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## Environmental factors driving infestations of a keystone winter fruit by an invasive and a native fruit fly

Gwenaëlle Deconninck, Méghan Boulembert, Patrice Eslin, Aude Couty, Anne Bonis, Nicolas Borowiec, Inessa Buch, Hervé Colinet, Lionel Delbac, Françoise Dubois, et al.

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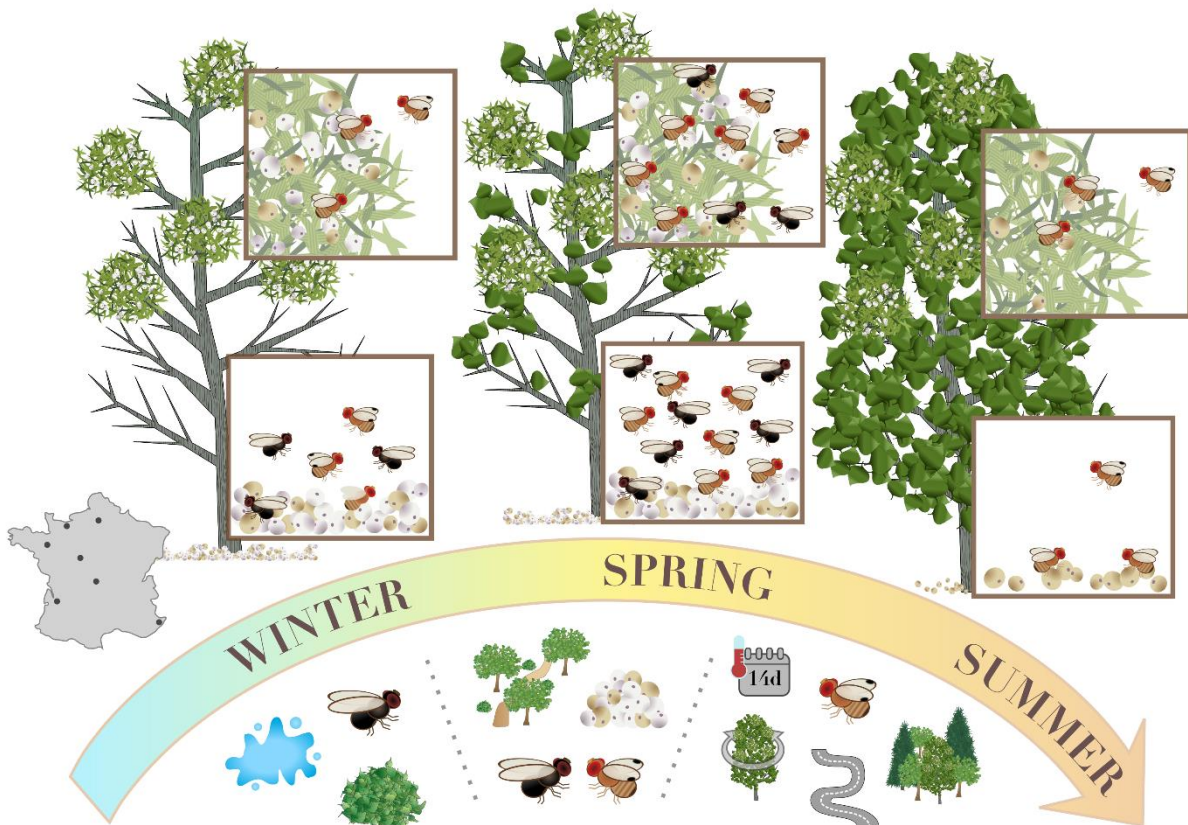
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13 **Graphical abstract:**



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17 **Environmental factors driving infestations of a keystone winter fruit by an invasive and a native**  
18 **fruit fly**

19

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73

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90

91 **Running title**

92 Infestation of a winter fruit by *Drosophila suzukii* and *D. subobscura*

93

94 **Abstract**

95 In temperate regions, most insect species overwinter in diapause while others continue to be  
96 active, feed and possibly reproduce despite adverse climatic conditions. For fruit flies which remain  
97 active winter long, the presence of winter-available fruit is crucial for population persistence. This study  
98 aimed to disentangle the relative effects of climatic, landscape and local factors on infestation rates of  
99 an important winter trophic resource, mistletoe (*Viscum album*) fruit, by drosophilid flies. Mistletoe fruit  
100 were sampled between January and July 2022 in seven regions of France, across a wide range of climatic  
101 conditions from Mediterranean to temperate oceanic. The fruit were used both by the invasive  
102 *Drosophila suzukii* and the native *D. subobscura* in the latter part of winter and throughout spring,  
103 suggesting that this resource may assist these species to overcome the winter bottleneck. Infestations by  
104 both flies were positively associated with the presence of fallen mistletoe fruit on the ground and semi-  
105 natural (forest, hedgerow) and anthropogenic (garden, park) habitats. The mistletoe's host tree species  
106 also influenced the fruit infestation rate. *Drosophila suzukii* infestation rate was positively impacted by  
107 the accumulated thermal energy ('degree days') in the previous 14 days. Mistletoe could act as a catalyst  
108 for the development of spring *D. suzukii* generations and should be considered in the context of  
109 integrative pest management strategies to prevent early infestation of crop fruit.

110

111 **Keywords**

112 Insect pest; biological invasion; mistletoe; *Viscum album*; non-crop host plants; *Drosophila suzukii*;  
113 *Drosophila subobscura*; landscape

114

115

116 **Highlights:**

- 117 • Trophic resources are scarce in winter for non-diapausing fruit flies
- 118 • We explored the roles of climatic, landscape and local factors affecting infestation rates of  
119 mistletoe fruit during winter by the invasive fly *D. suzukii* and the native *D. subobscura*
- 120 • Fly infestations were positively associated with presence of fruit on the ground, semi-natural  
121 and anthropic habitats and were influenced by the mistetoe's host trees
- 122 • Mistletoe could act as a catalyst for spring *D. suzukii* generations and are relevant for integrated  
123 pest management strategies

124

125 **Introduction**

126 In temperate regions, many insect species successfully overwinter through adopting specific  
127 strategies for synchronizing their cycle with food availability, such as diapause (Bale and Hayward  
128 2010; Gill et al. 2017; Lehmann et al. 2017). During diapause, development is suspended, which means  
129 no or little feeding during larval and adult stages (Sinclair 2015; Gill et al. 2017) and reliance on food  
130 reserves acquired in the pre-diapause phase for survival (Storey and Storey 2012; Gill et al. 2017). Other  
131 species, however, continue to feed and sometimes even reproduce throughout the winter (Danks 1978;  
132 Moore and Lee 1991; Wharton 2011), despite facing unfavorable climatic conditions. Resource selection  
133 in these species is therefore a crucial factor determining the extent to which a population is maintained  
134 (Danks 1978). The ability of insect herbivores to infest fruit resources during winter remains largely  
135 underexplored. These resources may also benefit invasive pest species, for which low temperature and  
136 resource scarcity make winter a critical bottleneck (Storey and Storey 2012).

137 *Drosophila suzukii* (Mastumara 1931) is a globally important invasive fly and a fruit pest  
138 (Asplen et al. 2015). Contrasting with other *Drosophila* species, *D. suzukii* is able to oviposit and  
139 develop in unripe and ripening fruit, causing important economic losses (Walsh et al. 2011; Tait et al.  
140 2021). This fly is highly polyphagous and uses wild as well as cultivated fruit (Lee et al. 2015; Poyet et

141 al. 2015; Kenis et al. 2016; Ulmer et al. 2022), including fruit of invasive plants (Poyet et al. 2014).  
142 Winter is a demographic bottleneck period for *D. suzukii*, mainly because the low temperatures and the  
143 lack of trophic resources reduce the population pool (Asplen et al. 2015; Hamby et al. 2016; Stockton  
144 et al. 2019). Even if remaining *D. suzukii* individuals are active during winter (e.g., foraging,  
145 displacement), so that they do not have a diapause *sensu stricto*, cold temperatures cause an ephemeral  
146 reproductive diapause (quiescence), which is reversible when climatic conditions become more  
147 favorable (Toxopeus et al. 2016; Wallingford et al. 2018). A major challenge for the fly is thus to find  
148 suitable hosts (usually wild fruit in natural habitats) both to provide food to allow populations that  
149 developed in the previous year to persist between winter and late spring, and to initiate the establishment  
150 of new generations (Poyet et al. 2015; Panel et al. 2018) before cultivated fruit become available as  
151 hosts. Among the few plant species bearing fruit in winter and early spring, *Viscum album* (mistletoe)  
152 is expected to be an important resource for *D. suzukii* since the fly can develop in the berries it produces  
153 (Panel et al. 2018; Poyet et al. 2015; Kenis et al. 2016) and because *V. album* and closely related species  
154 are widely distributed and often abundant across temperate regions worldwide (Watson 2001).

155 *Viscum album* L., 1753 is recognized as a keystone resource for various animal species in most  
156 temperate forests and woodlands (Watson 2001). It is an obligate hemiparasitic shrub that grows on a  
157 wide range of angiosperm and gymnosperm trees (Barney et al. 1998; Zuber 2004; Thomas et al. 2023).  
158 Native to Europe, it has a patchy distribution which depends on host availability, bird dispersal of seeds  
159 and human management (Zuber 2004; Thomas et al. 2023). Its fruit develop slowly, ripening in  
160 November to December in western Europe, with some remaining attached until spring (Thomas et al.  
161 2023). Depending on the host tree, the number of berries per kg of mistletoe ranges between 96 and 237  
162 (Preston 1977), providing resources for birds and small mammals (Thomas et al. 2023). It could also  
163 represent a potentially important breeding reservoir for insects in winter. Several arthropod species take  
164 advantage of *V. album* stems and leaves (Zuber 2004; Briggs 2011; Thomas et al. 2023). However, only  
165 a few utilize the fruit, among which are the larvae of *D. suzukii* (Thomas et al. 2023).

166 *Viscum album* is widely distributed across the area invaded by *D. suzukii* in Europe (Hultén and  
167 Fries 1986) and occurs in woodlands and hedges (Briggs 2021; Thomas et al. 2023) where *D. suzukii*

168 overwinters (Rossi-Stacconi et al. 2016; Briem et al. 2018; Santoiemma et al. 2019). The relationship  
169 between *V. album* and *D. suzukii* has been explored using field monitoring of infestation at the end of  
170 winter (Briem et al. 2016; Panel et al. 2018; Delbac et al. 2020a) and in laboratory experiments assessing  
171 the ability of *D. suzukii* to infest *V. album* berries (Poyet et al. 2015; Briem et al. 2016; Wolf et al. 2020).  
172 Its ability to utilize the fruit suggests that *D. suzukii* is able to overcome the toxicity of *V. album* berries  
173 (Gaidamashvili et al. 2012), as has been shown with other toxic fruit (Poyet et al. 2015, 2017). In winter  
174 and early spring, mistletoe fruit also constitutes a food resource for adult *D. suzukii* females that are  
175 active but with underdeveloped oocytes in ovaries (Briem et al. 2016). As the fly's reproductive diapause  
176 ends and the female's oocytes mature, the mistletoe fruit may provide suitable breeding sites at a time  
177 when other commercial fruit are not yet available (Poyet et al. 2015; Briem et al. 2016; Panel et al. 2018;  
178 Delbac et al. 2020a). Seed populations of *D. suzukii* in these fruit could therefore catalyze the  
179 development of new generations in spring.

180 *Drosophila suzukii* is the only Drosophilidae species known to oviposit and develop in *V. album*  
181 berries (Briem et al. 2016; Thomas et al. 2023) which may, thus, represent a low or free competition  
182 niche for the fly. This contrasts with other fruit where *D. suzukii* is known to facilitate other fly species:  
183 the fruit skin perforation by ovipositing *D. suzukii* females accelerates fruit decomposition and provides  
184 a point of entry for other species ovipositing preferentially in decaying organic matter (Poyet et al. 2014;  
185 Rombaut et al. 2017). This is the case for *D. melanogaster* in grapes (Rombaut et al. 2017) or *D.*  
186 *subobscura* in *Prunus serotina* (Poyet et al. 2014). The same process may occur in *V. album*, with *D.*  
187 *suzukii* facilitating other overwintering Drosophilidae species. Among them, the native European  
188 species *D. subobscura* could be expected to share *D. suzukii* winter niche. This species is highly cold  
189 tolerant (David et al. 2003; Delbac et al. 2020b), specialized on decomposing fruit (Begon 1975;  
190 Shorrock 1975), often dominant in Drosophilidae communities (Delbac et al. 2020b; Deconninck et al.  
191 2024), and has already been found associated with *D. suzukii* in fallen *Prunus serotina* fruit (Poyet et al.  
192 2014) and apple fruit (Deconninck et al. 2024).

193 To date, the influence of environmental factors on *V. album* infestation rate has not been  
194 explored, although they are expected to act at multiple scales. Global warming, resulting in mild winter



195 temperatures, may promote early winter fruit infestation, including those of *V. album*, by shortening the  
196 reproductive diapause period of *D. suzukii*. Thus, among climatic variables, those related to temperature  
197 may be important predictors of *V. album* infestation by *D. suzukii*. Landscape variables are also expected  
198 to influence fruit infestation. As wintering *D. suzukii* find shelter in hedges and woodland (Briem et al.  
199 2018; Rossi-Stacconi et al. 2016; Ulmer et al. 2022), *V. album* individuals close to forest habitats are  
200 therefore likely to have a higher risk of infestation. Local variables such as the quantity and quality of  
201 berries are also likely to influence infestation levels (Ulmer et al. 2022). Conversely, bird foraging can  
202 reduce the availability of *V. album* fruit, especially when temperatures are low and alternative resources  
203 are scarce (Briggs 2021). There is, therefore, a risk that *D. suzukii* may face a lack of this key resource  
204 in late winter, before the fly's eggs mature in early spring. In general, *D. suzukii* prefers to oviposit in  
205 ripening and ripe fruits (Walsh et al. 2011; Atallah et al. 2014). In laboratory assays, flies laid more eggs  
206 in artificially damaged than in undamaged berries (Briem et al. 2016). Damaged fruit are commonly  
207 observed in the field after the birds have foraged or after a storm event, but the distribution of *D. suzukii*  
208 between damaged or undamaged mistletoe berries in the field remains unknown.

209 This study aimed to disentangle the relative roles of climatic, landscape and local factors that  
210 could affect infestation rates of a wild host plant by *D. suzukii*. We focused on the mistletoe *V. album*  
211 because this major host plant is one of the few species bearing fruit in winter and early spring. This non-  
212 crop host plant could also support overwinter seed populations of *D. suzukii*, catalyzing the development  
213 of new generations in spring in advance of the availability of the first commercial fruit crops such as  
214 cherries, strawberries or raspberries. We hypothesized that (i) *D. suzukii* presence in *V. album* would be  
215 positively associated with the abundance of natural habitats such as woodland, which provide winter  
216 refuge for *Drosophila* species (Basden 1954) and particularly for *D. suzukii* (Ulmer 2022); and, (ii) *D.*  
217 *suzukii* infestation of *V. album* fruit would facilitate infestation by other *Drosophila* species such as *D.*  
218 *subobscura* (Poyet et al. 2014; Deconninck et al. 2024) or *D. melanogaster* (Rombaut et al. 2017;  
219 Deconninck et al. 2024). We determined the infestation rates across a large geographical area spanning  
220 1,000 km in France and including a large range of climatic conditions. At each sampling location, we

221 also measured several local (e.g., mistletoe host tree and mistletoe traits) and landscape variables (e.g.,  
222 vegetation cover, proportion of habitats) to identify the environmental drivers of mistletoe infestations.

## 223 **Methods**

### 224 *Sampling design*

225 Mistletoe fruit were sampled in seven regions of France across a wide range of climatic  
226 conditions from Mediterranean in the south to temperate oceanic in the north (Figure 1, Table 1). In  
227 Amiens, Bordeaux, Rennes and Tours, sampling took place every month between January and July 2022,  
228 while in Caen, Clermont-Ferrand and Nice, sampling took place only once at the optimum timing of  
229 fruit maturity in February/March. Indeed, no fruit remained at these sampling locations after March,  
230 likely as a result of bird foraging. An average of 10 mistletoe individuals were randomly sampled at  
231 each location and on each sampling day, with some variation depending on fruit availability. Where  
232 possible, a minimum of 100 berries was sampled from each individual mistletoe, but this number was  
233 not always reached on some sites at the end of the fruiting period.

### 234 *Traits of mistletoe and host trees*

235 Collected fruit were separated into three subsets to monitor *Drosophila* emergence: undamaged  
236 ('healthy') and damaged fruit collected on the plant and fruit collected on the ground (if present). Several  
237 traits of the sampled mistletoe individuals and their host trees were measured to characterize the local  
238 resources available for the flies and the microhabitat. The following reproductive and vegetative traits  
239 were measured: the maximum and minimum diameter of the mistletoe individual sampled, and an  
240 estimate of the number of fruit present. For each sampled mistletoe individual, five berries were  
241 randomly selected to measure their length and width and calculate their volume ( $4/3 \times \pi \times \text{mean radius}^3$ )  
242 and fruit skin area ( $4 \times \pi \times \text{mean radius}^2$ ). Five leaves were also taken, their length and width measured  
243 and the leaf surface index (length  $\times$  width; Ulmer et al. 2022) calculated. The height of the mistletoe  
244 individual on the host tree (from the ground) was also recorded. The tree species hosting the mistletoe  
245 was identified (Table S1) and its height, crown diameter and trunk circumference measured. The number  
246 of mistletoe individuals on the host tree was recorded. Variables, units and codes are listed in Table S2.

247 *Environmental variables*

248           Local environmental, landscape and climatic variables were measured at each sampling location  
249 or extracted from online databases to examine the effects of regional and local environmental conditions  
250 on infestation rates (Table S2).

251           Local environmental conditions were described as follows. First, within a 5 m-radius plot  
252 centered on the mistletoe host tree, the cover and height of the tree, shrub and herbaceous layers were  
253 estimated, as well as soil litter thickness (Table S2). Second, within a 20 m radius, the percentage of  
254 local habitat elements surrounding the host was recorded (e.g., orchard, woodland, grassland, swamp,  
255 crop, garden, shrub, building, hedgerow, river, pond, poplar plantation, park, road; see Table S2), as  
256 well as the number of *V. album* individuals around the host tree (i.e., on other trees than the host tree  
257 itself) and any presence of other plant species with maturing fleshy fruit.

258           The landscape composition around each sampled mistletoe was then characterized. A  
259 geographic database was created using a Geographic Information System (GIS; ArcGIS Pro v.2.5,  
260 ESRI). The sampled host trees were positioned in the GIS and buffers of 50, 100, 250, 500, 750, 1000,  
261 1250, 1500, 1750, 2000, 2500 and 3000 m radii around each host tree were created for subsequent  
262 analyses of landscape composition. Landscape elements (crop, water, woodland, heartland, grassland,  
263 road, urban area, orchard, industrial zone) were extracted from the OSO database (Centre d'Expertise  
264 Scientifique OSO, 2022) and updated using aerial photographs and field observations (in buffers < 100  
265 m).

266           Macroclimatic conditions were characterized for each sampling site using regional  
267 measurements. The daily meteorological data were retrieved from the three nearest meteorological  
268 stations to each site, from January 1st 2022 to each day of sampling ([https://www.historique-](https://www.historique-meteo.net/france/)  
269 [meteo.net/france/](https://www.historique-meteo.net/france/), details in Table S3). Daily minimum, mean and maximum temperatures, rainfall and  
270 snowfall were calculated for all sites using inverse-distance weighting (IDW) interpolation (Willmott et  
271 al. 1985) from the data from the three nearest weather stations (Table S3). Accumulated degree-days  
272 (“Growing Degree Days”, GDD) were calculated using a lower threshold of 0°C between January 1st

273 2022 and the day of sampling (Baskerville and Emin 1969). The baseline value of 0°C is a standard  
274 threshold commonly used to calculate GDD in insect and plant studies (White et al. 2012; McNeil et al.  
275 2020). It is particularly suitable to study the temporal synchrony between insects and plant resources  
276 (Iler et al. 2013). It was also chosen because active *D. suzukii* can be observed even at very low positive  
277 temperature (< 5°C) during winter, including during periods of snowfall (Ulmer 2022; Ulmer et al. 2022)  
278 and because mistletoe fruit can undergo freeze-thaw cycles before ripening ends. From daily  
279 precipitation values, we also calculated mean daily and cumulative precipitation between January 1st  
280 2022 and the day of sampling and within the 7- or 14-day periods before each fruit sampling day.

### 281 *Emergence of Drosophila species*

282 After collection, the mistletoe fruit were individually placed on wet cotton wool in cylindrical  
283 plastic transparent containers (diameter = 118 mm, height = 135 mm, volume = 1,476 cm<sup>3</sup>), covered  
284 with a nylon mesh, and maintained in a temperature-controlled room at 20 °C under a 16:8 L:D regime.  
285 Adult flies emerging from the fruit were placed in 70% ethanol. They were identified to species level  
286 using Bächli et al. (2005) and Withers and Allemand (2012). Individuals of the two major species found  
287 (*D. suzukii* and *D. subobscura*) were sexed and counted using a Leica M205C stereomicroscope equipped  
288 with a Leica MC170 HD camera and the Leica Application Suite software.

### 289 *Infestation variables*

290 We examined the relationships between environmental variables and two common infestation  
291 variables (Benavidez et al. 2021) that were either centered on the fruit (Fruit Infestation Rate: FIR =  
292  $100 \times \text{number of emerged } Drosophila \text{ individuals from fruit collected from a given } V. \text{ album individual}$   
293  $/ \text{total number of fruit collected from the same } V. \text{ album individual}$ ) or on the plant (Plant Infestation  
294 Rate: PIR =  $100 \times \text{number of infested } V. \text{ album individuals in a region or month} / \text{total number of } V.$   
295  $\text{album individuals sampled in the same region or month}$ ). A high FIR indicates that the majority of fruit  
296 on the plant are infested by the fly and a high PIR indicates that the majority of the plants in a region  
297 are infested by the flies. These variables can be interpreted as follows: a high FIR reflects the plant auto-  
298 contamination by the flies while a high PIR reflects fly dispersal (e.g., when the FIR and PIR are both

299 high, there is both auto-contamination of the plant and dispersal of the flies; when the FIR is high and  
300 the PIR is low, there is mostly plant auto-contamination; when the FIR is low and the PIR high, there is  
301 mostly fly dispersal; when both FIR and PIR are low, there is an absence of both contamination and  
302 dispersal). These infestation variables were also calculated for each fruit category (healthy or damaged  
303 fruit on the plant and fruit on the ground, following Deconninck et al. (2024)).

#### 304 *Statistical analyses*

305 For each of the two *Drosophila* species, we tested the influence of environmental variables (fruit  
306 and plant morphology, host tree characteristics, local abiotic conditions, habitat composition in the  
307 surrounding landscape and climatic variables) on FIR using mixed models (GLMMs). Region was also  
308 introduced as a random effect in GLMMs to account for the non-independence among sampling  
309 locations within the same region. For both *D. suzukii* and *D. subobscura* models, a preselection of  
310 explanatory variables was made by using the non-redundant variables that correlated (Pearson  
311 correlation) most strongly with fruit infestation rates at the assessed spatial scales (buffers from 5 m to  
312 3000 m radius around each sampling point), as recommended by Ulmer et al. (2022). Backward selection  
313 of explanatory variables and the second-order Akaike information criterion (AICc; Hurvich and Tsai  
314 1989) were used to select the most parsimonious model, i.e. the model with the lowest AICc.  
315 Homoscedasticity was checked using biplots of residuals and model predictions. As sample numbers  
316 were not balanced between mistletoe host trees (Table S1; due to high host tree diversity and random  
317 sampling, many host tree species included only one or a few samples in the dataset), separate GLMMs  
318 were performed to test the effect of host tree identity on FIR by *Drosophila* species using the four  
319 dominant host tree species, i.e. those for which the occurrence was greater than 5% of the total number  
320 of samples. As with previous GLMMs, region was introduced as a random effect in the models. To test  
321 whether the FIR varied across months, we used Kruskal-Wallis tests. When significant, *post-hoc*  
322 pairwise comparisons between months were then performed using Mann-Whitney U tests. All statistical  
323 analyses were performed using SPSS version 24.0 (IBM Corporation).

#### 324 **Results**

325 *Dynamics of Viscum album fruit resource*

326 A total of 33,536 fruit from 264 mistletoe individuals were sampled across all regions between  
327 January and July 2022 (Table 2). The number of fruit decreased progressively over the study period,  
328 from an average of 167 collected per mistletoe in January to an average of only 26 in July (Figure 1).  
329 From January to June, the majority of fruit were healthy on the plant (47–63%) and the proportion of  
330 damaged fruit on the plant progressively declined from 33% to 16% over the same period. The  
331 proportion of fruit on the ground initially decreased from 18% to 9% between February and March, then  
332 increased by June to reach 37%. In July, no healthy fruit remained on the plants and most fruit were  
333 either damaged (88%) or on the ground (12%).

334 *Regional infestation of Viscum album*

335 A total of 735 *D. sukuzii*, 53 *D. subobscura* and 1 *D. repleta* individuals emerged from the fruit  
336 sampled in all regions between January and July 2022 (Table 2). No flies emerged from fruit sampled  
337 in Clermont-Ferrand, Nice and Rennes. *Drosophila sukuzii* mean infestation rate (FIR) was the highest  
338 in Bordeaux ( $6.11 \pm 1.83\%$ ), with a mean of  $2.37 \pm 0.53\%$  across all regions. Among regions showing  
339 fruit infestation, the maximum fruit infestation rate (max FIR) by *D. sukuzii* ranged between 11.63%  
340 (Tours) and 72.86% (Amiens). Up to 39.13% of the *V. album* individuals sampled were infested by *D.*  
341 *sukuzii* (Bordeaux), with a mean plant infestation rate (PIR) of 20.08% across all regions.

342 *Drosophila subobscura* was only found in Amiens, Bordeaux and Tours, with mean FIR ranging  
343 between  $0.19 \pm 0.07\%$  in Bordeaux and  $0.31 \pm 0.15\%$  in Amiens. The maximum FIR by *D. subobscura*  
344 ranged between 1.96% in Bordeaux and 16.67% in Amiens. Up to 15.22% of the *V. album* individuals  
345 sampled were infested by *D. subobscura*, with a mean PIR of 7.20% across all regions. The single  
346 individual of *D. repleta* was obtained in Amiens.

347 *Seasonality of Viscum album infestation*

348 *Drosophila subobscura* was the earliest fly species to emerge from *V. album* fruit, emerging  
349 from fruit sampled in February in Amiens and Tours (Figure 2A, 2B). In February, its FIR was low  
350 ( $0.06 \pm 0.04\%$ ), then increased significantly in April and May to reach  $0.67 \pm 0.33\%$  and  $0.28 \pm 0.23\%$ ,

351 respectively (Kruskal-Wallis test,  $\chi^2 = 26.145$ ,  $p < 0.001$ ; Figure 2A). This species did not emerge from  
352 fruit collected after May, and was mostly found in fruit collected on the ground (95% of individuals),  
353 with only two individuals emerging from healthy fruit sampled on the plant (Figure 3B). The sex ratio  
354 of emerging *D. subobscura* flies was unbiased (chi-squared test:  $\chi^2 = 0.647$ ,  $p = 0.42$ ), with 30 females  
355 against 23 males.

356 *Drosophila suzukii* first emerged from fruit sampled in March, showing a FIR of  $0.79 \pm 3.71\%$ ,  
357 with infestation increasing significantly to reach  $9.20 \pm 3.05\%$  in May, followed by a decrease in June  
358 to  $0.92 \pm 0.66\%$ , and no further emergence in July (Kruskal-Wallis test,  $\chi^2 = 37.951$ ,  $p < 0.001$ ; Figure  
359 2A). A majority (58.3%) of *D. suzukii* emerged from fruit collected on the ground, then 36.8% from  
360 healthy fruit on the plant and 4.9% from damaged fruit on the plant. The highest fruit infestation rate  
361 was observed in May, with 15% for fruit on the ground, 8% for healthy fruit on the plant and 0.1% for  
362 damaged fruit on the plant (Figure 3B). Emerging *D. suzukii* flies had an unbiased sex-ratio overall (chi-  
363 squared test:  $\chi^2 = 0.647$ ,  $p = 0.42$ ), with 374 females and 361 males.

364 In February, 10% of *V. album* individuals were infested by *D. subobscura*, which decreased to  
365 3% in March, then increased to 23% in April and finally decreased to 6% in May (Figure 2B). In March,  
366 13% of *V. album* individuals were infested by *D. suzukii*, increasing to 39% and 40% in April and May,  
367 respectively, and then decreasing in June to reach 22%.

368 Throughout the seasons, the dynamics of infestation by *D. suzukii* and *D. subobscura* changed  
369 (Figure 4A, 4B). In February and March, both species had low FIR and PIR, suggesting that both auto-  
370 contamination (local infestation) of *V. album* individuals and dispersal were low. Then, in April, both  
371 species started to disperse. In May, *D. suzukii* was both auto-contaminating *V. album* individuals and  
372 dispersing while *D. subobscura* infestation decreased. In June, local infestation of *D. suzukii* increased  
373 again. Finally, starting from June for *D. subobscura* and July for *D. suzukii*, no further infestation was  
374 found in *V. album* fruit.

375 *Effect of environmental variables on Viscum album fruit infestation rate*

376 *Drosophila suzukii* fruit infestation rate was positively associated with the percentage of fruit  
377 collected on the ground, the canopy width of the host tree, the path cover in a 5 m radius, the garden and  
378 forest cover in a 20 m radius around sampling points and the GDD in the preceding 14 days (GLMM,  
379 Table 3). *Drosophila subobscura* fruit infestation was positively associated with the percentage of fruit  
380 collected on the ground, the cover of water, hedgerow and urban park in a 20 m radius around sampling  
381 points (GLMM, Table 3). The identity of the dominant host trees (*Crataegus monogyna*, *Malus*  
382 *domestica*, *Populus nigra*, *Robinia pseudoacacia*) significantly influenced FIR by *Drosophila* species  
383 (Table S1 and Figure S1). Mistletoe growing on *P. nigra* had the most heavily infested berries, with a  
384 FIR of  $4.11 \pm 1.57\%$  and  $0.65 \pm 0.32$  by *D. suzukii* and *D. subobscura*, respectively. *Drosophila suzukii*  
385 FIR was significantly reduced in *M. domestica* and *R. pseudoacacia* compared to *P. nigra*, and the  
386 lowest FIR was for mistletoe growing on *C. monogyna* (GLMM:  $F = 3.00$ ,  $p = 0.04$ ). *Drosophila*  
387 *subobscura* FIR was also significantly decreased in mistletoe growing on *C. monogyna* and *R.*  
388 *pseudoacacia*, and was zero on *M. domestica* (GLMM:  $F = 2.63$ ,  $p = 0.05$ ).

## 389 Discussion

390 Both *D. suzukii* and *D. subobscura* emerged from *Viscum album* fruit in the latter part of winter  
391 and throughout spring, confirming that this food resource likely helps them to overcome the winter  
392 bottleneck induced by low temperatures and limited availability of fruit of other species. Below, we  
393 address (i) how local and landscape factors affect *Drosophila* infestation, (ii) the potential role of *V.*  
394 *album* as a catalyst for the development of spring *D. suzukii* generations, (iii) the potential for *D. suzukii*  
395 to impact trophic fluxes in the context of invasion and climate change, and (iv) the relevance of our  
396 findings in the context of pest management strategies.

### 397 *Local and landscape drivers of fruit infestation*

398 Levels of infestation by both *D. suzukii* and *D. subobscura* were locally positively associated  
399 with the percentage of fruit on the ground, most likely a result of wind, bird foraging or abscission due  
400 to fruit maturity. *Drosophila subobscura* has not previously been reported to complete its life cycle in  
401 *V. album*, although it is known to utilize fallen fruit for breeding (Shorrocks 1975; Poyet et al. 2014;



402 Deconninck et al. 2024). Begon (1975) showed that the density of berries in an area increased the  
403 chances of breeding by *D. subobscura*. He studied *D. subobscura*'s peak of abundance in November  
404 and sampled several fleshy-fruited plants (e.g., hawthorn, rowan, woody nightshade), but not mistletoe  
405 which matures later. These plants are also present in our sampling regions (Poyet et al. 2015) and *D.*  
406 *subobscura* may have switched from them to *V. album* in February. *Drosophila subobscura* is also  
407 known to favor soft fruit for oviposition (Begon 1975), which is consistent with its preference for softer  
408 decaying fruit on the ground. In contrast, *D. sukukii* is known for its ability to oviposit in ripening and  
409 ripe fruit (Walsh et al. 2011) using its serrated ovipositor (Atallah et al. 2014), although was still more  
410 attracted by damaged than intact mistletoe berries in a laboratory experiment (Briem et al. 2016). The  
411 field patterns revealed by our study are consistent with this experimental result as the largest number of  
412 *D. sukukii* were found in fallen fruit (damaged), even if, on the plant itself, healthy fruit were preferred  
413 over damaged. Several hypotheses may support these observations: (i) the dietary requirements of *D.*  
414 *sukukii* may vary seasonally (Rendon et al. 2019; Jiménez-Padilla et al. 2020); ripe and rotting berries  
415 may be more suitable during winter as winter morphs seek resources richer in sugar (Rendon et al. 2019);  
416 (ii) the absence or low levels of interspecific competition even in decaying *V. album* berries may allow  
417 the larvae to complete their development; it has been suggested that the presence of other drosophilids  
418 in other decaying fruit may result in levels of competition that *D. sukukii* cannot tolerate (Kidera and  
419 Takahashi 2020); and (iii) more extreme winter environmental conditions may restrict the ability of flies  
420 to reach mistletoe individuals higher in the shrub or tree vegetation (Dillon and Frazier 2006; Frazier et  
421 al. 2008); this will result in the flies staying close to the ground where the temperature is buffered  
422 (Deconninck et al. 2024) and, therefore, to infest fallen fruit.

423 Landscape features affected the two *Drosophila* species differently. Garden and forest cover in  
424 the area of the sampling locations positively influenced levels of infestation by *D. sukukii*, while the  
425 cover of water, hedgerow and urban park positively influenced those of *D. subobscura*. Semi-natural  
426 habitats including woodland, grassland, hedgerow and shrubs are known to positively affect the  
427 abundance of Drosophilidae species by providing food resources, breeding sites and shelters with  
428 beneficial microclimatic conditions (Santoemma et al. 2018; Delbac et al. 2020b). The differences

429 between the semi-natural habitats affecting each species may be due to their diet and breeding  
430 preferences, as *D. suzukii* is mostly frugivorous (Walsh et al. 2011; Poyet et al. 2015; but see Stockton  
431 et al. 2019 for alternative resources), while *D. subobscura* is both frugivorous and fungivorous (Begon  
432 1975; Delbac et al. 2020b). The food and breeding resources the flies are seeking may not be found in  
433 the same semi-natural habitats. Similarly, the canopy width of the host tree only affected *D. suzukii*,  
434 which has a strong preference for the canopy layer (Tanabe 2002).

435 The importance of semi-natural habitats varied between the two species, with *D. subobscura*  
436 less affected by their presence than *D. suzukii* (Delbac et al. 2020b). This is consistent with the  
437 ‘generalist’ ecology of *D. subobscura*, as it is found across multiple habitats (Shorrocks 1975; Gross  
438 and Christian 1994). This species is also considered a ‘core’ species invariably dominating fruit fly  
439 species assemblages from autumn to early spring, at least in apples (Deconninck et al. 2024). The impact  
440 of semi-natural habitats on Drosophilidae abundance also varied between seasons.

441 *Mistletoe as a host for seed populations catalyzing new generations of D. suzukii in spring?*

442 *Viscum album* fruiting commences in November and berries can remain on the plant until May  
443 (Thomas et al. 2023; Delbac et al. 2020a). It is one of the few plant species providing resources to birds,  
444 mammals and some insect species in winter (Watson 2001; Thomas et al. 2023). *Drosophila suzukii*  
445 adults have previously been reported to feed on *V. album* berries in winter, and to start using them as a  
446 breeding substrate in April (Briem et al. 2016; Panel et al. 2018; Delbac et al. 2020a). In our study, *V.*  
447 *album* started to be infested by *D. suzukii* in March, slightly earlier than previously reported (Delbac et  
448 al. 2020a). Early-infested *V. album* berries could therefore generate the first generations of *D. suzukii*  
449 that will later attack early maturing commercial fruit such as cherries. In this part of Europe, cherries  
450 begin to mature mid-April (Santoemma et al. 2018) and are one of the most heavily-infested commercial  
451 plants by *D. suzukii* (Beers et al. 2011).

452 The fruit infestation rate (FIR) was quite low in our data, but the plant infestation rate (PIR) was  
453 very high (up to 40%). This discrepancy between the two metrics may be explained by a combination  
454 of the low survival rate of *D. suzukii* at the end of winter and by the high quantity of fruit on each plant,

455 diluting the overall infestation rate. Nonetheless, a host tree bearing numerous mistletoe individuals  
456 (e.g., a maximum of 110 mistletoe individuals was counted in a single poplar tree in this study) will  
457 generate a high number of flies even if its mean FIR is low. Therefore, commercial fruit fields  
458 surrounded by trees bearing mistletoe individuals may be exposed to a wave of *D. suzukii* around mid-  
459 April once the first crop fruit mature sufficiently to attract these flies, although this effect will depend  
460 on the location.

461         There were clear differences between the regions studied in the persistence of mistletoe fruit  
462 across months and in infestation rates. Regional contrasts may primarily result from overall climatic  
463 conditions impacting mistletoe phenology (Fontúrbel et al. 2018), as it is the case for flowering and  
464 fruiting periods of many plant species (reviewed by Menzel et al. 2006, 2020). More specifically, earlier  
465 and more rapid fruit maturation in some regions may not match the fly's phenology, leading to a  
466 phenological mismatch (Renner and Zohner 2018). Second, even if berries are at an appropriate stage  
467 of maturity for the flies to oviposit, the latter may not be able to do so due to reproductive diapause  
468 (Abarca and Fahn 2021). Finally, in some regions, mistletoe berries may be more rapidly consumed by  
469 birds due to a lack of availability of other resources (Visser et al. 2012). In our study locations, wood  
470 pigeons (*Columba palumbus*) and blackbirds (*Turdus merula*) were observed to eat mistletoe berries.  
471 Thrushes are known dispersers (Thomas et al. 2023), while it is unclear whether wood pigeons generally  
472 feed on berries or graze *V. album* leaves (Briggs 2021). Such mismatches between fruit and *Drosophila*  
473 sp. physiology and phenology have been reported between elderberries and *D. suzukii* (Ulmer et al.  
474 2022). In southern France, *Sambucus nigra* fruits in July and experiences a low infestation rate  
475 (mismatch), because the typically hot and dry weather is unfavorable for *D. suzukii* while, in northern  
476 France, *S. nigra* mostly fruits in September and experiences considerable infestation (match), as the mild  
477 and humid weather is favorable for the fly. In the context of contemporary climate change, which is  
478 already impacting *V. album* distribution (Bertin 2008), any advance in timing leading to an earlier match  
479 between fruit maturity and fly ability to reproduce may amplify the possibility of infestation and damage  
480 to spring-cultivated commercial fruit, but this requires further investigation.

481 *Potential impact of D. suzukii on ecosystem functioning*

482           The timing and pattern of mistletoe utilization differed between *D. suzukii* and *D. subobscura*.  
483 Both species initially adopted a similar strategy of local infestation at the end of winter, probably  
484 reducing energetic costs associated with dispersal. In April, when temperatures are milder, dispersal  
485 reaches a peak. As spring progressed, mistletoe utilization started to diverge: *D. suzukii* showed both a  
486 high level of local infestation and dispersal in May, coinciding with abundance at that time when various  
487 cultivated fruits are maturing (Estrella et al. 2007). *Drosophila suzukii* thus seemed to favor dispersal  
488 strategies while *D. subobscura* continued to infest at a local scale. Our data contrast with those of Poyet  
489 et al. (2014), who suggested facilitation of *D. subobscura* by *D. suzukii* in *Prunus serotina* fruits, thanks  
490 to the ability of *D. suzukii* to pierce fruit skin with its serrated ovipositor, a feature not possessed by *D.*  
491 *subobscura*. However, *D. subobscura* started to emerge from mistletoe fruit in February, one month  
492 earlier than *D. suzukii*, and was mainly found in fruit on the ground. This is likely because of *D.*  
493 *subobscura* oviposition requirements (Begon 1975; Shorrocks 1975) and because this fly species is  
494 unusual amongst the *Drosophila* community in being able to infest decaying fruit throughout the coldest  
495 period of the year (Deconninck et al 2024). As *D. subobscura* emerged before *D. suzukii*, our results did  
496 not provide evidence of a facilitating effect of *D. suzukii* benefiting *D. subobscura*, at least up to March.  
497 Other environmental factors (e.g., winds, birds, fruit maturity) caused mistletoe fruit damage and/or fall,  
498 facilitating *D. subobscura* infestation.

499           The number of GDD in the previous 14 days (GDDMC14j, Table 3) strongly influenced *D.*  
500 *suzukii* infestation rate. As temperature increases as a result of climate change, the increased thermal  
501 energy available offers *D. suzukii* the opportunity to start utilizing mistletoe fruit earlier in the year. This  
502 resource diversion benefiting *D. suzukii* is likely to impact fruit availability for other frugivores and  
503 could have cascading consequences on the trophic network equilibrium in the ecosystem (Roche et al.  
504 2023). Decaying fruit could be unattractive to some bird species (Manzur and Courtney 1984; Poyet et  
505 al. 2014) and/or become attractive to others (Greenleaf et al. 2023). Premature fruit abscission because  
506 of *D. suzukii*-induced fruit decay may also reduce ornithochoric seed dispersal (Bühlmann and Gossner  
507 2022) and, thus, the colonization capacity of mistletoe. Further behavioral studies are required to

508 experimentally test the attractiveness of infested *versus* uninfested fruit and their visual attractiveness  
509 and palatability for the birds that disperse their seeds.

#### 510 *Considerations about pest management strategies*

511 The data obtained in this study suggest that the use of mistletoe fruit by *D. suzukii* could catalyze  
512 an increase in fly populations available to infest early maturing cultivated fruit in spring. Developing  
513 integrated pest management strategies is essential (Tait et al. 2021) and the consideration of winter  
514 processes in these will become increasingly important. Better understanding of *D. suzukii* overwintering  
515 strategies is required in order to identify potential avenues for the development of pest management  
516 strategies applicable in winter (Panel et al. 2018). *Viscum album* fruit being an important trophic  
517 resource not only for *D. suzukii* but also for birds and mammals, it is not viable or acceptable to eradicate  
518 mistletoe generally. However, removal could be considered from trees adjacent to certain fruit crop  
519 production areas (e.g., cherry, strawberry, raspberry, etc), which could help reduce or delay the initial  
520 crop infestation. Notably, *V. album* host tree species influenced the fruit infestation rate: mistletoe on  
521 poplars were most heavily infested compared to those on hawthorn, apple or black locust which were  
522 eight, two and 0.33 times less infested, respectively. Pest management strategies should initially focus  
523 on the most heavily infested host plant species.

524 Further research is now required to better understand differences in *D. suzukii* infestation  
525 between the various mistletoe host tree species. They could be a result of the variability in biologically  
526 active phenolic compounds in mistletoe berries depending on the host tree species (Pietrzak et al. 2017).  
527 For example, mistletoe growing on *Populus nigra* trees are particularly rich in phenolic acids (Pietrzak  
528 et al. 2017). Such compounds may act as repellents or attractants for insects (Pratyusha 2022), including  
529 *D. suzukii* (Hussain et al. 2023). Further research could improve monitoring and behavior-based  
530 management tools. More generally, commercial fruit cultivation should be revisited from the lens of  
531 landscape structure, for instance by integrating the configurations that are least favorable for winter  
532 population growth of this invasive pest insect.

533

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538

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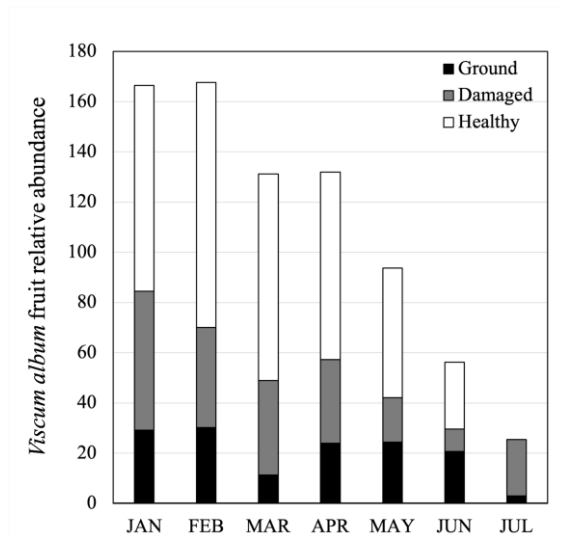
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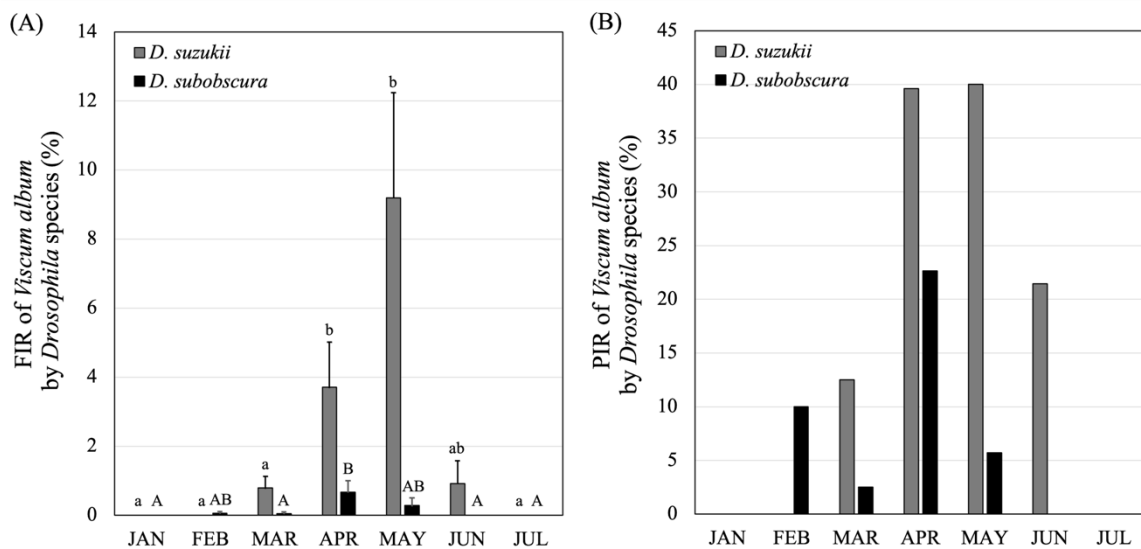
## 738 Tables and Figures



739

740 **Figure 1** Variation in *Viscum album* fruit relative abundance (number of collected fruit divided by the  
 741 number of plants sampled) between January and July 2022, in relation to their position and status: on  
 742 the ground (Ground), on the tree damaged (Damaged) or healthy (Healthy).

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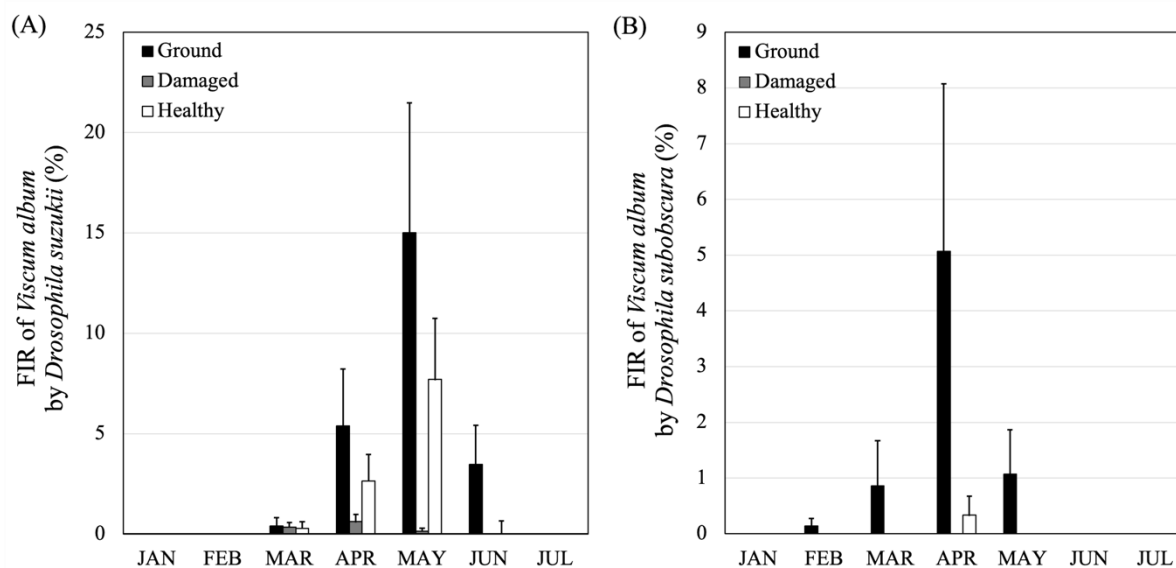


744

745 **Figure 2** Variation in FIR (A) and PIR (B) of *Viscum album* by *Drosophila suzukii* and *D. subobscura*  
 746 between January and July 2022. Fruit Infestation Rate:  $FIR = 100 \times \text{number of emerged } Drosophila \text{ sp.}$   
 747 from all fruit collected from a *Viscum album* individual / number of fruit collected from the same *V.*

748 *album* individual. Plant Infestation Rate:  $PIR = 100 \times$  number of infested *V. album* individuals in a  
 749 month / number of sampled *V. album* individuals in the same month. Significance of differences between  
 750 months are represented by different lowercase and capital letters for *D. suzukii* and *D. subobscura*  
 751 respectively.

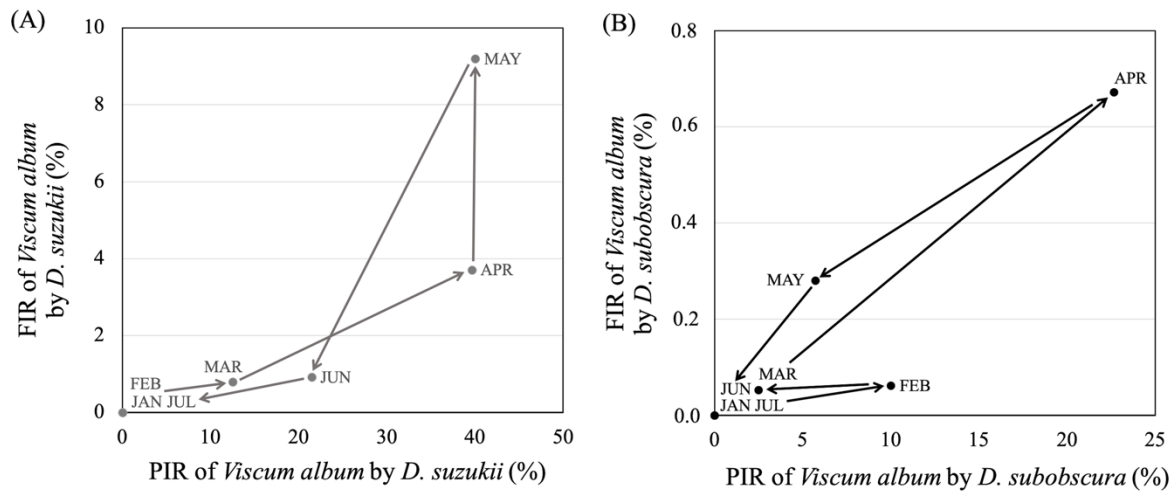
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753

754 **Figure 3** Variation in FIR of *Viscum album* by *Drosophila suzukii* (A) and *D. subobscura* (B) between  
 755 January and July 2022, in relation to their position and status: on the ground (Ground), on the tree  
 756 damaged (Damaged) or healthy (Healthy). Fruit Infestation Rate:  $FIR = 100 \times$  number of emerged  
 757 *Drosophila* sp. from all fruit collected from a *Viscum album* individual / number of fruit collected from  
 758 the same *Viscum album* individual, as described in Figure 2.





759

760 **Figure 4.** Mean fruit infestation rate (FIR) in relation to plant infestation rate (PIR) of *Viscum album*761 according to months between January and July 2022 for (A) *Drosophila suzukii* and (B) *D. subobscura*.

762 Interpretation: high FIR + high PIR = dispersion + auto-contamination; high FIR + low PIR = auto-

763 contamination; low FIR + high PIR = dispersion; low FIR + low PIR = low auto-contamination /

764 dispersal. Dispersal and auto-contamination are maximized in May for *D. suzukii* and in April for *D.*765 *subobscura*.

766 **Table 1** Main features of the studied regions from north to south of France. Latitude and longitude are  
 767 the mean values of geographic coordinates (WGS84 projection system) of the sampling locations in  
 768 each region. Mean daily T°C and rainfall (mm): mean daily temperatures and cumulative rainfall  
 769 calculated with daily data from meteorological stations in 2022.

<b>Region (main city)</b>	<b>Latitude (north)</b>	<b>Longitude (east)</b>	<b>Mean daily T°C</b>	<b>Rainfall (mm)</b>	<b>Sampling period (year 2022)</b>
Amiens	49.843391	2.161312	12.8	154.8	26/01–19/07
Caen	49.098724	-0.167531	12.92	208.8	28/03–24/05
Rennes	48.168850	-1.743138	13.8	135.7	17/01–05/04
Tours	47.373393	0.818669	14.6	164.6	21/01–18/05
Clermont-Ferrand	45.814265	3.205791	13.2	225.8	14/03–19/03
Bordeaux	44.787455	-0.595867	16.8	113.1	21/01–14/06
Nice	43.786175	6.802034	17.53	128.2	23/02–23/03

770

771 **Table 2** Number of mistletoe individuals sampled in all studied regions between January and July 2022 with number of fruit sampled, total number of emerged  
 772 *Drosophila* species, mean  $\pm$  SE and maximum fruit infestation rate. Regions are listed from north to south of France. Fruit Infestation Rate: FIR =  $100 \times$  number  
 773 of emerged *Drosophila* sp. from all fruit collected from a *Viscum album* individual / number of fruit collected from the same *V. album* individual. Plant Infestation  
 774 Rate: PIR =  $100 \times$  number of infested *V. album* individuals in a month / number of sampled *V. album* individuals in the same month.

Region (main city)	No mistletoes	No fruit	<i>D. suzukii</i>				<i>D. subobscura</i>				<i>D. repleta</i>
			No emerged	Mean FIR $\pm$ SE (%)	Max FIR (%)	PIR (%)	No emerged	Mean FIR $\pm$ SE (%)	Max FIR (%)	PIR (%)	No emerged
Amiens	126	16723	341	2.15 $\pm$ 0.77	72.86	20.63	33	0.31 $\pm$ 0.15	16.67	7.94	1
Caen	19	1870	16	2.66 $\pm$ 2.63	50.00	10.53	0	0.00	0.00	0.00	0
Rennes	30	3211	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0
Tours	22	3526	43	1.11 $\pm$ 0.61	11.63	31.82	8	0.26 $\pm$ 0.23	4.96	9.09	0
Clermont-Ferrand	15	1550	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0
Bordeaux	46	5673	335	6.11 $\pm$ 1.83	53.00	39.13	12	0.19 $\pm$ 0.07	1.96	15.22	0
Nice	6	983	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0
<b>Total</b>	<b>264</b>	<b>33536</b>	<b>735</b>	<b>2.37 <math>\pm</math> 0.53</b>	<b>72.86</b>	<b>20.08</b>	<b>53</b>	<b>0.20 <math>\pm</math> 0.08</b>	<b>16.67</b>	<b>7.20</b>	<b>1</b>

775

776 **Table 3** Effect of environmental variables on *Viscum album* fruit infestation rate (FIR) by *Drosophila*  
 777 *suzukii* and *D. subobscura* analyzed using GLMMs. GROUTOT: % fruit collected on the ground,  
 778 HLENGH: Canopy width of the host tree (m), PATH: Path cover (in a 5 m radius), GARDEN20: Garden  
 779 cover (in a 20 m radius), FOREST20: Forest cover (in a 20 m radius), GDDMC14J: Growing Degree  
 780 Days (of the last 14 days), WATE20: Water cover (in a 20 m radius), HEDGE20: Hedgerow cover (in  
 781 a 20 m radius), PARK20: Urban park cover (in a 20 m radius)

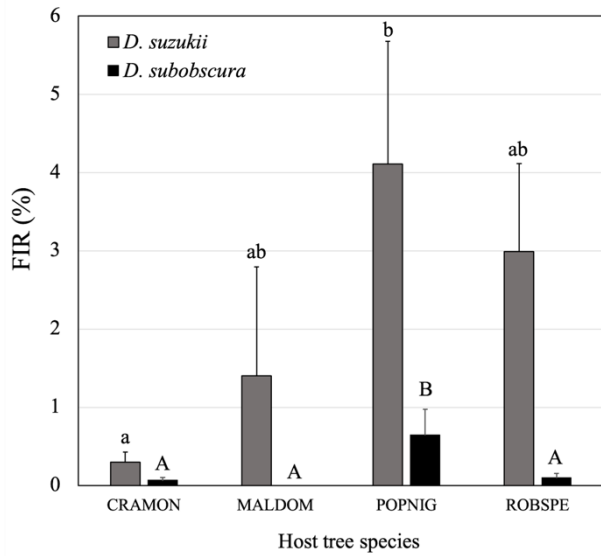
Dependent variables	Explanatory variables	Model parameters						
		F	Estimates	SE	d.f.	t	p	AICC
<i>Viscum album</i> fruit infestation rate by <i>Drosophila suzukii</i> (n=264 samples)	Model constant	18.895	-7.6485	1.7596	257.00	-4.347	<0.001	1848.96
	GROUTOT	14.684	0.0797	0.0208	257.00	3.832	<0.001	
	HLENGH	3.933	0.2230	0.1124	257.00	1.983	0.048	
	PATH	8.023	0.1402	0.0495	257.00	2.833	0.005	
	GARDEN20	15.847	0.1637	0.0411	257.00	3.981	<0.001	
	FOREST20	4.680	0.0887	0.0410	257.00	2.163	0.031	
	GDDMC14J	13.476	0.0402	0.0110	257.00	3.671	0.000	
<i>Viscum album</i> fruit infestation rate by <i>Drosophila subobscura</i> (n=264 samples)	Model constant	3.075	-0.1829	0.1043	259.00	-1.753	0.081	856.94
	GROUTOT	12.400	0.0101	0.0029	259.00	3.521	0.001	
	WATE20	17.729	0.1980	0.0470	259.00	4.211	<0.001	
	HEDGE20	6.514	0.0125	0.0049	259.00	2.552	0.011	
	PARK20	9.348	0.0092	0.0030	259.00	3.057	0.002	

782

783

784 **Supplementary Material**

785



786

787 **Figure S1** Mean fruit infestation rate (FIR)  $\pm$  SE (%) by *D. suzukii* and *D. subobscura* in *Viscum album*  
 788 individuals according to the major host tree species of *Viscum album*. CRAMON: *Crataegus monogyna*  
 789 ( $n = 66$  samples), MALDOM: *Malus domestica* ( $n = 36$ ), POPNIG: *Populus nigra* ( $n = 60$ ), ROBSPE:  
 790 *Robinia pseudoacacia* ( $n = 43$ ). Significance of differences between months are represented by different  
 791 lowercase and capital letters for *D. suzukii* (GLMM:  $F = 3.00$ ,  $p = 0.04$ ) and *D. subobscura* (GLMM:  $F$   
 792  $= 2.63$ ,  $p = 0.05$ ) respectively.

793 **Table S1** Host trees of *Viscum album* individuals sampled in the study and mean FIR  $\pm$  SE (%) by *D.*  
 794 *suzukii* (*Dsuz*) and *D. subobscura* (*Dsub*).

Species	Code	Number	%	<i>Dsuz</i> mean FIR $\pm$ SE (%)	<i>Dsub</i> mean FIR $\pm$ SE (%)
<i>Acer campestre</i>	ACECAM	13	4.9%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Acer opalus</i>	ACEOPA	3	1.1%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Acer saccharinum</i>	ACESAC	4	1.5%	9.64 $\pm$ 4.14	0.00 $\pm$ 0.00
<i>Acer</i> sp.	ACESP	7	2.7%	4.41 $\pm$ 4.10	0.28 $\pm$ 0.28
<i>Carpinus betulus</i>	CARBET	5	1.9%	12.28 $\pm$ 10.31	0.20 $\pm$ 0.20
<i>Corylus avellana</i>	CORAVE	1	0.4%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Crataegus monogyna</i>	CRAMON	66	25.0%	0.30 $\pm$ 0.13	0.07 $\pm$ 0.03
<i>Fraxinus</i> sp.	FRASP	4	1.5%	0.97 $\pm$ 0.97	0.33 $\pm$ 0.33
<i>Malus domestica</i>	MALDOM	36	13.6%	1.40 $\pm$ 1.39	0.00 $\pm$ 0.00
<i>Populus alba</i>	POPALB	3	1.1%	0.00 $\pm$ 0.00	0.29 $\pm$ 0.29
<i>Populus nigra</i>	POPNEG	60	22.7%	4.11 $\pm$ 1.57	0.65 $\pm$ 0.32
<i>Populus</i> $\times$ <i>canadensis</i>	POPCAN	1	0.4%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Prunus avium</i>	PRUAVI	1	0.4%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Prunus</i> sp.	PRUNUS	3	1.1%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Pyrus communis</i>	PYRCOM	1	0.4%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Quercus ilex</i>	QUEILE	3	1.1%	14.67 $\pm$ 14.67	0.00 $\pm$ 0.00
<i>Quercus pubescens</i>	QUEPUB	2	0.8%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Quercus rubra</i>	QUERUB	1	0.4%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Quercus</i> sp.	QUERCU	1	0.4%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Robinia pseudoacacia</i>	ROBSPE	43	16.3%	2.99 $\pm$ 1.12	0.10 $\pm$ 0.05
<i>Tilia platyphyllos</i>	TILPLA	2	0.8%	0.64 $\pm$ 0.23	0.00 $\pm$ 0.00
<i>Tilia</i> sp.	TILSP	4	1.5%	0.34 $\pm$ 0.34	0.00 $\pm$ 0.00
<b>TOTAL</b>		264	100%	2.37 $\pm$ 0.53	0.20 $\pm$ 0.08

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796 **Table S2** List of the variables assessed in the study. Abbreviations: s: measure from weather station, 7J  
797 and 14J: measures collected from the 7 and 14 days prior to sample collection.

CATEGORY	CODE	DESCRIPTION	UNIT
<b>DROSOPHILIDAE SPECIES</b>			
<b>INFESTATION INDICES</b>	FIR	Fruit Infestation Rate = $100 \times$ number of emerged <i>Drosophila</i> individuals from fruit collected from a <i>Viscum album</i> individual / total number of fruit collected from the same <i>Viscum album</i> individual	%
	PIR	Plant Infestation Rate = $100 \times$ number of infested <i>Viscum album</i> individuals in a region or month / total number of <i>Viscum album</i> individuals sampled in the same region or month	%
<b>MISTLETOE FRUIT CATEGORIES</b>			
<b>NUMBER</b>	HEAFRUIT	Number of healthy fruit collected on a <i>Viscum album</i> individual	Number
	DAMFRUIT	Number of damaged fruit (rotten or with open skin) collected on a <i>Viscum album</i> individual	Number
	PLAFRUIT	Sum of healthy and damaged fruit collected on a <i>Viscum album</i> individual	Number
	GROFRUIT	Number of fruit collected on the ground below a <i>Viscum album</i> individual	Number
	TOTFRUIT	Sum of <i>Viscum album</i> fruit collected on the plant and on the ground	Number
<b>PERCENTAGE</b>	%HEALPLA	$100 \times$ HEAFRUIT / PLAFRUIT	%
	%DAMAPLA	$100 \times$ DAMFRUIT / PLAFRUIT	%
	%HEALTOT	$100 \times$ HEAFRUIT / TOTFRUIT	%
	%DAMATOT	$100 \times$ DAMFRUIT / TOTFRUIT	%
	%FPLANT	$100 \times$ PLAFRUIT / TOTFRUIT	%
	%GROUTOT	$100 \times$ GROFRUIT / TOTFRUIT	%
<b>LIFE TRAITS OF MISTLETOE INDIVIDUALS</b>			
<b>FRUIT TRAITS</b>	MFWIDTH	Mean fruit width (n = 5 fruit)	cm
	MFVOL	Mean fruit volume (n = 5 fruit)	cm <sup>3</sup>
	MFSURF	Mean fruit skin area (n = 5 fruit)	cm <sup>2</sup>
<b>LEAVE TRAITS</b>	MLENGTH	Mean leaf length (from the base of the petiole to the top/apex of the blade; n = 5 leaves)	cm
	MLWIDTH	Mean leaf width (n = 5 leaves)	cm
	MLSURF	Mean leaf area (area = length $\times$ width; n = 5 leaves)	cm <sup>2</sup>
<b>INDIVIDUAL MORPHOLGY</b>	LENGTH	Maximum diameter of <i>Viscum album</i> individual	m
	WIDTH	Minimum diameter of <i>Viscum album</i> individual	m
	INDFRUIT	Total number of fruit present on a sampled <i>Viscum album</i> individual	Number
	HEIGHT	Height of <i>Viscum album</i> individual from the ground	m
<b>MISTLETOE HOST TREE</b>			

<b>MISTLETOE HOST TREE</b>	HOSTSPE	<i>Viscum album</i> host species	Species	
	HHEIGHT	Height of the host tree	m	
	HLENGH	Maximum diameter of the host tree canopy	m	
	HWIDTH	Minimum diameter of the host tree canopy	m	
	HTRUNK	Circumference of the host tree trunk	cm	
	HMISTLETOE	Number of <i>Viscum album</i> individuals on the host tree	Number	
	HMISTLETOE20	Number of <i>Viscum album</i> individuals in a 20 m radius around the host tree	Number	
	SUMHMIST20	Sum of <i>Viscum album</i> individuals on the host tree and in a 20 m radius around the host tree	Number	
<b>SITE AND LANDSCAPE CHARACTERISTICS</b>				
<b>LOCAL ENVIRONMENT (in a 5 m radius around the mistletoe host tree)</b>	ALTM	Site altitude	m	
	SLOM	Site slope	Degree	
	CTREE	Cover of tree layer (height > 8 m)	%	
	CSHRUB	Cover of shrub layer (1-8 m)	%	
	CHERB	Cover of herb layer (< 1 m)	%	
	HHERBMEAN	Height of herbaceous layer	cm	
	HLIGN	Height of woody species (shrubs, trees and lianas)	m	
	COMP	Cover of biowaste composter	%	
	SOIL	Cover of bare soil	%	
	DWOOD	Cover of dead wood debris on the ground	%	
	TLITTER	Depth of leaf litter	cm	
	LITTER	Cover of leaf litter	%	
	RIVER	Cover of stream	%	
	POND	Cover of pond	%	
	PATH	Cover of (unpaved) pathway	%	
	ROAD	Cover of road and paved surface	%	
	BUILD	Cover of building	%	
	<b>LOCAL HABITATS (in a 20 m radius around the mistletoe host tree)</b>	ORC20	Cover of orchard area (fruit trees and their associated grassland)	%
		FOREST20	Cover of woodland	%
		PASTURE20	Cover of grazed grassland	%
MOW20		Cover of mown grassland	%	
GRASS20		Cover of grassland (PASTURE20+MOW20)	%	
SWAMP20		Cover of swamp	%	
CROP20		Cover of conventional agriculture crop	%	
VEGGAR20		Cover of market garden	%	
GARDEN20		Cover of private garden	%	
SHRUB		Cover of shrub	%	
BUILD20	Cover of building	%		



	HEDGE20	Cover of hedgerow	%
	RIVER20	Cover of river	%
	POND20	Cover of pond	%
	POPLARP20	Cover of poplar plantation	%
	GREESP20	Cover of urban green space (small urban planted herbaceous or shrub strips)	%
	PARK20	Cover of park	%
	GGSP20	Total urban vegetated area (sum of garden, green space and park cover)	%
	RP_FC	Fleshy-fruited plant species richness	Number
<b>LANDSCAPE COMPOSITION</b> (from OSO 2022 data basis; cover percentages calculated within the following radii around the mistletoe host tree: 50 m, 100 m, 250 m, 500 m, 750 m, 1000 m, 1250 m, 1500 m, 1750 m, 2000 m, 2500 m and 3000 m)	CROP%	Cover of conventional agriculture crop	%
	WATE%	Cover of river and other water surface	%
	FORE%	Cover of woodland	%
	HETH%	Cover of heathland	%
	MOW%	Cover of grassland	%
	ROAD%	Cover of road and paved surface	%
	URB%	Cover of urban area	%
	ORC%	Cover of orchard area (fruit trees and their associated grassland)	%
	INDU%	Cover of industrial zone	%
	<b>METEOROLOGY</b>		
<b>TEMPERATURE AND PRECIPITATION VARIABLES</b> (from weather stations data; meanings of suffixes added to variable names: 7J = data from the 7 days preceding fruit sampling, 14J = data from the 14 days preceding fruit sampling)	GDDMC	Sum of daily positive temperature (Growing Degree Days) calculated from the mean temperatures of the 7 or 14 days before fruit sampling	°C
	NFD	Number of days with negative temperatures ( $\leq 0$ °C) during the 7 or 14 days before fruit sampling	Number
	RAIN	Sum of daily precipitation in the 7 or 14 days before the fruit sampling	cm
	SNOW	Sum of daily snowfall in the 7 or 14 days before the fruit sampling	cm
	MMIN	Mean minimum temperature during the 7 and 14 days before fruit sampling	°C
	MMAX	Mean maximum temperature during the 7 days before fruit sampling	°C
	MMEANCALC	Calculated mean of daily mean temperatures of the 7 or 14 days before the fruit sampling	°C
	MINMIN	Lowest minimum temperature during the 7 or 14 days before fruit sampling	°C
	MAXMAX	Highest maximum temperature during the 7 or 14 days before fruit sampling	°C
	SUMT_010122	Sum of daily positive temperature (Growing Degree Days) between 01/01/2022 and the sampling date	°C
	RAIN_010122	Sum of rain precipitation between 01/01/2022 and the sampling date	cm

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800 **Table S3** Weather station information. Geographic area: city of the research laboratory, station city:  
 801 postcode and the municipality name of the weather station location, Station coordinates: geographic  
 802 location of the city where the weather station is located, Label city: postcode and municipality name  
 803 according to Historique-Météo.net, Label city coordinates: geographic location of the label city, Mean  
 804 distance: mean distance between the weather station and sampled locations (in kilometers). Geographic  
 805 coordinate system: WGS 84.

806

Geographic area	Station city	Station city coordinates	Label city	Label city coordinates	Mean distance (m)
Amiens	80260_Flesselles	50.0 N, 2.25 E	80600_Doullens	50.15724 N, 2.34019 E	16,288
	80160_Essertaux	49.75 N, 2.25 E	80000_Amiens	49.894067 N, 2.295753 E	17,516
	80890_Condé-Folie	50.017 N, 2.017 E	80420_Flixecourt	50.01465 N, 2.08095 E	22,404
	80300_Albert	50.0 N, 2.65 E	80300_Albert	50.00091 N, 2.65096 E	28,868
	80140_Doudelainville	50.0 N, 1.767 E	80100_Abbeville	50.105467 N, 1.836833 E	30,264
	60130_Angivillers	49.5 N, 2.5 E	80500_Montdidier	49.65 N, 2.56667 E	29,046
Bordeaux	33400_Talence	44.817 N, -0.6 O	33400_Talence	44.802614 N, -0.588054 O	3,520
	33360_Quinsac	44.75 N, -0.5 O	33000_Bordeaux	44.837789 N, -0.57918 O	8,853
	33440_Ambarès-et-Lagrave	44.983 N, -0.517 O	33390_Blaye	45.13333 N, -0.66667 O	22,444
Caen	14000_Caen	49.183 N, -0.35 O	14000_Caen	49.182863 N, -0.370679 O	11,027
	14170_Saint-Pierre-en-Auge	49.0 N, 0.0 E	14170_Saint-Pierre-en-Auge	49.02022 N, -0.0316086 O	4,852
	14860_Amfreville	49.25 N, -0.248 O	14150_Ouistreham	49.276656 N, -0.258658 O	15,936
	14430_Danestal	49.25 N, 0.017 E	14950_Beaumont-en-Auge	49.278363 N, 0.111144 E	27,512
	14400_Bayeux	49.277 N, -0.704 O	14400_Bayeux	49.276437 N, -0.70314 O	22,532
	27270_Saint-Aubin-du-Thenney	49.017 N, 0.5E	27300_Bernay	49.08888 N, 0.59858 E	30,614
Clermont-Ferrand	03000_Moulins	46.567 N, 3.333 E	03000_Moulins	46.568059 N, 3.334417 E	12,255
	63410_Charbonnières-les-Vieilles	46.0 N, 3.0 E	03800_Gannat	46.10015 N, 3.19886 E	31,664
	03500_Louchy-Montfand	46.317 N, 3.25 E	03500_Saint-Pourçain-sur-Sioule	46.30927 N, 3.28787 E	26,725
	03320_Le Veudre	46.75 N, 3.0 E	58000_Nevers	46.990896 N, 3.162845 E	25,782
	63122_Saint-Gènes-Champanelle	45.75 N, 3.017 E	63000_Clermont-Ferrand	45.777222 N, 3.087025 E	18,178
	63120_Courpière	45.75 N, 3.55 E	63120_Courpière	45.75689 N, 3.54216 E	18,261
	63740_Gelles	45.767 N, 2.75 E	63230_Saint-Ours	45.817793 N, 2.947995 E	18,059
63320_Courgoul	45.517 N, 3.033 E	63450_Saint-Saturin	45.660653 N, 3.090363 E	22,473	

Journal: Arthropod-Plant Interactions

	63500_Le Broc	45.5 N, 3.25 E	63500_Issoire	45.54151 N, 3.248128 E	25,697
Nice	04120_Castellane	43.85 N, 6.517 E	04120_Castellane	43.85 N, 6.51667 E	5,755
	04120_Gorges-du-Verdon	43.7613593 N, 6.3788372 E	04120_La-Palud-sur-Verdon	43.783000 N, 6.333000 E	20,377
	04000_Digne-les-Bains	44.1 N, 6.233 E	04000_Digne-les-Bains	44.09252 N, 6.23199 E	35,130
	06130_Grasse	43.667 N, 6.917 E	06130_Grasse	43.66667 N, 6.91667 E	34,072
	06140_Vence	43.717 N, 7.117 E	06140_Vence	43.72254 N, 7.11183 E	16,624
	06250_Mougins	43.6 N, 7.0 E	06250_Mougins	43.6023319 N, 7.006491 E	18,610
	06700_Saint-Laurent-du-Var	43.667 N, 7.183 E	06700_Saint-Laurent-du-Var	43.67097 N, 7.17606 E	13,915
Rennes	35360_Landujan	48.25 N, -2.0 O	22100_Lanvallay	48.450000 N, -2.033330 O	20,409
	35520_Montreuil-le-Gast	48.25 N, -1.717 O	35630_Hédé-Bazouges	48.3 N, -1.8 O	11,064
	35340_Ercé-près-Liffré	48.25 N, -1.5 O	35270_Combourg	48.41267 N, -1.74424 O	20,780
	35150_Amanlis	48.0N, -1.483 O	35000_Rennes	48.117266 N, -1.6777926 O	18,869
Tours	37190_Azay-le-Rideau	47.267 N, 0.467 E	37190_Azay-le-Rideau	47.26177 N, 0.46574 E	20,161
	37400_Amboise	47.417 N, 0.983 E	37400_Amboise	47.413326 N, 0.984407 E	13,491
	37190_Cheillé	47.25 N, 0.483 E	37000_Tours	47.394144 N, 0.68484 E	24,074
	37310_Sublaines	47.25 N, 1.0 E	37150_Château de Chenonceau	47.3248696 N, 1.0703005 E	17,622
	37600_Loches	47.133 N, 1.0 E	37600_Loches	47.128158 N, 0.997664 E	27,232
	41120_Candé-sur-Beuvron	47.5 N, 1.25 E	41000_Blois	47.5860921 N, 1.3359475 E	25,144

807