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## Source of *Hyalesthes obsoletus* Signoret planthopper (Hemiptera: Cixiidae) in southern France and potential effects of landscape

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19 **Abstract**

20 Cixiid planthoppers are considered of major economic importance, as they can transmit  
21 phytoplasmas responsible for many plant diseases. While thoroughly studied in vineyards, the  
22 epidemiology of stolbur phytoplasma, transmitted by *Hyaolesthes obsoletus* Signoret, was  
23 rarely investigated on minor crops as lavender, where it leads to ‘yellow decline’ disease and  
24 large economic losses. The objective of this paper is to understand the effect of the local  
25 landscape characteristics on the presence and density of *H. obsoletus* in the ‘Plateau de  
26 Valensole’, southern France. Potential host plants of *H. obsoletus* were surveyed in three  
27 contrasted zones (in terms of crops and disease intensity), by uprooting plants and capturing  
28 adults in emergence traps. The localization and potential movements of *H. obsoletus* from the  
29 host plants towards lavandin (infertile hybrid of lavender) were determined using yellow  
30 sticky traps. Clary sage plants were found as major hosts of *H. obsoletus*. Flying insects were  
31 also caught in fields of lavandin, although emergence traps and plant uprooting did not  
32 confirm this crop as a winter host, i.e., as a reservoir for the insect. Based on one zone, we  
33 showed that attractiveness may depend on crop (clary sage or lavandin) and on its age, as well  
34 as on the distance to the supposed source field. These results suggest that clary sage could be  
35 an important host of *H. obsoletus*, whose density largely varies between zones. Genetic  
36 studies would be required to confirm the role of clary sage in the dissemination of yellow  
37 decline of lavandin.

38

39 **Keywords**

40 Lavandin yellow decline; Stolbur phytoplasma; landscape composition; insect sources; in-  
41 field measures

42

43

## 44 1. Introduction

45 Agricultural pests are harmful to crops worldwide, as they can generate up to 25-40% yield  
46 losses at the world scale (based on eight major crops in Oerke and Dehne, 2004; Oerke 2006),  
47 with similar impact in pre- and post-harvest (Flood, 2010). The impact of insects is regarded  
48 as a global threat for current and future agricultural production systems. In addition to the  
49 direct losses due to feeding activity, insects cause yield losses via indirect damages  
50 (Weintraub and Beanland, 2006). Spittlebugs can indeed transmit virus and bacteria (e.g.  
51 *Xylella fastidiosa* (Wells et al. 1987) transmitted by *Philaenus spumarius* L., and responsible  
52 for Pierce disease of grapevines (Nunney et al. 2010) and leaf scorch of olive trees (Saponari  
53 et al. 2014)). Leafhoppers and planthoppers can transmit phytoplasmas (e.g. Flavescence  
54 dorée of grapevines, transmitted by *Scaphoideus titanus* Ball, Chuche and Thiery, 2014),  
55 which are prokaryotes colonizing plant phloem (Weintraub and Beanland, 2006).  
56 Phytoplasmas transmitted by insects are responsible for diseases in hundreds of plant species  
57 (Lee et al. 2000; Weintraub and Beanland, 2006), e.g., grapevine (Chuche and Thiery, 2014;  
58 Johanessen et al. 2008), lavender (Danet et al. 2010; Germain et al. 2015), maize (Jovic et al.  
59 2007), and strawberry (Danet et al. 2003).  
60 Among them, cixiid planthoppers (Hemiptera: Cixiidae) are considered of great economic  
61 importance, as they can transmit phytoplasmas agents of prominent and emerging plant  
62 diseases worldwide (e.g., Danet et al. 2003; Jovic et al. 2007; Maniyar et al. 2013). One of the  
63 most studied planthopper is *Hyalesthes obsoletus* Signoret, which is the vector of the stolbur  
64 phytoplasma causing the grapevine yellow disease ‘bois noir’ (Bressan et al. 2007;  
65 Johanessen et al. 2008). *H. obsoletus* is a polyphagous species, which overwinters as nymphs  
66 on the roots of host plant species (Sforza et al. 1999), and completes one generation per year  
67 in Central and South Europe (e.g., Sforza et al. 1999). *H. obsoletus* adults’ flight occurs from  
68 June til late August, depending on meteorological conditions and host plants (Darimont and

69 Maixner, 2001; Sforza et al. 1999). The insect can acquire phytoplasma at two different  
70 periods: first at larval stage, when feeding in the phloem of host-plant species during  
71 overwintering (Johanessen et al. 2008); second at adult stage, when sucking infected plants  
72 (Weintraub and Beanland, 2006).

73 The population size, distribution and dispersal of *H. obsoletus* are largely influenced by the  
74 spatial structure of host plant species (Bressan et al. 2007) and by the range of their contacts  
75 (Maniyar et al. 2013). In vineyard systems of Central and Southern Europe, bindweed -  
76 *Convolvulus arvensis* L.- and stinging nettle -*Urtica dioica* L.- (both herbaceous species) are  
77 the major host species (Langer and Maixner, 2004; Sforza et al. 1998; Imo et al. 2013)  
78 considered as reservoir plants for stolbur phytoplasma (Maniyar et al. 2013), while grapevine  
79 is considered as ‘an erratic feeding host’ (Bressan et al. 2007; Maixner, 2011). More than 50  
80 species were identified as host species in Europe (Bulgaria, Crete, France, Greece, Italy),  
81 other Mediterranean countries (Israel, Liban, Maroc, Turkey), and Russia (Aleksic et al. 1967;  
82 Fos et al. 1992; Güçlü and Özbek, 1988; Hoch and Remane, 1986; Kovaceski, 1958; Leclant  
83 and Lacote, 1969; Sforza et al. 1998; Suchov and Vovk, 1946). Based on these studies, hosts  
84 of *H. obsoletus* cover a wide range of species, including tree species (e.g., *Populus* spp.,  
85 *Quercus* spp., *Ulmus* spp.), cultivated crops (e.g., *Medicago sativa* L., *Onobrychis viciifolia*  
86 Scop., *Zea mays* L.) and wild species (e.g., *Amaranthus retroflexus* L., *Cirsium arvense*  
87 Scop., *Melilotus officinalis* Des Rouss.). Lavender (*Lavandula angustifolia* Miller) and  
88 lavandin (infertile hybrid; *Lavandula hybrida* Reverchon) were also identified as host plants  
89 for *H. obsoletus* (Sforza et al. 1998, 1999), as well as clary sage (*Salvia sclarea* L.) very  
90 recently (Chuche et al., 2017). In addition, aromatic plants, such as immortelle (*Helichrysum*  
91 *stoechas* (L.) Moench) and thyme (*Thymus vulgaris* L.), can locally be suspected of being  
92 potential hosts for *H. obsoletus*, as some aromatic plants were identified as hosts (e.g.,  
93 *Lavandula* spp., *Vitex agnus castus* L.) (Sforza et al. 1998, 1999; Hoch and Remane, 1986).

94 In vineyards, Panassiti et al. (2015) assumed to 50 meters per year the range of active  
95 dispersal (i.e., flight) of an individual *H. obsoletus*. But dispersal of the insect both within-  
96 field and between crops were also found in other studies (Bressan et al. 2007; Orenstein et al.  
97 2003; respectively). Testing of push and pull strategy in Israel to avoid dispersal of *H.*  
98 *obsoletus* in adjacent vineyards even highlighted attraction of the insect by its preferred host  
99 plant for feeding (i.e., *Vitex agnus castus* L.) up to 400m, which was the maximum tested  
100 distance (Zahavi et al. 2007). The lack of attractiveness of *H. obsoletus* for *Vitis vinifera* L.  
101 could explain the short distances sometimes observed (e.g., in Panassiti et al. 2015). The  
102 presence of *H. obsoletus* on grapevine would result from random landing rather than selective  
103 flight (Bressan et al. 2007). As *H. obsoletus* flies mostly during the day, with a peak of  
104 activity between 15h and 21h (Bressan et al. 2007), a driving factor of its long-range dispersal  
105 could be wind speed, as demonstrated for species with diurnal flight activity (Larsen and  
106 Whalon, 1988; Orenstein et al. 2003).

107 In Provence (southern France), the stolbur phytoplasma (transmitted by *H. obsoletus*) causes a  
108 lavender and lavandin disease called ‘yellow decline’ (Danet et al. 2010; Gaudin et al. 2011;  
109 Germain et al. 2015), which is responsible for important economic losses (Gaudin et al.  
110 2011). When infected, lavender and lavandin plants become yellow, puny, and finally die,  
111 leading to an early uprooting due to lower and non-profitable yields (uprooting after 6-7 years  
112 instead of 12-15 years). This crop, grown in Provence since many generations, is adapted to  
113 dry and hot summers, and contributes € 30 million per year to the local economy (Germain et  
114 al. 2015). As no curative method exists against stolbur phytoplasma, farmers grow tolerant  
115 cultivars on part of the acreages (Gaudin et al. 2011). While symptom severity does not  
116 correlate either with the tolerance status of cultivars, or with the phytoplasma titer (Gaudin et  
117 al. 2011), Yvin (2011) showed that highly diseased areas were associated with high captures  
118 of *H. obsoletus* in lavender and lavandin fields.

119 Gathering knowledge on the epidemiological pattern of yellow decay caused by *H. obsoletus*  
120 in this area is essential to design effective strategies in lowering its impact. As a first step  
121 towards this aim, the objective of this paper is to understand the effect of the local landscape  
122 characteristics on the presence and density of *H. obsoletus* in the ‘Plateau de Valensole’,  
123 southern France. To this aim, this study was carried out to: (1) better characterise the  
124 polyphagous nature of *H. obsoletus*, i.e., the diversity of host plants whose location and  
125 abundance should be characterized, and (2) highlight the dynamic between sources and sinks  
126 for the crop species of interest by estimating likely distance travelled by *H. obsoletus*.

127

## 128 **2. Materials and Methods**

### 129 2.1. Study area

130 The ‘Plateau de Valensole’ is a dry plateau located in the south of France, in the NUTS-2  
131 region Provence-Alpes-Côte-d’Azur (coordinates  $\approx 43^{\circ}40'05''$  N -  $43^{\circ}58'41''$  N;  $5^{\circ}47'06''$  E  
132 –  $6^{\circ}17'32''$  E). It covers about 50,000 ha, with altitude ranging between 450-850 m, and it is  
133 spatially delimited by surrounding valleys. About one third of its area is covered by crops  
134 (15,500 ha in 2012), with the lavandin, the infertile hybrid of lavender crop (*Lavandula*  
135 *hybrida* Reverchon; *Lavandula latifolia* Medik x *Lavandula angustifolia* Miller), covering 22-  
136 24% of agricultural land (ASP, 2016; data for 2014 and 2010, respectively). The main  
137 lavandin cultivar is Grosso, while cultivar Sumian is less represented because of lower yields  
138 ( $70 \text{ kg ha}^{-1}$  vs.  $100 \text{ kg ha}^{-1}$ ; CIHEF, 2012). Both cultivars are considered tolerant to stolbur  
139 phytoplasma (Gaudin et al. 2011).

140

### 141 2.2. Field experimental design

142 The field campaign was carried out in 2015 on three zones (Brunet, Montagnac and Saint-  
143 Jurs). These three zones were chosen as representative of contrasted levels of lavandin yellow

144 decline (i.e., low, medium and high), of the presence of woods (where alternative hosts of *H.*  
145 *obsoletus* could be found), and of the presence of potential alternative plant hosts (i.e.,  
146 sainfoin -*Onobrychis viciifolia* Scop.- and clary sage -*Salvia sclarea* L.). All of them included  
147 one field of a 1-year old lavandin, cultivar Grosso (target field). *H. obsoletus* can not  
148 complete its reproduction cycle in these 1-year lavandin, as the plant transplanting occurs  
149 after the flying period of the insect. The altitude of the study zones was 620 m, 670 m and 740  
150 m for Montagnac, Brunet and Saint-Jurs, respectively. Weather conditions of the studied year  
151 (monthly rainfalls and monthly minimum, mean and maximum air temperatures) mostly did  
152 not differ from data of the 19 previous years (August 1995-July 2015). For the studied year,  
153 we considered the period August 2014 – July 2015 (i.e. from the beginning of laying period til  
154 the end of flying period; Appendix A). Weather data were recorded in Valensole (altitude of  
155 600 m, 43°50'18''N 6°00'00''E) from the beginning of 2015 by Meteo France, in a weather  
156 station located at 10 km, 15 km, and 19 km from Brunet, Montagnac, and Saint-Jurs,  
157 respectively.

158 The identification of the sources of *H. obsoletus* was performed with two types of in-field  
159 surveys: the identification of larvae on plant roots and the capture of emerging adults. The  
160 presence of potential sources of *H. obsoletus* on the surrounding fields was investigated by  
161 capturing flying adults and recording the composition of the local landscape. Local landscape  
162 was characterized in terms of location (field observations) and proportion (GIS computations)  
163 of the different land uses. Polygons figuring the field borders of land uses were digitized at a  
164 1:1000 scale using an IGN orthophoto (<https://www.geoportail.gouv.fr/>; Lambert 93  
165 coordinates) dated from 2015 with a resolution of 20 cm. Classification of the polygons in  
166 different land uses was done manually on the basis of an homogeneity of texture and color,  
167 and verified with field observations to distinguish the following categories: woods, and  
168 cultivated crops: alfalfa (*Medicago sativa* L.), clary sage (*Salvia sclarea* L.), durum wheat



169 (*Triticum durum* Desf.), grassland (mixed species), lavandin (*Lavandula hybrid* Reverchon),  
170 pea (*Pisum sativum* L.) rapeseed (*Brassica napus* L.), sainfoin (*Onobrychis viciifolia* Scop.),  
171 and sunflower (*Helianthus annuus* L.). Crop age was also recorded for perennial species  
172 (lavandin and clary sage, cropped for 6-15 years and 3-4 years, respectively), based on  
173 farmers' interview. The covered landscape area including target field was chosen according to  
174 the potential sources of *H. obsoletus*. In-field measurements were performed in an area of 500  
175 m radius around the target field for Montagnac and Saint-Jurs, while the area in Brunet was  
176 larger (1 km) in order to include one plot of an additional potential source of *H. obsoletus*  
177 (clary sage). Due to the larger area in Brunet, not all fields around the target field were  
178 surveyed; survey included all the fields between supposed source and target, as well as their  
179 direct neighbouring fields.

180

181 # Figure 1 approximately here #

182

### 183 2.2.1. Searching for larvae and emerging adults

184 Potential host plants for *H. obsoletus* were searched based on studies performed in France  
185 (Sforza et al. 1999) and abroad (Aleksic et al. 1967; Güçlü and Özbek, 1988; Hoch and  
186 Remane, 1986; Kovaceski, 1958), including both cultivated and non-cultivated plants. Extra  
187 aromatic plants – that were not included in the above-mentioned studies – were also  
188 investigated, as they were suspected hosts according to local knowledge of farmers and  
189 technical advisers. Potential hosts, identified in previous studies or suspected by local  
190 authorities, were investigated in the three studied areas: (1) *cultivated crops*, i.e., lavandin,  
191 clary sage, alfalfa, sainfoin, alfalfa; and (2) *natural vegetation*, i.e., immortelle (*Helichrysum*  
192 *stoechas* (L.) Moench), thyme (*Thymus vulgaris* L.), bindweed (*Convolvulus arvensis* L.),  
193 yellow melilot (*Melilotus officinalis* Des Rouss.), dandelion (*Taraxacum* spp.), lamb's

194 quarters (*Chenopodium album* L.), amaranth (*Amaranthus retroflexus* L.), bedstraw (*Galium*  
195 spp.), creeping thistle (*Cirsium arvense* Scop.), stinging nettle (*Urtica dioica* L.) and wild  
196 lavender (i.e., found in woods or in field edges). The surrounding fields with other crops were  
197 also searched: grassland (mixed species), durum wheat, and rapeseed.

198 Larvae were searched and counted on plant roots. Plants uprooting was performed on June  
199 2015 for larvae to be on L5 stage, i.e., when they are grouped in a white molt (Breck, 1979)  
200 and thus easily identifiable (Figure 1A). For cultivated plants (lavandin and clary sage),  
201 around five plants per field were randomly uprooted. For natural vegetation (wood, field  
202 edge), 10 plants were uprooted for each species. Fields cropped with 1-year lavandin were not  
203 tested, as *H. obsoletus* could not complete its reproduction cycle.

204 Capture of *H. obsoletus* emerging adults was realized with emergence traps. Emergence traps  
205 consisted of a yellow sticky trap, surrounded by a net held by two metal hoops (Figure 1B).

206 The yellow sticky trap is a PVC tube, 40 cm high, surrounded by a sticky yellow strip, and  
207 held by a stem of Provence rod of 50 cm embedded in the soil. Each trap covered 1 m<sup>2</sup>.

208 Emergence traps were placed around mid-June in fields of lavandin, sainfoin, alfalfa (1-2  
209 traps per field of the studied zone) and natural zones (4-5 traps per studied zone) at the same  
210 time than larvae surveys. In natural zones the abundance of potential host plants was recorded  
211 as the percentage of area covered by these plants in the emergence trap. These traps could not  
212 be set up for clary sage because of a too dense vegetation (except for the 2-year clary sage of  
213 Saint-Jurs, where crop cover was less dense).

214

#### 215 2.2.2. Capturing flying adults

216 Flying adults of *H. obsoletus* were captured with yellow sticky traps (Figure 1C) located in  
217 cultivated crops and natural zones. About 40 traps were set up in each study zone, during the  
218 last week of June (i.e., before the start of the flying period of *H. obsoletus*). 3-5 traps were

219 randomly placed within each field in clary sage (presumed source) and young lavandin (host),  
220 while 1-2 traps in durum wheat, rapeseed, grassland, and woods. The traps were weekly  
221 monitored from the end of June till the end of July, and the number of adults of *H. obsoletus*  
222 was counted.

223

### 224 2.3. Characterization of lavandin management and surrounding landscape

225 Local farmers were interviewed to gather information on the management of lavandin fields  
226 located in the three studied zones. Surveys focused on the management practices that may  
227 affect the presence and abundance of *H. obsoletus*: the age of the lavandin crop, the cultivar,  
228 the harvest date, the use of irrigation, and clay spraying (a prevention technique consisting  
229 covering the plants' leaves with clay (in powder) to prevent *H. obsoletus* bites). Note that  
230 spraying insecticide on lavandin is not allowed during the flying period of *H. obsoletus*, as it  
231 coincides with the flying period of bees. Landscape characteristics in terms of cultivated crops  
232 and natural areas (i.e., woods) were recorded in the three study zones (Table 1).

233

234 # Table 1 approximately here #

235

### 236 2.4. Statistical analyses

237 Based on the results of larvae search and emergence traps, the sources of *H. obsoletus* were  
238 identified. Firstly, the spatial autocorrelation of weekly and total catches of *H. obsoletus* in  
239 yellow sticky traps was determined using Moran's I spatial statistics (Cliff and Ord, 1981).  
240 The values of this index range between -1 (i.e., perfect negative correlation between  
241 observations) and 1 (i.e., perfect positive correlation between observations). No spatial  
242 autocorrelation is associated to a Moran's I index of 0, i.e., indicating that observations are  
243 independent ( $P < 0.05$ ). This analysis was performed in the study zones where *H. obsoletus*

244 was captured. For this analysis, we considered clary sage field as the source of *H. obsoletus*,  
245 and lavandin field as the target. Secondly, we fitted negative binomial and Poisson models  
246 using the logarithm of the sum of captures over the season as dependent variable to assess the  
247 dispersion pattern of *H. obsoletus*. These two models have the same number of parameters  
248 (i.e., intercept + slope parameters, depending on the number and type of explanatory  
249 variables) (Ver Hoef and Boveng, 2007). Negative binomial model assumes an over-  
250 dispersion of the dependent variable (i.e., conditional variance higher than conditional mean),  
251 and the Poisson model corresponds to a negative binomial model with variance equal to  
252 mean, by setting the over-dispersion parameter to 0 (Greene, 2008). We considered two  
253 explanatory variables in the tested models, both together and separately: (1) the minimum  
254 distance between the trap and the border of the source field (m); and (2) the host type in  
255 which the trap was placed (Crop\_code), including information about the crop (clary sage or  
256 lavandin), the cultivar (for lavandin only), and the age. Such categorization was performed  
257 because of the uneven distribution of crop characteristics (i.e., not every combination crop ×  
258 cultivar × age).

259 The overall performances of Poisson and negative binomial models *per se* were compared  
260 with Akaike criterion (AIC, a measure of model goodness of fit penalizing more complex  
261 models; Burnham and Anderson, 2002). As these models do not share the same likelihood  
262 function, they were compared via a likelihood ratio test corrected for degrees of freedom (Self  
263 and Liang, 1987). We assessed the goodness-of-fit of the best model (according to AIC and  
264 likelihood ratio test) and the significance of the explanatory tests with  $\chi^2$  test on residual  
265 deviance. The comparison between coefficients associated to the different modalities of the  
266 Crop\_code explanatory variable was performed with Wald test, by considering 95%  
267 confidence intervals for each coefficient in the best model. Model residuals were visually  
268 checked for independence from fitted values. Poisson and negative binomial models were

269 fitted for the study zone Brunet, due to missing values in Saint-Jurs, as these models require  
270 an identical length and timing of observation. No field source of *H. obsoletus* was found in  
271 Montagnac.

272 Statistical analyses and figures were performed with R software (R Development Core Team,  
273 2013). Between-trap distances for computing Morans' I were calculated with the function  
274 "dist", and minimal distances between each trap and the pre-identified source field were  
275 computed with the "gDistance" function of the R package rgeos (Bivand and Rundel, 2016),  
276 based on trap and field coordinates. Maps and land uses proportions were realised with the  
277 QGIS software version 2.10.1-Pisa (QGIS development team, 2015). Morans' Indices were  
278 computed with the function "Moran.I" of the R package ape (Paradis et al. 2004). Poisson  
279 models were fitted with the R function "glm" (R Development Core Team, 2013), and  
280 negative binomial models were fitted with the R function "glm.nb" of the package MASS  
281 (Venables and Ripley, 2002). Likelihood ratio tests for comparing Poisson and negative  
282 binomial models were performed with the R function "lrtest" of the package lmtest (Zeileis  
283 and Hothorn, 2002). Akaike values,  $X^2$  test analysis of deviance, and Wald test were  
284 computed with the R functions "AIC", "pchisq", "anova", and "summary", respectively.

285

### 286 **3. Results**

#### 287 3.1. Host plants of *Hyalesthes obsoletus* at larval and emergence stages

288 In Brunet study zone, bindweed was the most widespread potential natural host of *H.*  
289 *obsoletus*, as it was found in all the tested zones (including the cultivated grasslands and the  
290 field edges of durum wheat), except in the woods and in the field of durum wheat. Other  
291 potential natural hosts for *H. obsoletus* were yellow melilot, dandelion, lamb's quarters and  
292 amaranth, which were less frequently found as compared to bindweed. No larva of *H.*  
293 *obsoletus* was detected on these natural species (Table 2). For these species, emerging adults

294 were captured in only one trap located in cultivated grassland, where bindweed covered about  
295 10% of the trap surface (four and one individuals in the weeks 2-9 and 9-17 July,  
296 respectively). Among the four lavandin fields (two 3-year and two 4-year fields), random  
297 plant's uprooting did not reveal to find any larva of *H. obsoletus*. However, a few adults  
298 (three) were caught during the survey of week 2-9 of July in a 3-year lavandin field (cultivar  
299 Grosso). Larvae of *H. obsoletus* were also found in the 4-year clary sage field, on about 70%  
300 of the uprooted plants with an average of 13 larvae per plant (between 4 and 23 larvae per  
301 plant). No larvae were found in the 2-year clary sage field.

302 In the natural zones of Saint-Jurs, wild lavender and thyme species were found in the woods,  
303 and yellow melilot was present in the field edge between 1-year and 5-year lavandin fields.  
304 Bindweed was identified in all areas but in rapeseed and durum wheat fields. No larva of *H.*  
305 *obsoletus* was found in the roots of these species, and no adult was captured in the emergence  
306 traps (Table 2). In the cultivated areas, no *H. obsoletus* was found in lavandin fields, neither  
307 by uprooting plants nor with the emergence traps. For clary sage, the six fields located in the  
308 study zone were tested for the presence of *H. obsoletus* (one field of 2-year clary sage, four  
309 fields of 3-year clary sage, and one field of 4-year clary sage). The insect was found in the 4-  
310 year clary sage only, on 30% of the plants, for an average of 7 larvae per host plant (between  
311 2 and 15 larvae per plant). All positive plants were located in a strip in the middle of the field.  
312 In Montagnac natural areas, the potential hosts of *H. obsoletus* were thyme and bedstraw  
313 species in woods, and sainfoin and lavandin (4, 9 and 10 years-old) in cropped areas. Based  
314 on both plant uprooting and emergence traps, no source of *H. obsoletus* was identified in  
315 Montagnac during the survey (Table 2).

316

317 # Table 2 approximately here #

318

319 3.2. Density and pattern of *Hyalesthes obsoletus* flying adult captures

320 Most *H. obsoletus* flying adults were captured in Brunet, which were found in all the traps in  
321 lavandin and clary sage fields, for 34% and 65% of insects, respectively (Table 3). The peak  
322 of *H. obsoletus* flight was shifted by one week in these two crops (9<sup>th</sup> and 17<sup>th</sup> of July for  
323 lavandin and clary sage, respectively) (Figure 2), probably because of the lavandin harvest in  
324 this period (lower attractiveness). In clary sage, more insects were captured in 4-year than in  
325 2-year fields, while in lavandin, the relation between the number of captures and the age of  
326 the crop was less clear (Figure 2). The insect was marginally found in the other areas tested,  
327 i.e., grassland, wood and durum wheat (average of 1, 1 and 1.5 insect per trap over the whole  
328 period, respectively). Spatial autocorrelation was significantly positive ( $I \in [0.085; 0.229]$ ;  $P$   
329 = 0.001) in all observation dates but for the first one (2<sup>nd</sup> of July,  $I=0.048$ ,  $P = 0.069$ ).  
330 Moran's  $I$  was significantly positive when considering the total number of captured *H.*  
331 *obsoletus* ( $I=0.176$ ;  $P < 0.001$ ).

332

333 # Figure 2 approximately here #

334

335 In Saint-Jurs, 189 adults of *H. obsoletus* were captured, 58% in lavandin fields, and 40% in  
336 clary sage fields (Table 3). For the latter, most insects (66 out of 75) were found in the 4-year  
337 clary sage field, with a large variability between the traps (standard deviation (s.d.) = 34  
338 insects). In lavandin fields, 39% of captures (43 out of 109) were done in 4-year lavandin (s.d.  
339 = 7 insects) and 43% (47 out of 109) in 1-year lavandin fields irrigated and sprayed with clay  
340 (s.d. = 6 insects), with a lower number in 3-year fields. Almost no *H. obsoletus* were captured  
341 in durum wheat, field edges, in the wood, and in rapeseed (average of 1, 2.5, 0, and 1 insect  
342 per trap, respectively). The peak of insects captures occurred at the beginning of July. Spatial  
343 autocorrelation was not significantly different from 0 at any observation date ( $P > 0.227$ ).

344 In Montagnac, almost no flying adults of *H. obsoletus* were captured with the yellow sticky  
345 traps (Table 3), which were found only in lavandin fields, in two out of five surveyed dates.

346

347 # Table 3 approximately here #

348

349 3.3. Potential source-target relationships in the study zone Brunet

350 In Brunet, the 4-year clary sage was considered as the source of *H. obsoletus*, according to  
351 larva and adult emergence detection, thus considering 2-year clary sage and lavandin as target  
352 fields. Both negative binomial and Poisson models highlighted better fitting of captures when  
353 including the minimum distance between the trap and the source, and the type of crop as  
354 explanatory variables (see the values of AIC in Appendix B). Negative binomial performed  
355 better than Poisson models ( $X^2$  test based on log-likelihood, Appendix B). Both the minimal  
356 distance to the source and the crop type had a significant effect on *H. obsoletus* captures  
357 (Table 4). Increasing the minimum distance between the source and the trap significantly  
358 decreased the number of adults (Table B1 in Appendix C), while the differences between the  
359 crop types were not always significant. The number of insects did not significantly differ ( $P =$   
360 0.05) between 1-year, 3-year lavandin (cultivar Grosso), and 2-year clary sage (Table B2 in  
361 Appendix C). A significantly smaller number of adults was captured in 3-year and 4-year  
362 lavandin (cultivar Sumian and Grosso, respectively), as compared to both 2-year clary sage  
363 and 1-year lavandin. The difference between the insects caught in 3-year Sumian and Grosso  
364 fields was significant ( $P = 0.05$ ), with a lower number of captures for Sumian (Table B2 in  
365 Appendix C).

366

367 # Table 4 approximately here#

368



369 This negative binomial model highlighted a high goodness-of-fit (Figure B1 in Appendix C)  
370 leading to a small non-significant residual deviance ( $P = 0.172$ ). However, the coefficient of  
371 the minimum distance to the source displayed a large 95% confidence interval (Table B1 in  
372 Appendix C), leading to a large uncertainty in predicting *H. obsoletus* presence, especially at  
373 short minimum distances between the source and the trap (Figure 3). Such uncertainty was  
374 higher for 1-year lavandin as compared to 2-year clary sage, due to their distances with  
375 respect to the source field (4-year clary sage). While the 2-year clary sage's traps were very  
376 close to the source (distance  $\in [66; 72]$  m), the two fields of 1-year lavandin were located  
377 further (two fields, distance  $\in [525; 762]$  m).

378

379 # Figure 3 approximately here#

380

## 381 4. Discussion

### 382 4.1. Hosts of *Hyalesthes obsoletus*

383 The paper presented here brought to light the effect of local characteristics on the presence  
384 and density of *H. obsoletus*, by focusing on larvae and emerging adults for the host plant  
385 species, and on the adult for feeding and egg-laying.

386 Overall, larvae detection and emergence traps provided consistent results regarding the host  
387 species of *H. obsoletus*. Most individuals were found in fields of old clary sages, either as  
388 larvae on roots or as flying adults. As far as we know, this crop was not previously identified  
389 as a host for this insect. In European vineyards, bindweed and stinging nettle are the two main  
390 host species of *H. obsoletus* (Langer and Maixner, 2004; Sforza et al. 1998; Imo et al. 2013).  
391 In our study, although bindweed was largely represented in two out of three study zones, no  
392 larvae were found on its roots, and emergence traps caught a very low number of individuals,  
393 only in Brunet. This result could be linked to the potentially higher attractiveness of clary

394 sage. Stinging nettle was not found in the study zones, probably due to the high altitude (620-  
395 740 m), the dryness of the climate, and the low fertility of the soils. Indeed, stinging nettle  
396 prefers nutrient-rich soils (Siebel and Bouwma, 1998), especially regarding nitrogen, and a  
397 relatively wet and fresh environment (Rameau et al. 1999; 2008). Moreover, *H. obsoletus* is  
398 found, at high altitudes in Europe (above 1000 m) where soil enrichment has occurred, e.g., in  
399 cattle shelters (Davis, 1989). No insect was found in the woods, and in sainfoin and alfalfa;  
400 whereas these two last crops were reported as potential hosts of *H. obsoletus* in Turkey  
401 (Güçlü and Özbek, 1988). No larva was found in the lavandin fields, and no adult was caught  
402 in the emergence trap, except for 3 individuals in the 3-year field of cultivar Grosso. This  
403 result is consistent with (unpublished) trials of local technical institute, which found that the  
404 insect hardly overwinters on tolerant cultivars Grosso and Sumian, with no larva found on  
405 their roots. These results thus suggest that these cultivars are dead-end host plant, and not a  
406 substrate for nymphs (Sforza, 1998). These results suggest that, in the studied areas,  
407 landscape characterization should focus on clary sage and lavandin, and could omit a detailed  
408 study of woods, alfalfa and sainfoin.

409 Most flying adults were found in 4-year clary sage fields, and a smaller proportion was caught  
410 on lavandin. In Brunet, the peak of the flight in lavandin was anticipated by one week as  
411 compared to clary sage. The decrease of captures in lavandin could then be due to harvesting,  
412 in turns lowering its attractiveness for the insect. This is consistent with findings by Riolo et  
413 al. (2007), reporting that the dispersion of *H. obsoletus* can change when the primary host is  
414 unavailable. Attractiveness properties could also explain the larger number of adults found in  
415 1-year lavandin fields, as compared to older fields. Host preference tests, such as performed  
416 by Kessler et al. (2011) for bindweed and stinging nettle, could give insights on plant  
417 attractiveness ranking and explore the potential differences between the two cultivars Grosso  
418 and Sumian, where less flying adults were captured. The three detection methods of *H.*

419 *obsoletus* ranked similarly across study zones. While captures were consistent with historical  
420 observations in Montagnac, where no yellow decline was recorded, the ranking of the insect  
421 pressure in Brunet and Saint-Jurs differed from expectations. Indeed, Saint-Jurs, located in the  
422 extreme North of the Plateau, is currently the most affected zone, whereas Brunet is  
423 considered as a moderate diseased zone. Different hypotheses could be drawn from these  
424 results: a shifting of the geographic distribution of the vector from North to South-East, the  
425 impact of clay spraying as prophylactic measure in Saint-Jurs, or the weather conditions that  
426 occurred during this study and the previous winter. Indeed, larvae development, adult  
427 emergence and flight depend on temperatures and thermal sums (Boudon-Padieu and  
428 Maixner, 2007; Imo et al. 2013; Maixner and Langer, 2006), and warmer temperatures are  
429 associated to a higher insect activity (Orenstein et al. 2003).

430

#### 431 4.2. Inference at field and small-landscape scales

432 Based on the planting densities provided by the farmers, field size, and on the spatial  
433 heterogeneity of the captures within the field, the raw extrapolation at field scale of the  
434 average uprooting captures of larvae would give a potential of about 5 millions and 0.3  
435 millions individuals of *H. obsoletus* in the 4-year clary sage fields in Brunet and Saint-Jurs,  
436 respectively. Such estimation could be lowered by larval mortality, even if it mainly occurs at  
437 earlier larval instars than in our survey (Sforza et al, 1999). At the peak of *H. obsoletus* flight,  
438 up to 30 and 150 individuals were found for lavandin and clary sage, respectively, in Brunet.  
439 These numbers are higher than in previous studies carried out inside and around vineyards  
440 with sticky traps (e.g., Sforza et al. 1998; Orenstein et al. 2003; Mori et al. 2008; Kessler et al.  
441 2011).

442 Spatial autocorrelation of *H. obsoletus* captures in clary sage and lavandin fields, tested with  
443 Moran's I, was significant ( $p = 0.05$ ) at almost all sampling dates in Brunet, while never in

444 Saint-Jurs. On the contrary Orenstein et al. (2003) found no spatial pattern for *H. obsoletus* in  
445 vineyards. Our findings could be linked to the different plant attractiveness for *H. obsoletus*,  
446 as grapevine is not a favorite host (Bressan et al. 2007), while little is known about the  
447 attractiveness of the potential host plants found in Brunet, i.e., clary sage, lavandin and, to a  
448 lower extent, bindweed. It is indeed demonstrated that the interaction between the vector and  
449 the plant pathogen could influence the specialization or preference for specific hosts (Biere  
450 and Tack, 2013), thus influencing dissemination (Maixner et al. 2014).

451 Under the hypothesis that the clary sage fields were the sources of *H. obsoletus*, we derived  
452 potential dispersion curves towards potential targeted hosts, i.e., lavandin, showing significant  
453 effects of both distance to the source and host type (crop; age and cultivar of lavandin).

454 Similarly to a previous study on one Cicadellidae of grapevine (Lessio et al. 2014), we fitted  
455 exponential regression using the minimum distance to the source as explanatory variable. Our  
456 curve displayed a large variability in small distances from the source, whatever the considered  
457 host. We did not find any significant difference between the fitted curves for the two host  
458 species clary sage (3-year) and lavandin (1-year), which could suggest their similar  
459 attractiveness for the insect. The higher attractiveness of young lavandin, as compared to  
460 older ones, could be linked to the higher proportion of bare soil leading to higher soil  
461 temperatures, more attractive for *H. obsoletus* (xerothermic insect). However, we investigated  
462 only one field of the two crops, located close and far to the source for clary sage and lavandin,  
463 respectively. Moreover, no host plants were present in the middle, as there was a field  
464 cropped with durum wheat, a non-host crop. The uncertainty in the minimum distance from  
465 the source could be reduced by studying homogenous landscapes in terms of crops/age, and  
466 including infected clary sage as reservoir. However, since clary sage does not show any  
467 symptoms of the disease, targeting such situations may be difficult. In addition, such  
468 landscapes can hardly be designed for experimenting in reality due to their large scale.

469 Therefore model parameters should be fitted under real situations, to be able to set up pest-  
470 limiting or even pest-suppressive landscapes (i.e., location of sources and hosts, e.g., Hossard  
471 et al. 2015). Another important factor that was not taken into account here is the influence of  
472 wind speed in the dispersal of *H. obsoletus*, which could not have been done due to the lack of  
473 a very close weather station, this parameter being highly variable in space. Finally, while our  
474 survey allowed to determine the largest sources of *H. obsoletus*, no certain conclusion can be  
475 made on dispersal, as the captured insects were not marked (as in e.g., Lessio et al. 2014).

476

#### 477 4.3. Prospects for future studies on lavandin yellow decline

478 As we highlighted that clary sage was a major host for *H. obsoletus*, the next necessary step  
479 would be to test its role as a reservoir host for pathogen proliferation. This could be  
480 performed by testing (1) if over-wintering on clary sage lead to insects that can transmit  
481 stolbur phytoplasma (although it could also be acquired by sucking infested lavandin); and (2)  
482 if the phytoplasma's genotype is similar with the one found in diseased lavandins. Current  
483 knowledge indicates that lavender yellow decline is supposed to propagate in southern France  
484 only through the dispersal of *H. obsoletus* between lavender and lavandin fields (Danet,  
485 2010). Indeed, the genotyping of the stolbur phytoplasma, retrieved from diseased plants of  
486 lavender and lavandin, revealed that 14 out of the 17 genotypes were specific to  
487 lavender/lavandin, and did not correspond to the ones commonly found in vineyards or wild  
488 reservoirs in France (Danet, 2010). Further genotyping of both plants and insects would then  
489 be required for testing the lavandin-clary sage compatibility. This could be of primary  
490 importance, as the infection may be determined by the size of the reservoir, represented by the  
491 number of insects able to transmit the phytoplasma (Lee et al. 2000), and its spatial  
492 distribution within landscapes (e.g., for fungus, Bousset et al. 2015). For instance, previous  
493 plant genotyping already showed that bindweed may not be responsible for yellow decline of

494 lavender, as the main phytoplasma strains found in lavandin differed from that of bindweed  
495 and other wild plants (Chaisse et al. 2012). Such information on clary sage would be the next  
496 step towards the understanding of the yellow disease propagation in lavenders, preliminary to  
497 the design of control strategies. First results showed that clary sage could be a source of  
498 stolbur vector and carry the phytoplasma (Chuche et al. 2017), but the lavandin-clary sage  
499 compatibility need to be further investigated. Finally, the yellow disease of lavandin is present  
500 in the area since decades. It would then be interesting to gather the locations of clary sage  
501 fields in the past, which could be done by exploiting satellite images, in order to assess its  
502 potential linkage with the spatio-temporal intensity of the disease.

503

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511

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Table 1. Main characteristics of observed landscape composition in the three studied zones. Other crops include rapeseed, durum wheat, sunflower and pea. Local landscape was characterized in terms of location (field observations), and proportion (GIS computations) of the different crops. The age of perennial crops (lavandin and clary sage) were also recorded (farmers' interview).

Study zone	Brunet	Saint-Jurs	Montagnac
Total cropped surface considered (ha)	194.52	86.39	91.79
Central 1st year lavandin (%)	12.4	4.27	5.04
Lavandin (%)	27.13	62.48	41.36
Clary sage (%)	9.85	24.54	0.00
Sainfoin (%)	0.00	0.00	9.22
Grasslands (%)	10.26	0.00	0.6
Other crops (%)	52.77	12.97	48.82

Table 2. Summary of potential host plants found in the three study zones, and the associated results for plants' uprooting and captures of *H. obsoletus* in the emergence traps.

Type of host	Study zone	Brunet			Saint Jurs			Montagnac		
		Presence	Larva	Adult	Presence	Larva	Adult	Presence	Larva	Adult
Natural	Amaranth	x	-	-	-	-	-	-	-	-
	Bedstraw	-	-	-	-	-	-	x	-	-
	Bindweed	x	-	x*	x	-	-	-	-	-
	Creeping thistle	-	-	-	-	-	-	-	-	-
	Dandelion	x	-	-	-	-	-	-	-	-
	Immortelle	-	-	-	x	-	-	-	-	-
	Lamb's quarter	x	-	-	-	-	-	-	-	-
	Stinging nettle	-	-	-	-	-	-	-	-	-
	Thyme	-	-	-	x	-	-	x	-	-
	Wild lavender	-	-	-	x	-	-	-	-	-
	Yellow melilot	x	-	-	x	-	-	-	-	-
Cultivated	Clary sage	x	x	-	x	x	-	-	-	-
	Lavandin	x	-	x	x	-	-	x	-	-
	Sainfoin	-	-	-	-	-	-	x	-	-

x: presence; -: absence; empty case: non tested. \*Bindweed located in the cultivated grassland.



Table 3. Summary of *Hyalesthes obsoletus* flying adults found in the yellow sticky traps.

	Study zone	Brunet	Saint-Jurs	Montagnac
	Number of plots with occurrence of <i>H. obsoletus</i> ( <i>total number of plots</i> )	5 (5)	6 (6)	2 (5)
Lavandin	Number of traps with occurrence of <i>H. obsoletus</i> ( <i>total number of traps</i> )	21 (21)	15 (17)	2 (18)
	Number of dates with <i>H. obsoletus</i>	5	5	2
	Number of plots with occurrence of <i>H. obsoletus</i> ( <i>total number of plots</i> )	2 (2)	3 (6)	-
Clary sage	Number of traps with occurrence of <i>H. obsoletus</i> ( <i>total number of traps</i> )	5 (5)	15 (22)	-
	Number of dates with <i>H. obsoletus</i>	5	4*	-
Total	number of Lavandin plots; Clary sage plots; Other areas; All	437; 827; 3 <sup>§</sup> ; 1267	109; 75; 5 <sup>#</sup> ; 189	8; -; -; 8

-: no such crop in the considered study zone; \*: 2 surveyed dates (among the 5 performed on most fields) were partial, i.e., missing fields at the beginning of the season (2 first surveys), <sup>§</sup>: trapped in wood and grassland, <sup>#</sup>trapped in the edge between wood and 5-year infertile lavandin..

1 Table 4. Analysis of variance of the best performing model fitted for the study site Brunet,  
 2 i.e., negative binomial model including both the Minimum distance to the source and the Crop  
 3 code (Distance and Crop code, respectively).

4

Variable	Df	Deviance	Residual Df	Residual deviance	Pr(>Chi)
Null			22	108.934	
Distance	1	57.970	21	50.964	<0.001
Crop code	4	28.635	17	22.329	<0.001

5 Df : number of degrees of freedom.

6 Figure 1. In-field measurements performed for larvae detection (A), capture of emerging  
7 adults (B) and flying adults (C).

8

9 Figure 2. Number of trapped *Hyalesthes obsoletus* in lavandin and clary sage fields for the  
10 study site Brunet. Means per trap are shown in order to take into account the different  
11 numbers of traps within each field.

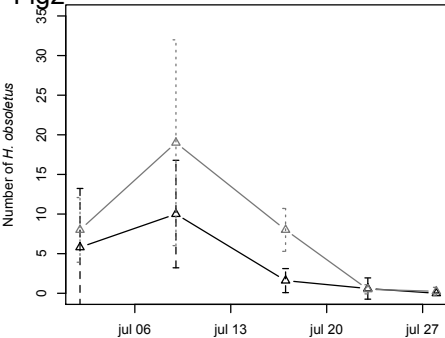
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13 Figure 3. Fitted number of *Hyalesthes obsoletus* obtained with the negative binomial model  
14 including both the Minimum distance to the source and the Crop code for Brunet study zone.  
15 Full lines correspond to fitted curves, and dashed lines correspond to 95% confidence  
16 intervals for simulation in 1-year lavandin (cultivar Grosso, in black, L1) and 2-year clary  
17 sage (in grey).

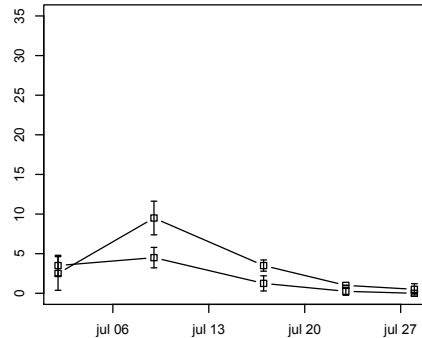


Fig 2

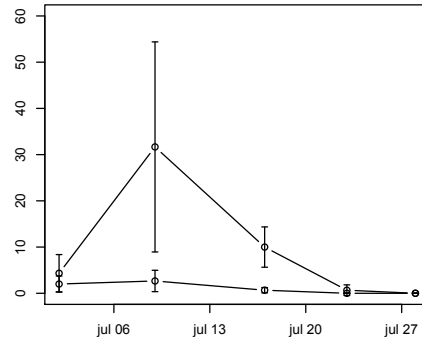
1-year Lavandin



3-year Lavandin



4-year Lavandin



Clary sage

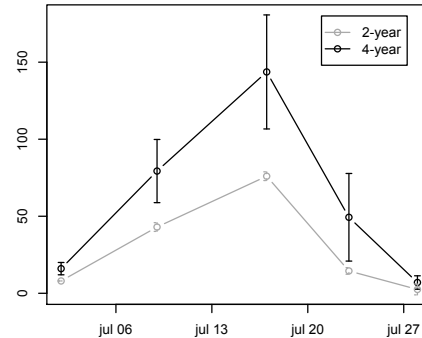
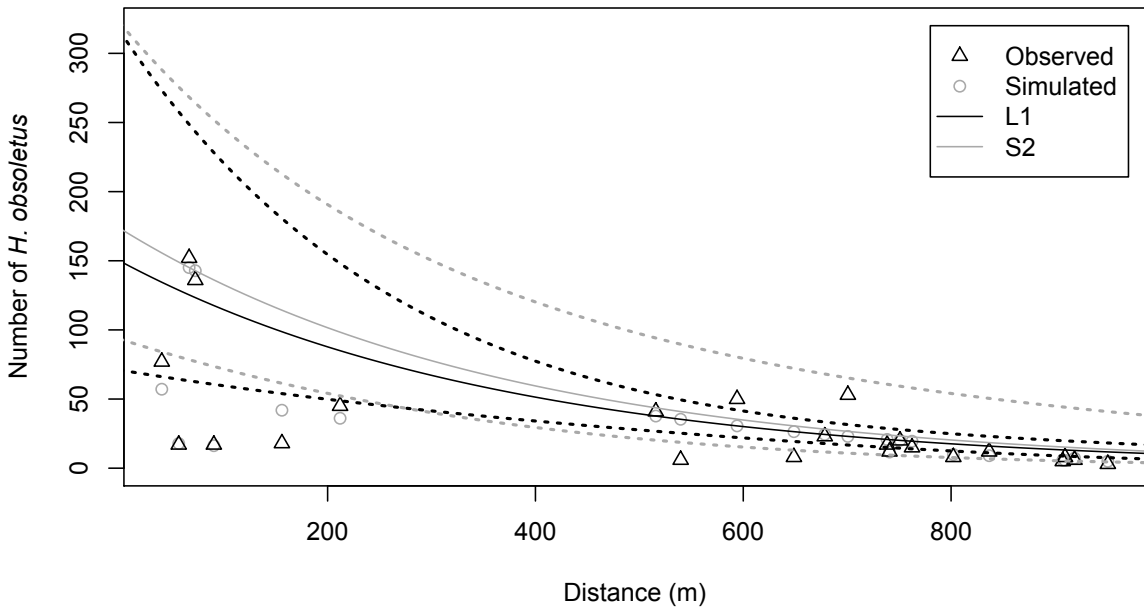
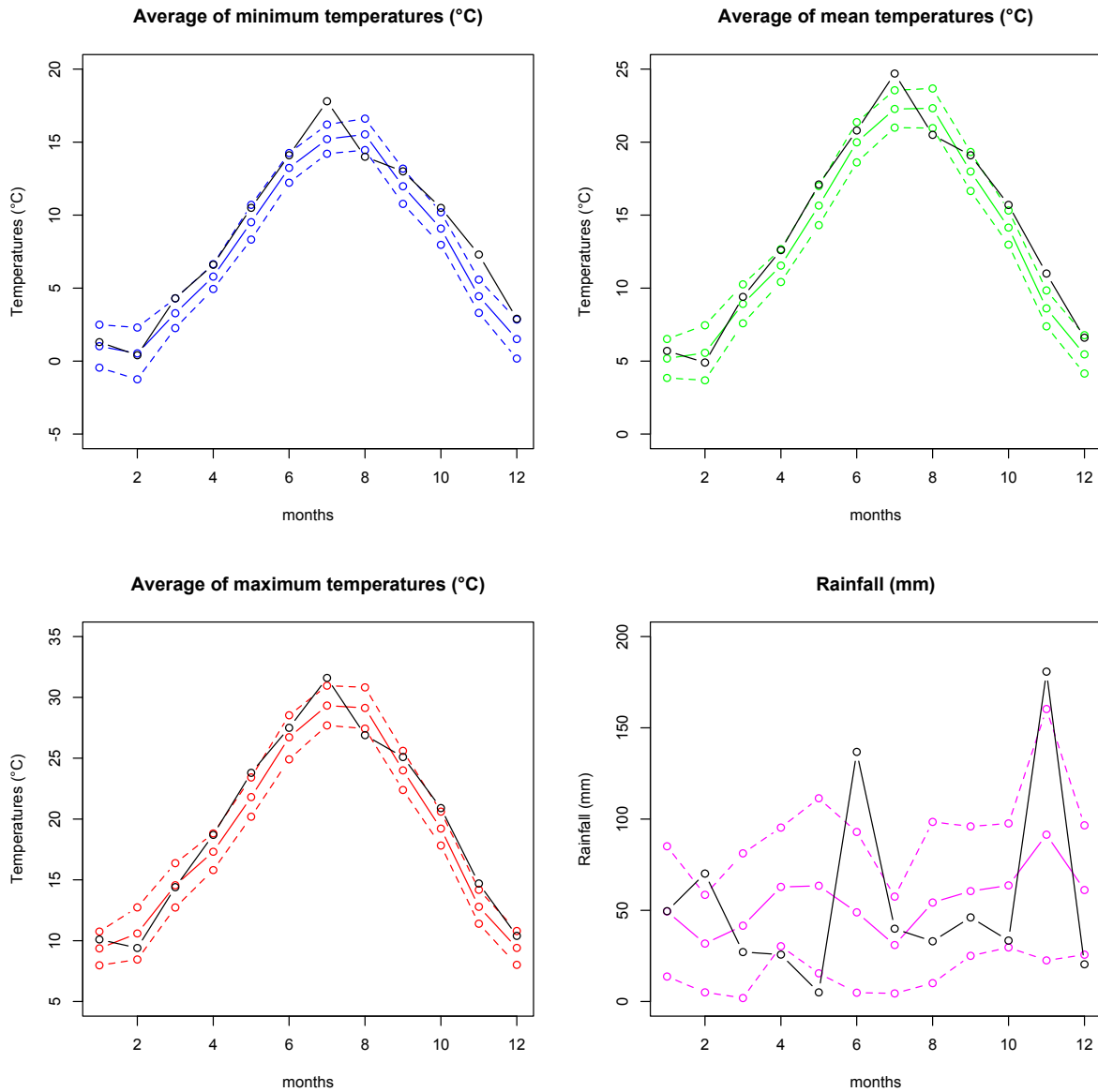


Fig3



1 Appendix A. Weather characteristics, based on MeteoFrance data.

2



3

4 Black dots correspond to the studied year. Colored dots correspond to 19-years  
 5 averaged data, with the full line indicating the mean, and the dotted lines indicating the  
 6 mean - standard deviation (below line) and the mean + standard deviation (upper line).

7 Appendix B. Model comparison (Model of line n+1 is compared with model of line n)

Function	Model	Log-lik	Chi <sup>2</sup>	Pr(>Chi)	AIC*
Poisson models	NULL	-453.42			909
	Distance	-256.03	394.77	< 0.001	516
	Crop code	-182.78	146.50	< 0.001	376
	Distance +Crop code	-117.91	129.75	< 0.001	248
Negative binomial models	NULL	-103.44	28.94	< 0.001	211
	Distance	-94.17	18.54	< 0.001	194
	Cropcode	-93.89	0.56	0.905	200
	Distance +Crop code	-84.84	19.11	< 0.001	184

8 \*AIC : Akaike. AIC values should not be compared between Poisson and negative binomial

9 models, as their likelihood functions differ (i.e., Poisson function and Normal Density

10 function, respectively).



11 Appendix C. Characteristics of the best model for the study site Brunet, i.e., negative  
 12 binomial model including both the Minimum distance to the source and the Crop code, and  
 13 associated tests.

14

15 Table C1. Model coefficients and confidence interval (CI) for Distance.

Variable	Coefficient	CI 95% (lower; upper bound)
Distance	$-2.675 \cdot 10^{-3}$	$-3.727 \cdot 10^{-3}; -1.656 \cdot 10^{-3}$

16

17 Table B2. Model coefficients (in bold) and associated Wald tests and 95% confidence  
 18 intervals (in italics) between Crop codes (qualitative variable).

Crop code	L1-cvG	L3-cvG	L3-cvS	L4-cvG
L3-cvG	<b>-0.570</b> <i>-1.205; 0.080</i>	/	/	/
L3-cvS	<b>-0.856***</b> <i>-1.443; -0.274</i>	<b>-1.409*</b> <i>-2.570; -0.235</i>	/	/
L4-cvG	<b>-1.979**</b> <i>-2.939; -0.986</i>	<b>-0.287</b> <i>-1.094; 0.508</i>	<b>1.122*</b> <i>0.224; 1.995</i>	/
S2	<b>0.146</b> <i>-0.761; 1.094</i>	<b>0.716</b> <i>-0.402; 1.852</i>	<b>2.125***</b> <i>1.192; 3.063</i>	<b>1.003*</b> <i>0.190; 1.951</i>

19 L1-cvG : 1<sup>st</sup> year infertile lavender hybrid cultivar Grosso; L3-cvG: 3<sup>rd</sup> year infertile lavender  
 20 hybrid cultivar Grosso; L3-cvS: 3<sup>rd</sup> year infertile lavender hybrid cultivar Sumian; L4-  
 21 cvG: 4<sup>th</sup> year infertile lavender hybrid cultivar Grosso; S2:2<sup>nd</sup> year clary sage. \*: significant at  
 22 P = 0.05; \*\*: significant at P = 0.01; \*\*\*: significant at P = 0.001. Model coefficients are  
 23 indicated in bold 95% confidence intervals are indicated in italics.

24 The difference between two crop codes has to be read by line, e.g., the parameter of Crop  
 25 code of L3-varG is equal to the corresponding parameter of L3-varG minus 0.570.

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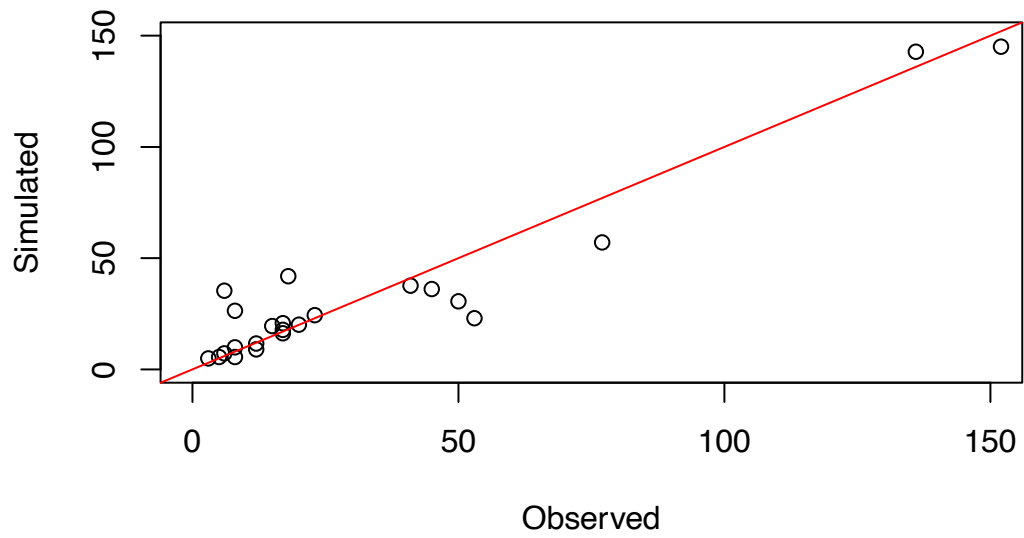
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36 Figure C1. Observed vs. simulated number of *Hyalesthes obsoletus*.

37 The red line corresponds to the 1:1 line (perfect fit).

38

39

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41