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

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Abstract

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

Keywords

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

1. Introduction

Agricultural pests are harmful to crops worldwide, as they can generate up to 25-40% yield losses at the world scale (based on eight major crops in Oerke and Dehne, 2004; Oerke 2006), with similar impact in pre- and post-harvest (Flood, 2010). The impact of insects is regarded as a global threat for current and future agricultural production systems. In addition to the direct losses due to feeding activity, insects cause yield losses via indirect damages (Weintraub and Beanland, 2006). Spittlebugs can indeed transmit virus and bacteria (e.g. *Xylella fastidiosa* (Wells et al. 1987) transmitted by *Philaenus spumarius* L., and responsible for Pierce disease of grapevines (Nunney et al. 2010) and leaf scorch of olive trees (Saponari et al. 2014)). Leafhoppers and planthoppers can transmit phytoplasmas (e.g. Flavescence dorée of grapevines, transmitted by *Scaphoideus titanus* Ball, Chuche and Thiery, 2014), which are prokaryotes colonizing plant phloem (Weintraub and Beanland, 2006). Phytoplasmas transmitted by insects are responsible for diseases in hundreds of plant species (Lee et al. 2000; Weintraub and Beanland, 2006), e.g., grapevine (Chuche and Thiery, 2014; Johanessen et al. 2008), lavender (Danet et al. 2010; Germain et al. 2015), maize (Jovic et al. 2007), and strawberry (Danet et al. 2003).

Among them, cixiid planthoppers (Hemiptera: Cixiidae) are considered of great economic importance, as they can transmit phytoplasmas agents of prominent and emerging plant diseases worldwide (e.g., Danet et al. 2003; Jovic et al. 2007; Maniyar et al. 2013). One of the most studied planthopper is *Hyalesthes obsoletus* Signoret, which is the vector of the stolbur phytoplasma causing the grapevine yellow disease ‘bois noir’ (Bressan et al. 2007; Johanessen et al. 2008). *H. obsoletus* is a polyphagous species, which overwinters as nymphs on the roots of host plant species (Sforza et al. 1999), and completes one generation per year in Central and South Europe (e.g., Sforza et al. 1999). *H. obsoletus* adults’ flight occurs from June til late August, depending on meteorological conditions and host plants (Darimont and

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

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

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

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

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

2. Materials and Methods

2.1. Study area

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

2.2. Field experimental design

The field campaign was carried out in 2015 on three zones (Brunet, Montagnac and Saint-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

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

Figure 1 approximately here

2.2.1. Searching for larvae and emerging adults

Potential host plants for *H. obsoletus* were searched based on studies performed in France (Sforza et al. 1999) and abroad (Aleksic et al. 1967; Güçlü and Özbek, 1988; Hoch and Remane, 1986; Kovaceski, 1958), including both cultivated and non-cultivated plants. Extra aromatic plants – that were not included in the above-mentioned studies – were also investigated, as they were suspected hosts according to local knowledge of farmers and technical advisers. Potential hosts, identified in previous studies or suspected by local authorities, were investigated in the three studied areas: (1) *cultivated crops*, i.e., lavandin, clary sage, alfalfa, sainfoin, alfalfa; and (2) *natural vegetation*, i.e., immortelle (*Helichrysum stoechas* (L.) Moench), thyme (*Thymus vulgaris* L.), bindweed (*Convolvulus arvensis* L.), 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 doica* 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 (Brcak, 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^2.
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 lavendin (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*

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

The overall performances of Poisson and negative binomial models *per se* were compared with Akaike criterion (AIC, a measure of model goodness of fit penalyzing more complex models; Burnham and Anderson, 2002). As these models do not share the same likelihood function, they were compared via a likelihood ratio test corrected for degrees of freedom (Self and Liang, 1987). We assessed the goodness-of-fit of the best model (according to AIC and likelihood ratio test) and the significance of the explanatory tests with X^2 test on residual deviance. The comparison between coefficients associated to the different modalities of the Crop_code explanatory variable was performed with Wald test, by considering 95% confidence intervals for each coefficient in the best model. Model residuals were visually 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

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

In the natural zones of Saint-Jurs, wild lavender and thyme species were found in the woods, and yellow melilot was present in the field edge between 1-year and 5-year lavandin fields. Bindweed was identified in all areas but in rapeseed and durum wheat fields. No larva of *H. obsoletus* was found in the roots of these species, and no adult was captured in the emergence traps (Table 2). In the cultivated areas, no *H. obsoletus* was found in lavandin fields, neither by uprooting plants nor with the emergence traps. For clary sage, the six fields located in the study zone were tested for the presence of *H. obsoletus* (one field of 2-year clary sage, four fields of 3-year clary sage, and one field of 4-year clary sage). The insect was found in the 4-year clary sage only, on 30% of the plants, for an average of 7 larvae per host plant (between 2 and 15 larvae per plant). All positive plants were located in a strip in the middle of the field.

In Montagnac natural areas, the potential hosts of *H. obsoletus* were thyme and bedstraw species in woods, and sainfoin and lavandin (4, 9 and 10 years-old) in cropped areas. Based on both plant uprooting and emergence traps, no source of *H. obsoletus* was identified in Montagnac during the survey (Table 2).

Table 2 approximately here

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

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

Figure 2 approximately here

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

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

Table 3 approximately here

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

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

Table 4 approximately here#

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

Figure 3 approximately here#

4. Discussion

4.1. Hosts of *Hyalesthes obsoletus*

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

Overall, larvae detection and emergence traps provided consistent results regarding the host species of *H. obsoletus*. Most individuals were found in fields of old clary sages, either as larvae on roots or as flying adults. As far as we know, this crop was not previously identified as a host for this insect. In European vineyards, bindweed and stinging nettle are the two main host species of *H. obsoletus* (Langer and Maixner, 2004; Sforza et al. 1998; Imo et al. 2013). In our study, although bindweed was largely represented in two out of three study zones, no larvae were found on its roots, and emergence traps caught a very low number of individuals, 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 occured, 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 lavendin. 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.*

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

4.2. Inference at field and small-landscape scales

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

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

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

Under the hypothesis that the clary sage fields were the sources of *H. obsoletus*, we derived potential dispersion curves towards potential targeted hosts, i.e., lavandin, showing significant effects of both distance to the source and host type (crop; age and cultivar of lavandin). Similarly to a previous study on one Cicadellidae of grapevine (Lessio et al. 2014), we fitted exponential regression using the minimum distance to the source as explanatory variable. Our curve displayed a large variability in small distances from the source, whatever the considered host. We did not find any significant difference between the fitted curves for the two host species clary sage (3-year) and lavandin (1-year), which could suggest their similar attractiveness for the insect. The higher attractiveness of young lavandin, as compared to older ones, could be linked to the higher proportion of bare soil leading to higher soil temperatures, more attractive for *H. obsoletus* (xerothermic insect). However, we investigated only one field of the two crops, located close and far to the source for clary sage and lavendin, respectively. Moreover, no host plants were present in the middle, as there was a field cropped with durum wheat, a non-host crop. The uncertainty in the minimum distance from the source could be reduced by studying homogenous landscapes in terms of crops/age, and including infected clary sage as reservoir. However, since clary sage does not show any symptoms of the disease, targeting such situations may be difficult. In addition, such 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 highlighed 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

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

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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.

	Study zone	Brunet			Saint Jurs			Montagnac		
Type of host	Potential host	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	-	-	-		
	Clary sage	x	x		x	x		-		
Cultivated	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
Lavandin	Number of plots with occurrence of H. obsoletus (*total number of plots*)	5 (*5*)	6 (*6*)	2 (*5*)
	Number of traps with occurrence of H. obsoletus (*total number of traps*)	21 (*21*)	15 (*17*)	2 (*18*)
	Number of dates with H. obsoletus	5	5	2
Clary sage	Number of plots with occurrence of H. obsoletus (*total number of plots*)	2 (*2*)	3 (*6*)	-
	Number of traps with occurrence of H. obsoletus (*total number of traps*)	5 (*5*)	15 (*22*)	-
	Number of dates with H. obsoletus	5	4*	-
Total number of *H. obsoletus*	Lavandin plots; Clary sage plots; Other areas; All	437; 827; 3[§]; 1267	109; 75; 5[#]; 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), [§]: trapped in wood and grassland, #trapped in the edge between wood and 5-year infertile lavandin..

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

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

Df : number of degrees of freedom.

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

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

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

Fig1

A
1 cm
© S. Guimier
B
40 cm
© S. Guimier
C
40 cm
http://rhone-alpes.synagri.com

Fig2

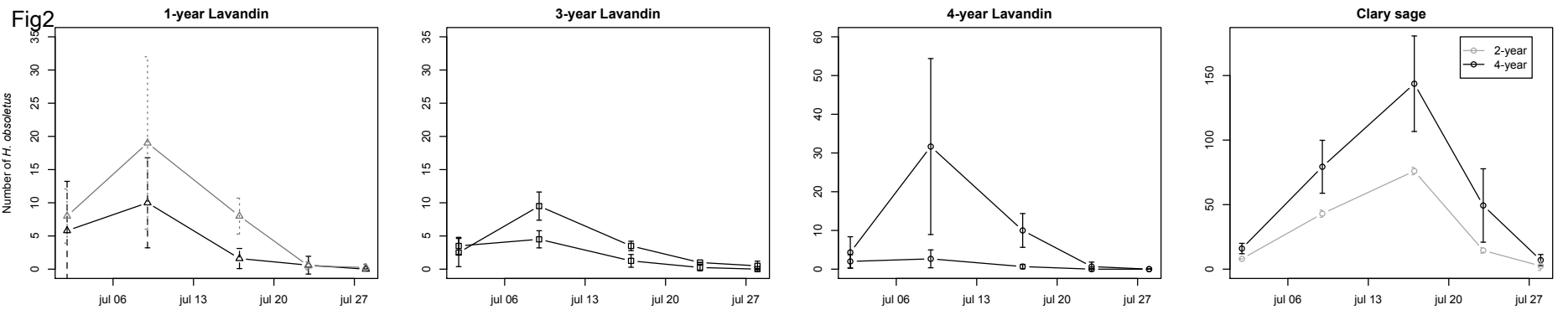
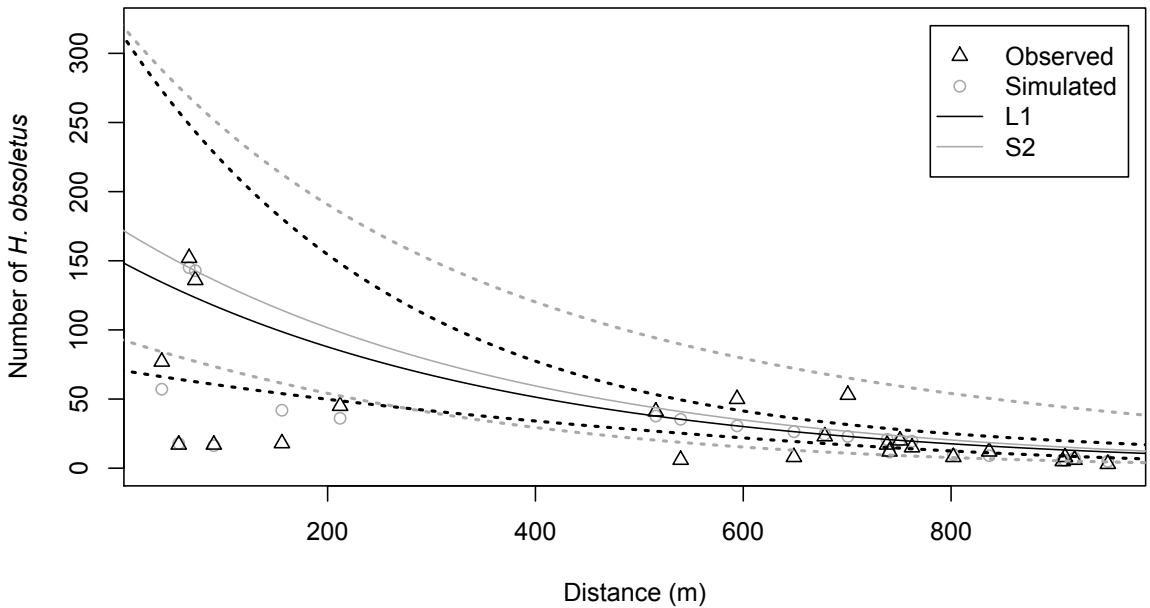
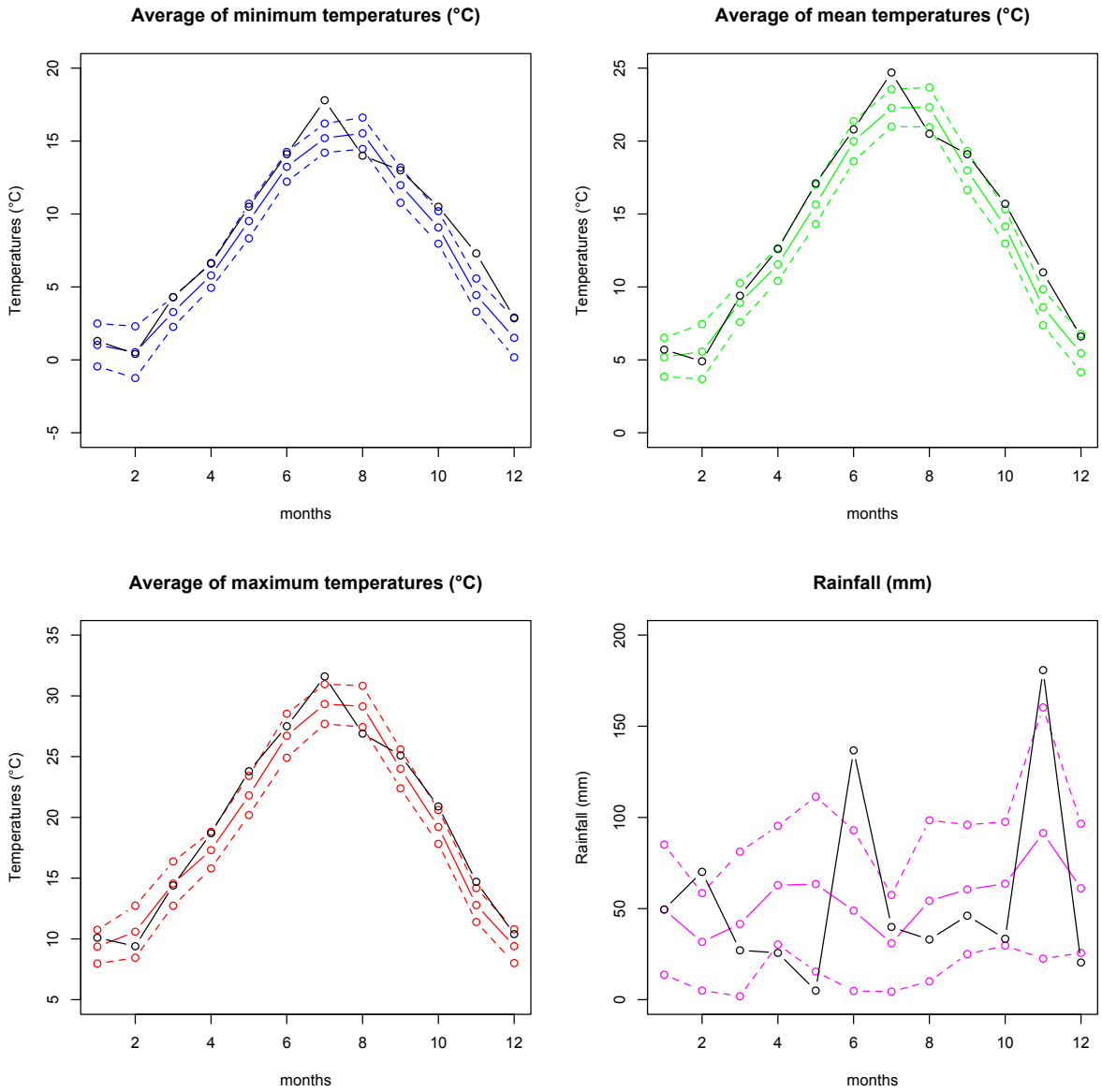

1-year Lavandin
3-year Lavandin
4-year Lavandin
Clary sage
Number of H. obsoletus
2-year
4-year
jul 06
jul 13
jul 20
jul 27

Fig3


Observed
Simulated
L1
S2
Number of *H. obsoletus*
0
50
100
150
200
250
300
200
400
600
800
Distance (m)

Appendix A. Weather characteristics, based on MeteoFrance data.



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

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

Function	Model	Log-lik	Chi^2	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

*AIC : Akaike. AIC values should not be compared between Poisson and negative binomial models, as their likelihood functions differ (i.e., Poisson function and Normal Density function, respectively).

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

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

Variable	Coefficient	CI 95% (lower; upper bound)
Distance	$-2.675.10^{-3}$	$-3.727.10^{-3}$; $-1.656.10^{-3}$

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

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

L1-cvG : 1st year infertile lavender hybrid cultivar Grosso; L3-cvG: 3rd year infertile lavender hybrid cultivar Grosso; L3-cvS: 3rd year infertile lavender hybrid cultivar Sumian; L4-cvG: 4th year infertile lavender hybrid cultivar Grosso; S2:2nd year clary sage.*: significant at P = 0.05; **: significant at P = 0.01; ***: significant at P = 0.001. Model coefficients are indicated in bold 95% confidence intervals are indicated in italics.
The difference between two crop codes has to be read by line, e.g., the parameter of Crop code of L3-varG is equal to the corresponding parameter of L3-varG minus 0.570.

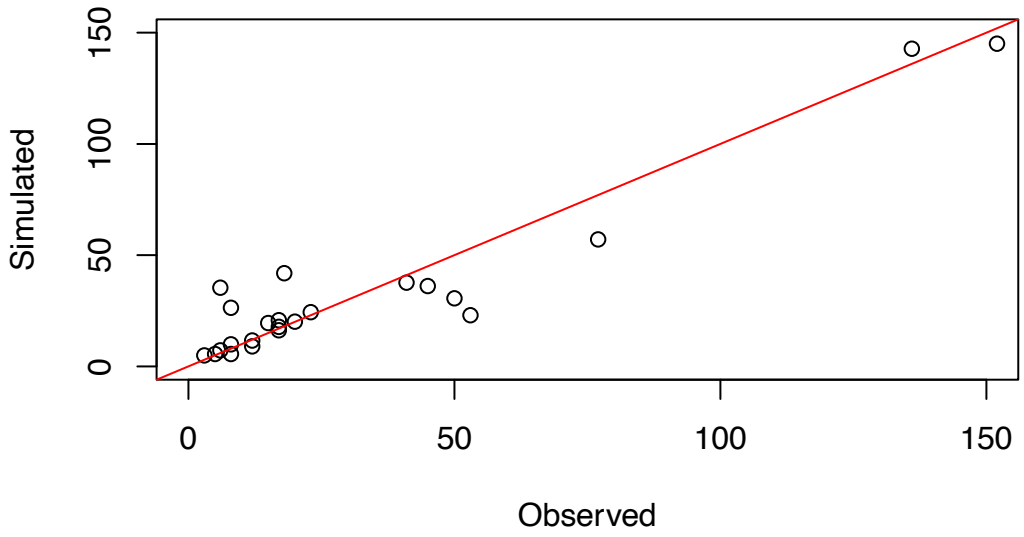


Figure C1. Observed vs. simulated number of *Hyalesthes obsoletus*. The red line corresponds to the 1:1 line (perfect fit).