table 3) and of *ca.* 1.9×10^{-2} individuals per
354 olive tree (0.14 individuals for 7.5 trees). Although a rigorous comparison of these densities is
355 difficult due to different sampling methods, data suggest that the density of *P. spumarius*
356 adult is 100 to 1000 times higher in Italian olive groves than in Corsican olive or clementine
357 groves (confirmed by observations in Apulia, Cruaud & Rasplus, pers. com.). Understanding

358 what landscape features (see *e.g.* Santoiemma et al., 2019) and/or farming practices (see *e.g.*
359 Sanna et al., 2021) explain the difference between these two contexts is one of the
360 perspectives opened by our study.

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

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

375 Finally, spittlebug frequency on crop foliage was higher in October than in June, contrary
376 to Italy, where maximum densities are observed in June-July (Bodino et al., 2020a). This
377 result has two contrasting implications for *Xf* epidemics in Corsica. On the one hand,
378 spittlebugs occur on crop foliage when they are the most infective, because insect infectivity
379 *in natura* globally rises from their emergence in spring to following winter (Beal et al., 2021).
380 On the other hand, several authors found that the probability of *Xf* winter curing is higher
381 when *Xf* inoculation date occurs late (Cao et al., 2011; Feil et al., 2003). Consequently
382 corsican clementine and olive trees would be more likely to recover thanks to winter curing

383 than if they were infected earlier in the season. However, climatic conditions, specific features
384 of plant species and *Xf* subspecies may modulate overwinter recovery and specific studies are
385 also needed on that topic.

386

387 4.3 Implications for the agroecological management of *Xf* vectors

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

406 Finally, soil tillage has been advocated in Italy to kill *P. spumarius* nymphs (Dongiovanni
407 et al., 2019b) that develop on ground vegetation. Recent work has shown that soil tillage

408 indeed limits *P. spumarius* density on ground vegetation (Sanna et al., 2021), but only in the
409 short term (differences disappeared within *ca.* 2 months). Here, we found that the
410 predominance of the *P. spumarius*-*C. monspeliensis* interaction was the strongest in April,
411 with very few nymphs developing on the ground vegetation. This result suggests that soil
412 tillage in the spring would likely be inefficient to limit spittlebug populations in Corsican
413 olive and clementine groves.

414 Instead, release of *Ooctonus vulgatus* (Hymenoptera: Mymaridae) in autumn (Mesmin et
415 al., 2020), of *Verrallia aucta* (Diptera: Pipunculidae) in late spring/early summer (Molinatto
416 et al., 2020), and/or of *Zelus renardii* (Hemiptera: Reduviidae) in autumn (Liccardo et al.,
417 2020) in the close vicinity of groves, could be efficient to reduce *P. spumarius* pressure.
418 However, while these three natural enemies naturally occur in mainland France (Garrouste,
419 2019; Mesmin et al., 2020; MNHN and OFB, 2021), information are still missing regarding
420 the occurrence of the last two in Corsica. Complementary studies are needed to avoid
421 releasing allochthonous species and reduce risk of non-target effects (Van Driesche and
422 Hoddle, 2016).

423

424 **5 Conclusion**

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

433

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443

444 **7 Data statement**

445 Data used to perform all statistics and graphics shown in the article are freely available at
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447

448 **8 References**

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689

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

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

697 **Table 3 Area of each sampled vegetation type, distance among sampled vegetation**
698 **types and area of available vegetation types in the microlandscapes.** Median values are
699 provided. Variation in sampled areas for adults (larger) and nymphs was due to the difference
700 in sampling methods (sweeping net versus on sight count). Available areas were assessed
701 based on aerial photographs, field knowledge and photographs made in the field, but not on a
702 comprehensive on-field cartography. They are therefore accurate for most vegetation types
703 but should be seen as an order of magnitude for *C. monspeliensis* bushes and *D. viscosa*
704 covers. “Forests” are mainly oak forests in our meso-mediterranean context (Reymann et al.,
705 2016, p. 9). Riparian forests were defined as 5 m buffers around stream banks (Sawtschuk et
706 al., 2014). An interactive and comprehensive description of the spatial distribution of sampling
707 sites can be found in the Supplementary maps.

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

715 Wald chi square tests are shown. Non significant fixed effects were dropped in model
716 selection and are depicted with a “-“ in χ^2 , df and P columns. For all significant interactions,
717 text in exponent refers to tables of Appendix 5 that detail pairwise comparisons of factor
718 levels. CWM : community weighted mean (see text).
719

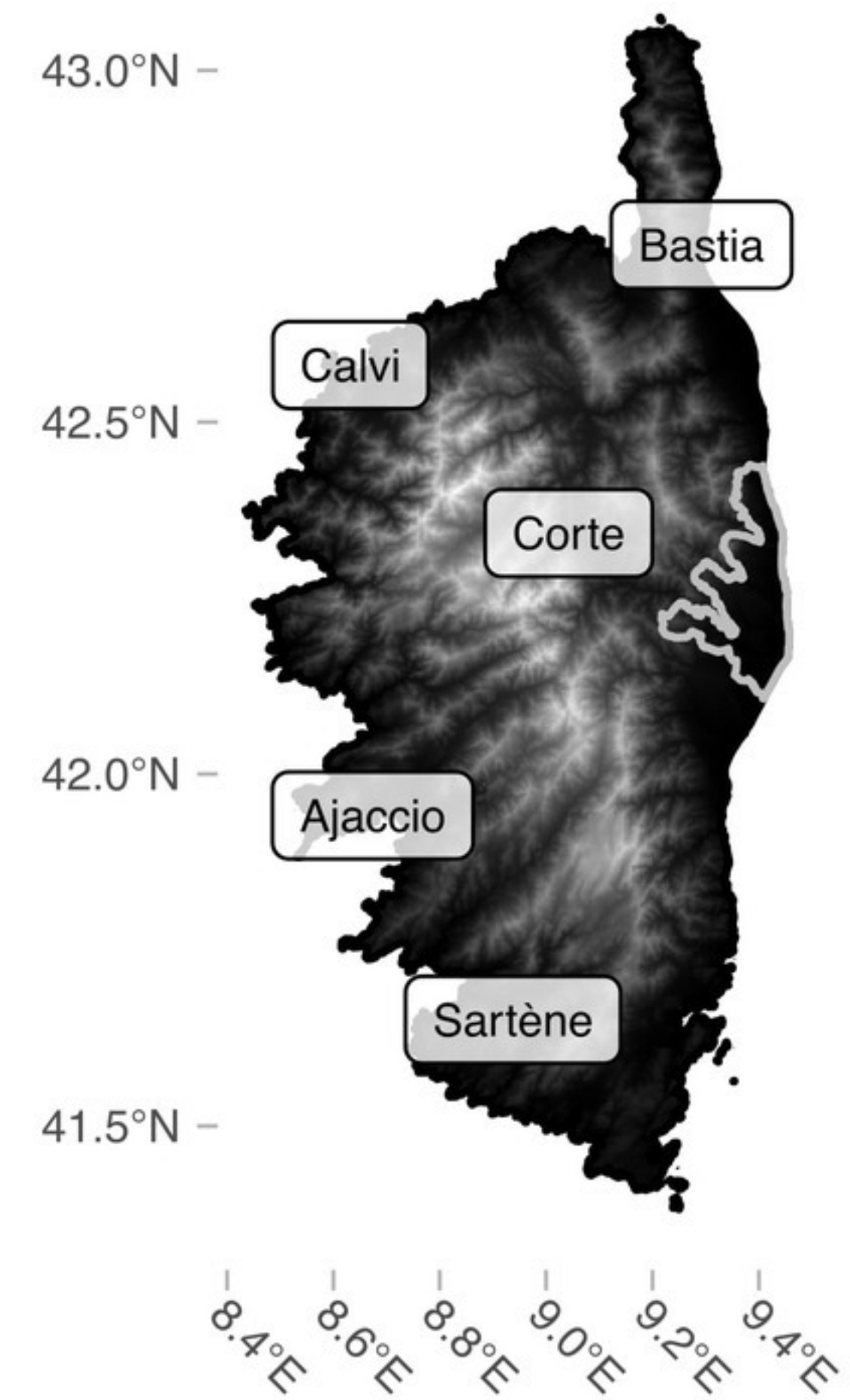
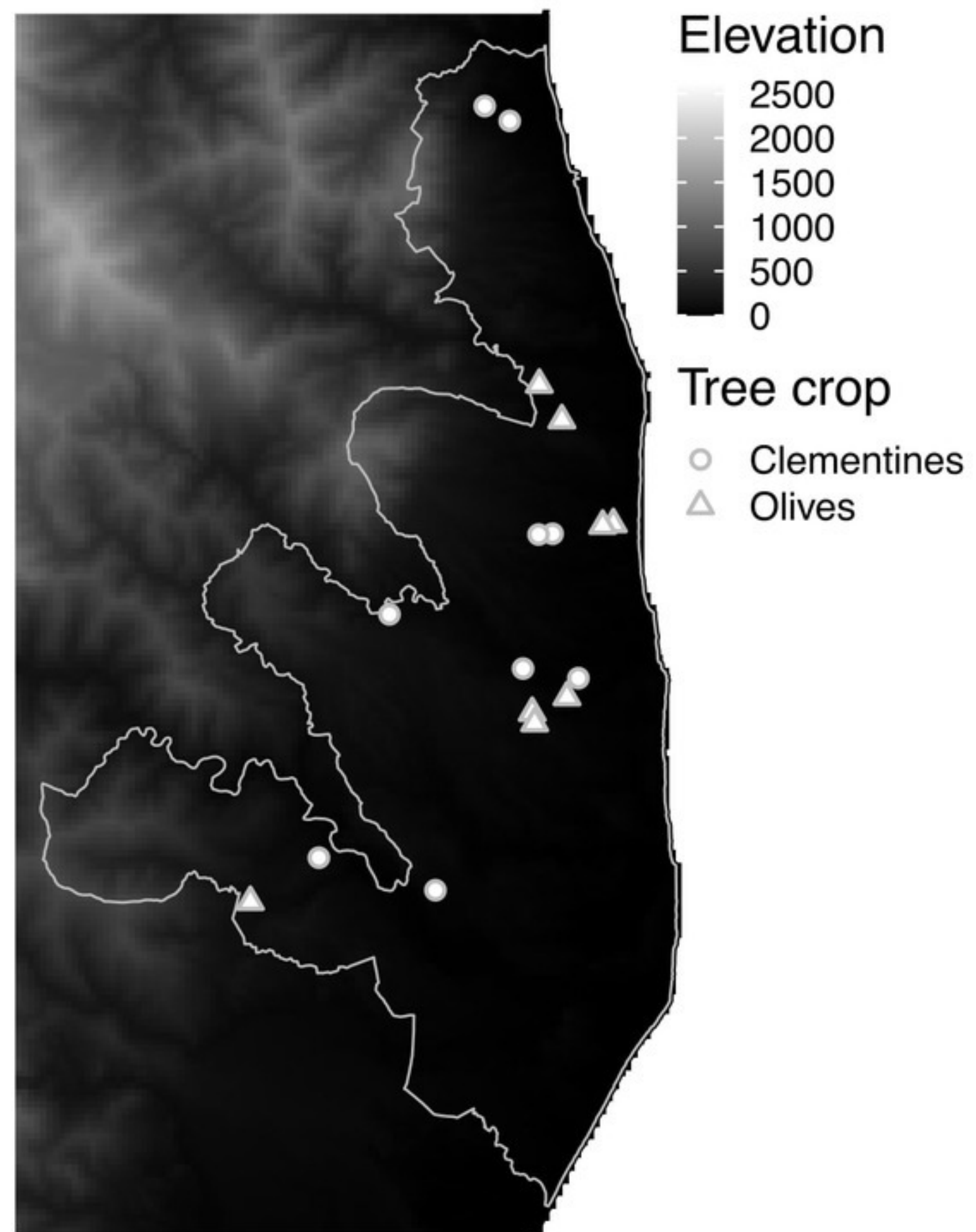
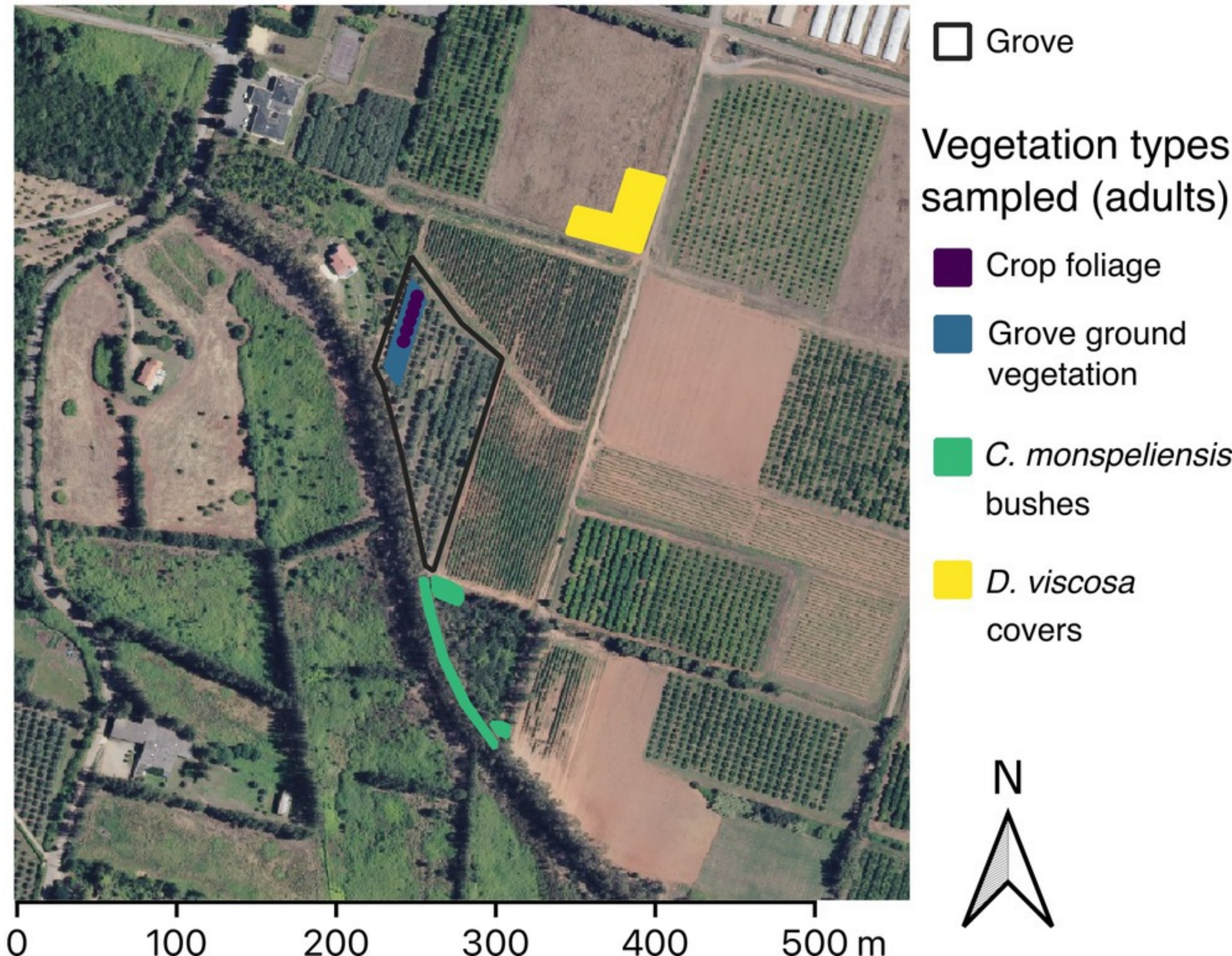
720 **Figure 1 Sampling sites.** A and B, studied area (white circles and triangles for clementine
721 and olive groves, respectively); C, details of one olive grove (see Supplementary maps for a
722 comprehensive description of the spatial distribution of sampling sites). Elevations and
723 orthophotographs are from BD ALTI® 25M (© IGN – 2022) and ORTHO HR® (© IGN –
724 2022), respectively.

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

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

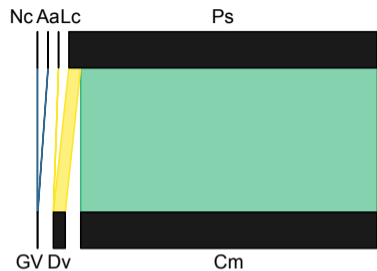
736 **Figure 4 Values of connectance, interaction evenness and *P. spumarius*-**
737 ***C. monspeliensis* predominance depending on sampling month and crop.** Each point
738 represents a network established on a given microlandscape for a given sampling session
739 (circles and triangles for clementine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

744 **Figure 5 Comparaison of ground vegetation between olive and clementine crops.**
745 Correspondance analysis performed on the botanical composition of the quadrats (A) and
746 functional characterization of the vegetation based on the Ellenberg indicator values for
747 moistness and nutrients (CWM; community weighted means). In A, each point is a vegetation
748 quadrat (circles and triangles for clementine and olive groves, respectively); each abbreviation
749 depicts a plant species (initials of the genus and species names; see Table S6.1 for complete
750 names) and ellipses show 75% confidence enveloppes of quadrats (computed with the R
751 package ‘FactoMineR’; Lê et al., 2008). In A, only species found on at least 5% of the
752 quadrats are shown. In B, data are shown as density traces (“violin plots”; Hintze and Nelson,
753 1998) highlighting the distribution of the data. The significance of correlation between each
754 variable and crop is shown with asterisks (***<p=0.001<***<p=0.01<*<p=0.05<NS).

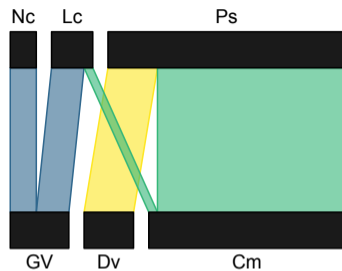
A**B****C**

A**B****C****D**

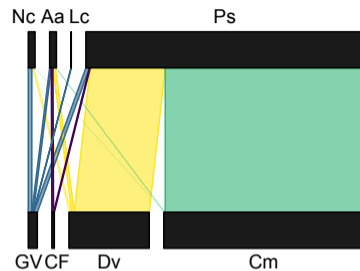
April (nymphs) - clementines (Ntot = 3613)



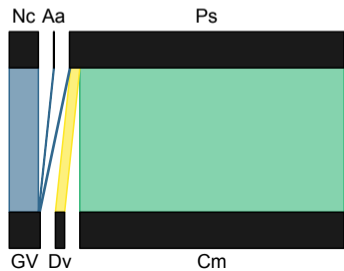
June (adults) - clementines (Ntot = 36)



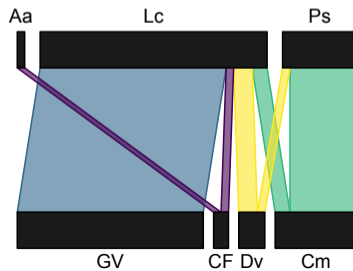
October (adults) - clementines (Ntot = 790)



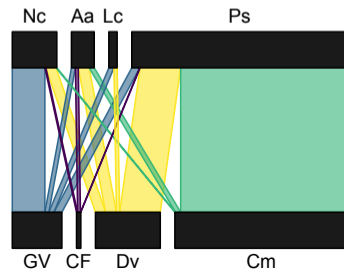
April (nymphs) - olives (Ntot = 3034)



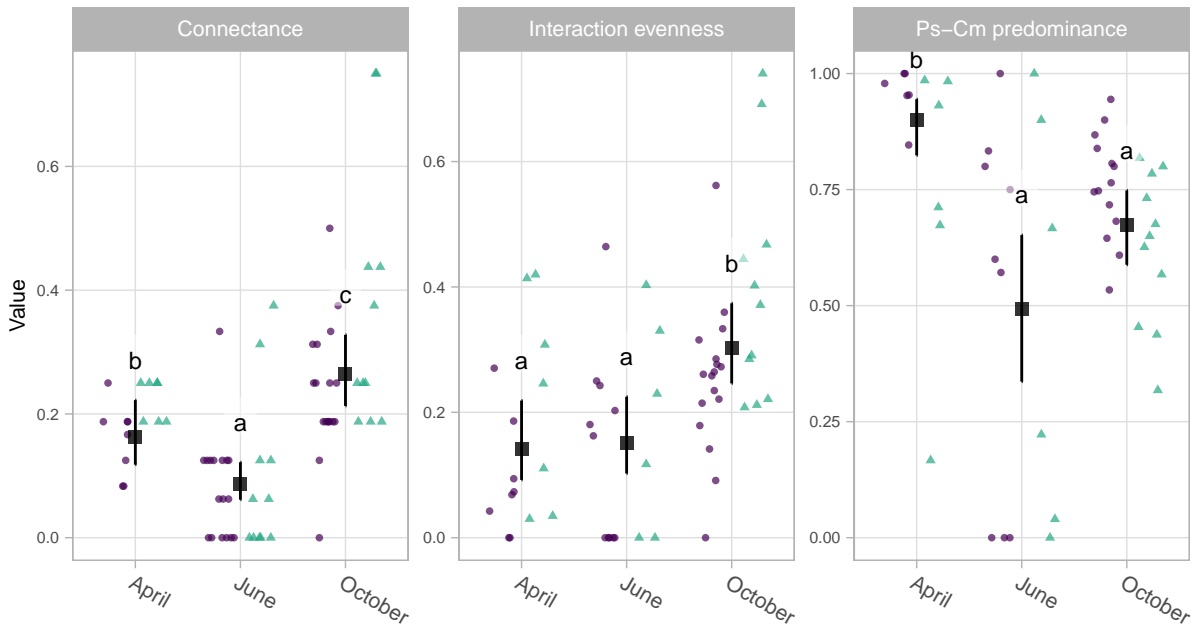
June (adults) - olives (Ntot = 83)



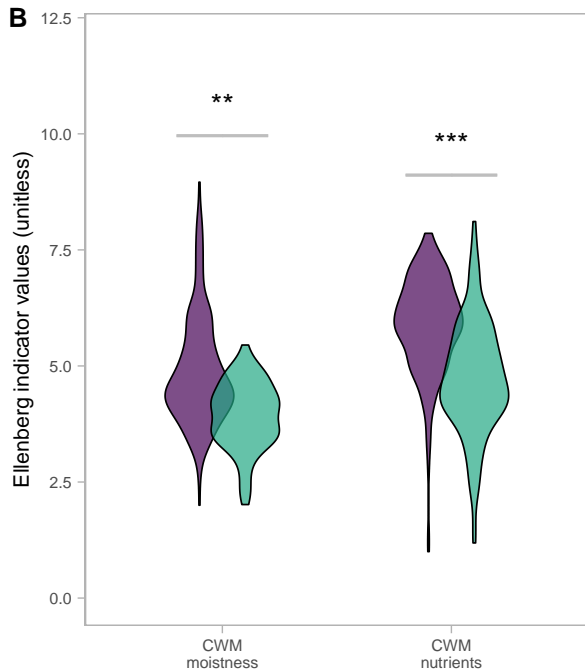
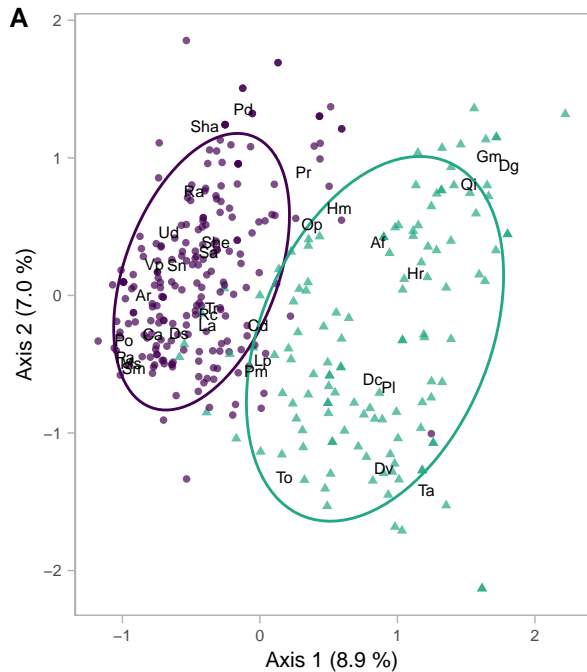
October (adults) - olives (Ntot = 805)



Tree crop ● Clementines ▲ Olives



Tree crop ■ Clementines ▲ Olives



Tree crop		Olives		Clementines	
		2019	2020	2019	2020
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				
	2019			2020		2019			2020	
Year	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
<i>C. monspeliensis</i> bushes	6	6	6	5	5	6	6	7	7	7
<i>D. viscosa</i> 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	<i>C. monspeliensis</i> bushes	<i>D. viscosa</i> covers	
Crop foliage	64	76	0	74	53	14.5 %
Ground vegetation	72	390	-	62	51	14.5 %
<i>C. monspeliensis</i> bushes	210	232	-	-	26	0.3 %
<i>D. viscosa</i> 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 ^{SS.1}	69.4	6	< 0.001	
		Insect species : Vegetation type ^{SS.2}	222.4	9	< 0.001	
		Insect species : Tree crop	-	-	-	
C <i>P. spumarius</i> abundance	259	Sampling month	-	-	-	
		Vegetation type	155.2	3	< 0.001	
		Tree crop	-	-	-	
		Vegetation type : Sampling month ^{SS.3}	313.6	8	< 0.001	
	<i>N. campestris</i> 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	-	-	-
	<i>A. alni</i> abundance	259	Sampling month	-	-	-
			Vegetation type	-	-	-
			Tree crop	-	-	-
			Vegetation type : Sampling month	-	-	-
<i>L. coleoptrata</i> 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	