



**HAL**  
open science

## Winter fleshy-fruited plants are the catalysts for spring populations of an invasive fruit fly

Gwenaëlle Deconninck, Méghan Boulembert, Patrice Eslin, Aude Couty, Françoise Dubois, Emilie Gallet-moron, Sylvain Pincebourde, Olivier Chabrerie

### ► To cite this version:

Gwenaëlle Deconninck, Méghan Boulembert, Patrice Eslin, Aude Couty, Françoise Dubois, et al.. Winter fleshy-fruited plants are the catalysts for spring populations of an invasive fruit fly. *Ecological Entomology*, 2024, 10.1111/een.13397 . hal-04775930

**HAL Id: hal-04775930**

**<https://u-picardie.hal.science/hal-04775930v1>**

Submitted on 10 Nov 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

1       **Winter fleshy-fruited plants are the catalysts for spring populations of an invasive fruit fly**

2

3       Gwenaëlle Deconninck<sup>1</sup>, Méghan Boulembert<sup>2</sup>, Patrice Eslin<sup>2</sup>, Aude Couty<sup>2</sup>, Françoise Dubois<sup>2</sup>, Emilie  
4       Gallet-Moron<sup>2</sup>, Sylvain Pincebourde<sup>1</sup>, Olivier Chabrerie<sup>2</sup>

5

6       <sup>1</sup>Institut de Recherche sur la Biologie de l’Insecte, IRBI UMR7261, CNRS - Université de Tours, Tours,  
7       France

8       <sup>2</sup>EDYSAN, Ecologie et Dynamique des Systèmes Anthropisés, UMR 7058 CNRS, Université de  
9       Picardie Jules Verne, Amiens, France

10

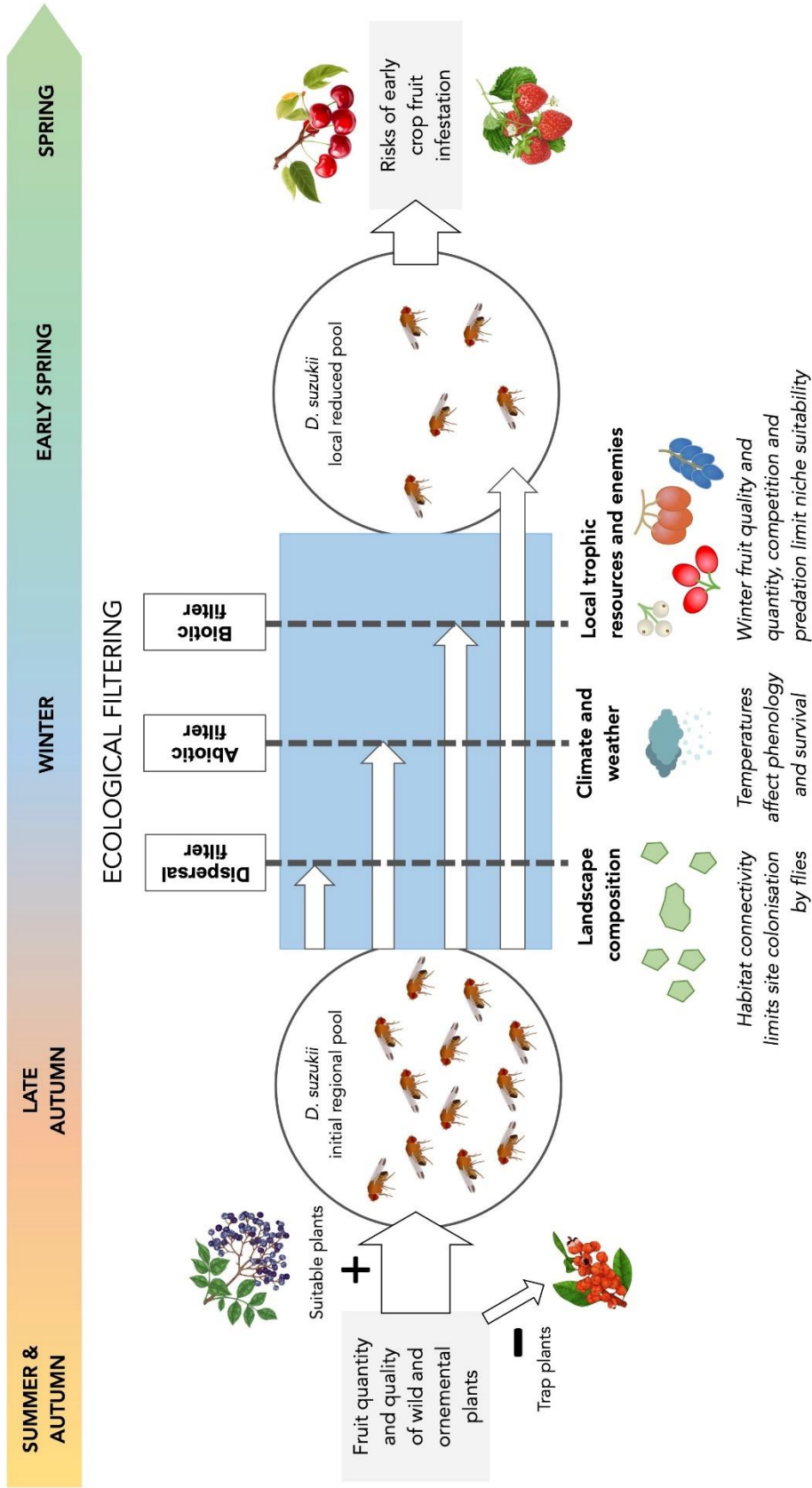
11       \*: Corresponding author: [olivier.chabrerie@u-picardie.fr](mailto:olivier.chabrerie@u-picardie.fr)

12

13       How to cite this article: Deconninck, G., Boulembert, M., Eslin, P., Couty, A., Dubois, F., Gallet-Moron,  
14       E. et al. (2024) Winter fleshy-fruited plants are the catalysts for spring populations of an invasive fruit  
15       fly. *Ecological Entomology*, 1–16. Available from: <https://doi.org/10.1111/een.13397>

16

17



21 Authors' ORCID:

- 22 ● Gwenaëlle Deconninck: 0000-0003-2002-0992
- 23 ● Méghan Boulembert: 0009-0005-8932-1373
- 24 ● Patrice Eslin: 0000-0002-1300-5092
- 25 ● Aude Couty: 0000-0002-6734-0400
- 26 ● Françoise Dubois: 0000-0002-2651-1795
- 27 ● Emilie Gallet-Moron: 0000-0003-1579-5013
- 28 ● Sylvain Pincebourde: 0000-0001-7964-5861
- 29 ● Olivier Chabrerie: 0000-0002-8949-1859

30

31 **Data availability:** The datasets generated during and/or analysed during the current study are available  
32 from the Dryad repository using the doi:10.5061/dryad.9p8cz8ws7

33

34 **Funding statement:** This work was supported by the ANR (Agence Nationale de la Recherche  
35 française) in the context of the project ANR DROTHERMAL (Grant Number: ANR-20-CE02-0011-  
36 01).

37

38 **Ethics approval and Conflict of interest statements:** The authors declare that the manuscript is not  
39 submitted or published elsewhere and confirm that all the research meets the ethical guidelines. The  
40 authors have no relevant financial or non-financial interests to disclose.

41

42 **Author contribution statement:** **Gwenaëlle Deconninck:** Writing – original draft preparation, Data  
43 curation, Formal analysis; **Méghan Boulembert:** Writing & editing, Sampling, Investigation, Data  
44 curation; **Patrice Eslin:** Writing – review & editing; Supervision; **Aude Couty:** Writing – review &  
45 editing; **Françoise Dubois:** Writing – review & editing, Sampling; **Emilie Gallet-Moron:** Writing –  
46 review & editing, Data curation, Formal analysis; **Sylvain Pincebourde:** Writing – review & editing,  
47 Supervision, Funding acquisition; Project administration; **Olivier Chabrerie:** Writing – original draft  
48 preparation, Validation, Supervision, Methodology, Sampling, Data curation, Formal analysis,  
49 Conceptualization, Funding acquisition; Project administration. All authors read and approved the final  
50 manuscript.

51

52

53 **Running title**

54 *Winter fruit infested by Drosophila suzukii*

55

56 **Abstract (247 words)**

- 57 1. Winter is a critical bottleneck period for many insects and is particularly pivotal for pest species,  
58 being a major regulator of their populations. In winter, insect fruit pests such as the invasive fly,  
59 *Drosophila suzukii*, not only have to cope with harsh environmental conditions but also need to  
60 find alternative resources when cultivated fruit are scarce.
- 61 2. This study aimed to disentangle the relative roles of climatic, landscape and local factors  
62 affecting fruit infestation rates of winter and spring host plants by *D. suzukii*. We assessed  
63 infestation in *Aucuba japonica*, *Elaeagnus ×submacrophylla* (syn. *Elaeagnus ×ebbingei*),  
64 *Mahonia aquifolium*, *M. japonica* and *Viscum album* fruit in the north of France, between  
65 January and July 2022.
- 66 3. *Drosophila suzukii* emerged from fruit of all plant species except *M. aquifolium*. The fly was  
67 the only species that emerged from fruit of *A. japonica*, *E. ×submacrophylla* and *M. japonica*,  
68 but co-occurred in *V. album* fruit with *D. subobscura*.
- 69 4. Climatic factors (e.g., cumulative precipitation, the number of frost hours), landscape  
70 composition (e.g., grassland, shrubland and water cover) and local variables (e.g., resource  
71 abundance, vegetation architecture) influenced *D. suzukii* infestation, with effects varying  
72 between host plants.
- 73 5. The fruiting succession of these five plants effectively provides a resource continuum from  
74 March to June, in which *E. ×submacrophylla*, in particular, plays a pivotal role before  
75 commercial fruit become available (e.g., strawberries, cherries). Non-crop plants should be  
76 considered in integrative pest management strategies as they could catalyse *D. suzukii*  
77 populations early in the season.

78

79 **Keywords**

80 *Drosophila suzukii*, *Drosophila subobscura*, environmental filtering, fruit infestation rate, insect  
81 invasion, non-crop plants, ornamental species.

82

83

## 84 Introduction

85 Winter is a critical bottleneck period for most temperate insects (Danks 1978; Moore and Lee  
86 1991). Driven by the harsh environmental conditions, many species overwinter by entering diapause  
87 (Bale and Hayward 2010; Gill et al. 2017; Lehmann et al. 2017), during which development is slow or  
88 suspended, do not feed or reproduce and rely on reserves accumulated in the pre-diapause phase to  
89 survive (Storey and Storey 2012; Sinclair 2015; Gill et al. 2017). Other species, however, continue to  
90 be active throughout winter (Danks 1978; Moore and Lee 1991; Wharton 2011). These species must  
91 find resources in order to survive and sometimes to complete their development. For species relying on  
92 seasonal fruit, this can be a challenge, as they will likely need to be polyphagous, switching between  
93 different resources over time (Kennedy and Storer 2000; Butterworth et al. 2023). Winter is also critical  
94 for insect pest species, as it plays a role in population regulation (Kennedy and Storer 2000; Gajski et  
95 al. 2023; Cuff et al. 2024). Insect fruit pests that are able to survive the harsh environmental conditions  
96 of winter, avoid predation and find alternative resources when cultivated fruit are scarce, are likely to  
97 gain an advantage at the beginning of the growth season. In this study we examine some elements of  
98 this hypothesis in the widespread pest species, *Drosophila suzukii* (Matsumura, 1931).

99 *Drosophila suzukii* is an invasive fruit fly and a pest worldwide (Asplen et al. 2015). Originating  
100 in Asia, it was first reported in Europe in 2008, followed by very rapid range expansion (Walsh et al.  
101 2011; Cini et al. 2012; Asplen et al. 2015). While winter is undeniably challenging for its survival  
102 (Hamby et al. 2016; Stockton et al. 2019; Ulmer et al. 2024), *D. suzukii* shows remarkable behavioural  
103 and physiological adaptations (Tait et al. 2021). With the onset of winter, it is able to switch from  
104 cultivated fruit to the late maturing fruit of wild plants (Poyet et al. 2015; Lee et al. 2015; Kenis et al.  
105 2016; Ulmer et al. 2022), including non-native plants (Poyet et al. 2014), at the same time changing its  
106 distribution in the landscape, finding sheltered microhabitats in woodland and hedgerows (Rossi-  
107 Stacconi et al. 2016; Tait et al. 2021; Ulmer et al. 2024). The adult fly's circadian rhythm changes, with  
108 maximum activity at mid-day, when temperatures are generally warmest, thereby reducing the risk of  
109 exposure to extreme cold (Shaw et al. 2019). Winter temperatures and short photoperiod also induce a  
110 winter morphotype which shows increased cold tolerance (Panel et al. 2020). Nevertheless, finding  
111 suitable host plants on which to feed and reproduce during winter remains a major challenge for *D.*  
112 *suzukii* (Stockton et al. 2019).

113 In natural habitats, wild fruit provide food and allow the persistence of seed populations of *D.*  
114 *suzukii* between winter and late spring, enabling the establishment of new generations (Poyet et al. 2015;  
115 Panel et al. 2018), before cultivated fruit become available as hosts. Nutrition is a critical driver of cold  
116 tolerance in *Drosophila* species (Henry et al. 2020; Jiménez-Padilla et al. 2020). Protein-rich diets can  
117 enhance the melanization response (Lee et al. 2008) which would help the reparation process and protect  
118 tissues after cold exposure (Sinclair et al. 2013). Specific amino-acids such as proline and arginine are  
119 also known to have a cryoprotective effect in *D. melanogaster* (Košťál et al. 2012, 2016). Finally, sugar-

120 rich diets can improve resistance to starvation, by increasing the lipid content of the fly (Ballard et al.  
121 2008), thus enabling flies to survive longer when resources are scarce (Henry et al. 2020). Consequently,  
122 availability of winter fruit resources may be an important determinant of *D. suzukii* persistence in winter.  
123 However, not only do few plant species bear fruit in winter and early spring, but only part of them are  
124 known to be susceptible to *D. suzukii* infestation. In Europe, these include *Aucuba japonica*, *Elaeagnus*  
125 *×submacrophylla*, *Hedera helix*, *Lonicera nitida*, *Mahonia* spp., *Rosa canina*, *Skimmia japonica*,  
126 *Symphoricarpos* spp. and *Viscum album* (Grassi et al. 2018; Panel et al. 2018; Poyet et al. 2015; Kenis  
127 et al. 2016). The phenology of these plants, however, varies tremendously.

128 Among these winter plants susceptible to *D. suzukii*, *Aucuba japonica*, *E. ×submacrophylla*,  
129 *Mahonia* spp. and *V. album* fruit are among the most heavily infested in laboratory experiments and  
130 allow both larval development and a higher rate of adult emergence than from any other plant (Poyet et  
131 al. 2015). *Aucuba japonica* (Thunb.), *Mahonia japonica* (Thunb.) DC. and *E. ×submacrophylla*  
132 (Servett) (syn. *E. ×ebbingei* (J.Door)) are native to Asia while *M. aquifolium* (Thunb.) is native to North  
133 America (Prior 1881; Bayton 2017; Edwards 2017). All are introduced ornamental shrubs that have long  
134 been planted in urban parks, partly because of their resistance to harsh environmental conditions (e.g.,  
135 pollution, wind exposure; Prior 1881; Coklar and Akbulut 2017; Edwards 2017; Abdalla 2019; Blanuša  
136 et al. 2020; Quadir et al. 2021). *Viscum album* L., 1753 (mistletoe) is an obligate hemiparasitic shrub  
137 native to Europe that grows on a wide range of angiosperm and gymnosperm trees (Barney et al. 1998;  
138 Zuber 2004; Thomas et al. 2023). All these plants can be found from winter to spring, with overlapping  
139 periods of fruiting (Terabayashi 1978; Abe 2001; Francis 2004; Edwards 2017; Thomas et al. 2023).

140 Most of these fruit contain compounds that are toxic to insects (e.g., aucubin; Rombouts and  
141 Links 1956), but *D. suzukii* seems to be able to overcome at least some of these plant species' defences.  
142 Poyet et al. (2015) confirmed that *D. suzukii* can develop on several toxic plants and that it even uses  
143 toxic compounds to perform medication when in the presence of parasitoids (Poyet et al. 2017).  
144 Knowledge of the detoxification processes involved is lacking and research on which compounds *D.*  
145 *suzukii* is able to overcome could help improve pest management strategies. Although chemical (Asplen  
146 et al. 2015; Dam et al. 2019; Tait et al. 2021) and biological (Iacovone et al. 2015; Ulmer et al. 2020,  
147 2021) control strategies have been and are still widely explored, knowledge relating to the phenology  
148 and ecology of *D. suzukii* species in natural systems is limited and is required to better predict and  
149 possibly control the risks of early infestation in cultivated crops. In particular, the species' population  
150 dynamics at the end of winter, several months before the fruiting period of most commercially cultivated  
151 plants, are largely unknown.

152 This study aimed to disentangle the relative roles of climatic, landscape and local factors that  
153 could affect infestation rates of winter host plants by *D. suzukii*. We focused on *A. japonica*, *E.*  
154 *×submacrophylla*, *M. aquifolium*, *M. japonica* agg. and *V. album* because they are known to be  
155 susceptible to *D. suzukii* and are representatives of the very limited group of plant species bearing fruit  
156 in winter and early spring. We hypothesised that (i) *D. suzukii* infestation rates would differ between

157 plant species as they produce different types of fruit varying in quantity, quality and phenology; (ii)  
158 other species could be facilitated by the presence of *D. suzukii* in these fruit, such as *D. subobscura*  
159 (Poyet et al. 2014; Deconninck et al. 2024a) or *D. melanogaster* (Rombaut et al. 2017); (iii) *D. suzukii*  
160 presence in wild fruit would be positively associated with the abundance of natural habitats such as  
161 woodland which are known to provide a winter refuge for *Drosophila* species (Basden 1954), and  
162 specifically for *D. suzukii* (Ulmer et al. 2024); (iv) environmental factors controlling fruit infestation  
163 may vary between plant species differing in their ecology and fruiting phenology; and (v) these non-  
164 crop host plants could support overwintering seed populations of *D. suzukii*, catalysing the development  
165 of new generations in early spring in advance of the availability of the first commercial fruit crops such  
166 as cherries, strawberries or raspberries. To test these hypotheses, we measured fruit infestation rates in  
167 these four plant species in northern France from winter to summer. Each sample was accompanied by  
168 measurements of climatic and local and landscape variables in order to identify the environmental  
169 drivers of host fruit infestations.

170

## 171 **Materials and Methods**

### 172 *Study area*

173 The study was conducted between January and July 2022 in the region of Amiens (49°53'40"  
174 N, 2°18'07" E) in northern France. The region's climate is oceanic with a mean annual temperature of  
175 10.7°C and an average annual rainfall of 691.9 mm (data from meteorological station Dury-les-Amiens,  
176 StatIC network). The landscape of this region is generally characterised by agricultural production and  
177 consists of a mosaic of open fields cultivated for cereals, rapeseed and sugar beet, interspersed with  
178 orchards, grasslands, woodland patches and rivers.

### 179 *Sampling design*

180 *Aucuba japonica* var. *variegata*, *Elaeagnus* × *submacrophylla*, *Mahonia aquifolium*, *Mahonia*  
181 *japonica* agg. (including a complex of related cultivars and hybrids) and *V. album* fruit were sampled  
182 every month, with individual plants of each species randomly sampled within a landscape area of 35 ×  
183 45 km (Figure S1). The number of individuals sampled per species and per month varied depending on  
184 fruit availability (from 8 to 119 individuals, see Table 1 and results below). When possible, a minimum  
185 of 100 fruit were randomly sampled from each plant individual, with some variation depending on  
186 seasonal availability of fruit.

### 187 *Traits of host plant species and fruit*

188 Collected fruit were separated into three subsets to monitor *Drosophila* emergence: undamaged  
189 ('healthy') and damaged fruit collected on the plant ('damaged') and on the ground ('ground'; if  
190 present). The fruit were categorized as 'damaged' when they were opened / injured (incised skin) and/or



191 rotten (brown spots). Several traits of the sampled plants were measured to characterise the local  
192 resources available for the flies and the local microhabitat. For each sampled plant, five berries were  
193 randomly selected to measure length and width and calculate volume ( $4/3 \times \pi \times \text{mean radius}^3$ ) and fruit  
194 skin area ( $4 \times \pi \times \text{mean radius}^2$ ). Five leaves were also taken, their length and width measured and the  
195 leaf surface index (length  $\times$  width; Ulmer et al. 2022) calculated. Individual morphology of each plant  
196 species was characterised by measuring the minimum and maximum plant canopy diameter, the  
197 circumference of the largest trunk (except for *V. album*) and the total number of fruit present on the  
198 plant. Mistletoe being a parasitic shrub, we also recorded the host tree species and measured the height  
199 of the mistletoe individual on the tree (from the ground), the tree height, the crown diameter, the trunk  
200 circumference, and the number of mistletoe individuals present on the host tree and in a 20 m radius  
201 around it. Variables, units and codes are listed in Table S1.

## 202 *Environmental variables*

203 Local, landscape and climatic variables were measured at each sampling site or extracted from  
204 online databases to examine the influence of regional and local environmental conditions on infestation  
205 rates (Table S1).

206 Local environmental conditions were described as follows. First, within a 5 m radius plot  
207 centred on the sampled plant, the cover and height of the tree, shrub and herbaceous layers were  
208 estimated, as well as soil litter thickness (Table S1). Second, within a 20 m radius, the percentage of  
209 local habitats surrounding the host was recorded (e.g., orchard, woodland, grassland, swamp, crop,  
210 garden, shrub, building, hedgerow, river, pond, poplar plantation, park, road; see Table S1), as well as  
211 the percentage of other plant species with maturing fruit.

212 The landscape composition around each sampled plant was then characterised. A geographic  
213 database was created using a Geographic Information System (GIS; ArcGIS Pro v.2.5, ESRI). The  
214 sampled plants were positioned in the GIS and buffers of 50, 100, 250, 500, 750, 1000, 1250, 1500,  
215 1750, 2000, 2500 and 3000 m radii around each host tree were created for subsequent analyses of  
216 landscape composition. Landscape elements (crop, water, woodland, shrubland, grassland, road, urban  
217 area, orchard, industrial zone) were extracted from the OSO 2022 database (THEIA 2023) and updated  
218 using aerial photographs and, in buffers <100 m, field observations.

219 Macroclimatic conditions were characterised for each sampling site using regional  
220 measurements. Daily meteorological data were retrieved from the three meteorological stations closest  
221 to each site, from 1 January 2022 to each sampling date (<https://www.historique-meteo.net/france/>;  
222 details in Table S2). Daily minimum, mean and maximum temperatures, rainfall and snowfall were  
223 calculated for all sites using inverse-distance weighting (IDW) interpolation (Willmott et al. 1985) from  
224 the data from the three nearest weather stations (Table S2). Accumulated degree-days (“Growing Degree  
225 Days”, GDD) were calculated using a lower threshold of 0°C between 1 January 2022 and the sampling

226 date (Baskerville and Emin 1969). The baseline value of 0°C is a standard threshold commonly used to  
227 calculate GDD in insect and plant studies (White et al. 2012; McNeil et al. 2020). It is particularly  
228 suitable to study the temporal synchrony between insects and plant resources (Iler et al. 2013; Ulmer et  
229 al. 2022). It was also chosen because (i) active *D. suzukii* can be observed even at very low positive  
230 temperature (< 5°C) during winter, including during periods of snowfall (Ulmer et al. 2024), (ii) flies  
231 are able to recover from chill coma after exposure to -1°C (Wallingford et al. 2016) and (iii) mistletoe  
232 fruit can undergo freeze-thaw cycles before ripening ends (Thomas et al. 2023). From daily precipitation  
233 values, we also calculated mean daily and cumulative precipitation between 1 January 2022 and each  
234 sampling date, and within the 7- or 14-days periods preceding each sampling date.

235 Microclimate temperatures were recorded at each sampling site using Hobo loggers (TIDBIT  
236 data logger V2 TEMP TBI-001, ONSET Company, Bourne MA, USA), recording every 60 min. In each  
237 sampling site a logger was suspended 1.5 m above the ground in the plant canopy, under the shade of a  
238 branch to avoid direct exposure to solar radiation and oriented northward. The minimum, mean and  
239 maximum air temperatures were extracted every day to compute the mean daily minimum, mean and  
240 maximum temperatures. As described for macroclimate data, GDD were calculated using Hobo logger  
241 data to characterise the local microclimate under the canopy of the sampled plants.

#### 242 *Emergence of Drosophila species*

243 After collection, the fruit sampled from each plant were placed on wet cotton wool in cylindrical  
244 plastic transparent containers (diameter = 118 mm, height = 135 mm, volume = 1,476 cm<sup>3</sup>), covered  
245 with a nylon mesh, and maintained in a temperature-controlled room at 20°C under a 16:8 L:D regime.  
246 Adult flies emerging from the fruit were placed in 70% ethanol. They were identified to species level  
247 using Bächli et al. (2004) and specific criteria published for *D. suzukii* (Withers and Allemand 2012).  
248 Individuals of each species were sexed and counted using a Leica M205C stereomicroscope equipped  
249 with a Leica MC170 HD camera and the Leica Application Suite software.

#### 250 *Infestation variables*

251 We examined the relationships between environmental variables and two common infestation  
252 variables (Benavídez et al. 2021) that were either centred on the fruit (Fruit Infestation Rate for a given  
253 *Drosophila* species:  $FIR = 100 \times \text{number of emerged individuals from fruit collected from a given plant}$   
254  $\text{individual} / \text{total number of fruit collected from the same plant individual}$ ) or on the plant species (Plant  
255 Infestation Rate:  $PIR = 100 \times \text{number of infested plant individuals of a species in a month} / \text{total number}$   
256  $\text{of plant individuals of this same species sampled in a month}$ ). These variables can be interpreted as  
257 follows: FIR reflects the plant auto-contamination by the flies while PIR reflects fly dispersal between  
258 host plant individuals (e.g., when the FIR and PIR are both high, both auto-contamination within the  
259 plant individual and dispersal of the flies between plant individuals take place; when the FIR is high and  
260 the PIR is low, there is mostly plant auto-contamination; when the FIR is low and the PIR high, there is

261 mostly fly dispersal; when both FIR and PIR are low, there is an absence of both auto-contamination  
262 and dispersal). These infestation variables were calculated for each fruit category (healthy or damaged  
263 fruit on the plant and fallen fruit on the ground) following Deconninck et al. (2024b).

#### 264 *Statistical analyses*

265 We tested for the influence of environmental variables (fruit and plant morphology, local abiotic  
266 conditions, habitat composition in the surrounding landscape and climatic variables) on *D. suzukii*  
267 ( $\log_{10}+1$ -transformed) FIR using mixed models (GLMMs) with host plant species included as a random  
268 effect in models to identify environmental variables responsible for infestations whatever the host plant  
269 species considered. Then, to identify environmental variables that specifically influenced infestation of  
270 each plant species, generalized linear models (GLMs) were built for each of the host plant species that  
271 were infested by *D. suzukii*. For infestation of *V. album*, we used mixed models (GLMMs) with host  
272 tree species parasitised by *V. album* included as a random effect to identify environmental variables  
273 responsible for fly infestations whatever host tree of *V. album* considered. Preselection of explanatory  
274 variables was made by using the variable that most strongly correlated (Pearson correlation) with FIR  
275 across the spatial scales assessed (buffers from 5 m to 3,000 m radius around each sampling point), as  
276 recommended by Ulmer et al. (2022). A backward selection of explanatory variables and the second-  
277 order Akaike information criterion (AICc; Hurvich and Tsai 1989) were used to select the most  
278 parsimonious model, i.e. the model with lowest AICc. Homoscedasticity was checked using biplots of  
279 residuals and model predictions. We used Kruskal-Wallis tests to test whether the FIR varied across  
280 months or between host plant species. *Post-hoc* pairwise comparisons between months were then  
281 performed using Mann-Whitney U tests. The same analyses were performed on *D. subobscura* FIR in  
282 *V. album* and are available in supplementary materials. All statistical analyses were performed using  
283 SPSS version 24.0 (IBM Corporation).

284

## 285 **Results**

### 286 *Availability of fruit resources across winter and spring*

287 Between January and July 2022, totals of 1385, 1357, 690, 2280 and 16,632 fruit were sampled  
288 from 43, 25, 8, 17 and 119 plants of *A. japonica*, *E. ×submacrophylla*, *M. aquifolium*, *M. japonica* and  
289 *V. album*, respectively (Table 1). Plant phenology differed between species (Table 2). *Aucuba japonica*  
290 and *V. album* bore ripe fruit throughout the entire sampling period, *E. ×submacrophylla* bore fruit from  
291 January to May, and *M. aquifolium* and *M. japonica* only from May to July.

### 292 *Host plant fruit infestation*

293 Between January and July 2022, a total of 636 *D. suzukii*, 27 *D. subobscura*, and 1 *D. repleta*  
294 emerged from all the sampled fruit (Table 1, Table S3). No flies emerged from *M. aquifolium* fruit.

295 *Drosophila subobscura* was only found in *V. album* fruit, with a mean FIR of  $0.23 \pm 1.58\%$  (Table S3).  
296 Fruit of *E. ×submacrophylla* were the most heavily infested by *D. suzukii* (FIR =  $17.68 \pm 38.74\%$ ),  
297 followed by *V. album*, *A. japonica* and *M. japonica*, in decreasing order. Plant infestation rate (PIR)  
298 ranged between 11.76% and 32.00%, consistent with the FIR pattern, with *E. ×submacrophylla* plants  
299 having the highest PIR.

#### 300 *Seasonality in host plant fruit infestation*

301 Although some fruit were available from January, fruit fly infestation began only in February.  
302 *Viscum album* fruit were the earliest to be infested, first by *D. subobscura* from February to May (Table  
303 S4, Figure S2), then by *D. suzukii* from March to June (Table 2, Figure 1). The FIR of *V. album* fruit  
304 remained low (mean < 2%), with highest values of 42.55% for *D. suzukii* (Table 1). PIR was relatively  
305 high, 18.49% for the entire study, and increasing to 40.63% for *D. suzukii* in April (Figure 1B).  
306 Infestations of *A. japonica* and *E. ×submacrophylla* by *D. suzukii* started in April (Table 2, Figure 1A,  
307 B). *Aucuba japonica* fruit were used until May, with a low FIR below 10.00%, but a relatively high  
308 global PIR of 13.95% (Table 1), peaking at 28.57% in April (Figure 1B). *Drosophila suzukii* that  
309 emerged from *E. ×submacrophylla* fruit were only found in fruit collected in April (Table 2; Figure 1)  
310 but showed the highest FIR (146.97%; i.e., the number of emerging flies was  $\sim 1.5\times$  greater than the  
311 number of collected fruit in a sample; Table 1) and PIR (32.00%; Table 1, Figure 1B) compared to the  
312 other species (Kruskal-Wallis test on FIR,  $\chi^2 = 7.00$ ,  $p = 0.030$ ). Finally, *M. japonica* was used in May  
313 and June by *D. suzukii*, with low FIR values of 0.61% and 4.41%, respectively, and the lowest PIR of  
314 11.76% (Table 1).

#### 315 *Environmental variables correlating with fruit infestation*

316 The quality of the fruit from which *D. suzukii* emerged ('healthy', 'damaged', or 'ground')  
317 differed significantly according to the host plant species (Kruskal-Wallis test,  $\chi^2 = 323.42$ ,  $p < 0.0001$ ;  
318 Figure 2). In *M. japonica*, adult flies only emerged from healthy fruit collected on the plant. In *A.*  
319 *japonica*, flies emerged only from fruit collected on the plant, both healthy (54%) and damaged (46%).  
320 In *V. album*, adult flies emerged from healthy fruit on the plant (43%) and from fruit on the ground  
321 (57%). Finally, in *E. ×submacrophylla*, flies emerged from fruit sampled either on the plant (88%,  
322 comprising healthy (17%) or damaged (71%)), or on the ground (12%; Figure 2).

323 Independent of the host plant species, *D. suzukii* fruit infestation was negatively associated with  
324 the cumulative precipitation and the number of frost hours recorded by Hobo microclimatic sensors in  
325 the 7 days preceding fruit sampling, with the cover of grassland in a radius of 20 m, and with the cover  
326 of shrubland in a 3 km radius; infestation was positively associated with the area of water in a radius of  
327 100 m (GLMM, Table 3). Environmental variables affecting *D. suzukii* FIR differed between plant  
328 species (GLM, Table 4; GLMM, Table 5). In *A. japonica*, the cover of bare soil in a radius of 10 m and  
329 the richness of fleshy-fruited plant species in a radius of 20 m had a positive association, while the cover

330 of grassland in a radius of 20 m and the area of water in a radius of 250 m had a negative association  
331 (GLM, Table 4). In *E. ×submacrophylla*, the number of frost days recorded by weather stations in the  
332 preceding 14 days and the cumulative precipitation in the preceding 7 days were negatively associated  
333 with *D. suzukii* FIR, while the cover of road surface in a radius of 250 m had a positive association  
334 (GLM, Table 4). In *M. japonica*, only plant trunk circumference was associated with *D. suzukii* FIR,  
335 with a negative correlation (GLM, Table 4). In *V. album*, *D. suzukii* FIR was positively associated with  
336 the percentage of fruit collected on the ground, the mean leaf area index of *V. album* and the cumulative  
337 precipitation between 1 January 2022 and the sampling date (GLMM, Table 5). The cover of poplars  
338 (POPLARP20;  $R = 0.292$ ;  $p = 0.001$ ) and hedges (HEDGE20;  $R = 0.252$ ;  $p = 0.006$ ) in a radius of 20 m  
339 were positively associated with *D. suzukii* infestation in *V. album*, although the variables were not  
340 retained in the final model.

341 Microclimatic variables also correlated with *D. suzukii* FIR, but were not retained in the final  
342 models after the backward selection of competing explanatory factors. For example, FIR of *V. album*  
343 was positively correlated with the highest hourly maximum temperature (MAXMAX7Jh;  $R = 0.293$ ;  $p$   
344  $< 0.001$ ) and with Growing Degree Days (GDDM7Jh;  $R = 0.276$ ;  $p = 0.002$ ) recorded by Hobo loggers  
345 during the 7 days preceding fruit sampling. FIR of *A. japonica* was negatively correlated with the  
346 number of frost days recorded by weather stations during the 14 days preceding fruit sampling  
347 (NFD14Js;  $R = -0.350$ ;  $p = 0.022$ ) but it was not retained in the final model. Finally, recent weather  
348 metrics, i.e. temperatures during the preceding two weeks, were more correlated with infestation than  
349 the overall climate of the entire study period, i.e. the cumulative temperature (GDD) calculated from 1  
350 January 2022, which showed no significant correlation with FIR.

351 The main environmental variables correlating with *V. album* fruit infestation by *Drosophila*  
352 *subobscura* were shown in Table S5 and discussed below this table.

353

## 354 **Discussion**

355 Our study demonstrates that *D. suzukii* is able to use the vernal fruit of the plant species *A.*  
356 *japonica*, *E. ×submacrophylla*, *M. japonica* and *V. album* in the latter part of winter and throughout  
357 spring, confirming that these plants are likely to help the fly to overcome the winter bottleneck induced  
358 by low temperatures and fruit resource scarcity. Here, we (i) address how multi-scale environmental  
359 factors influence *D. suzukii* infestation, (ii) discuss the role of ornamental and non-crop plant species as  
360 catalysts for the development of spring *D. suzukii* populations, and (iii) summarise the hierarchy of  
361 ecological filters influencing the dynamics of *D. suzukii* populations in winter, highlighting its value in  
362 the context of early pest management strategies.

363 *Climate and weather effects on fruit infestation*

364 Several climatic variables correlated with *D. suzukii* infestation. These variables acted at  
365 different temporal scales (cumulative climate of the year *versus* weather in the weeks immediately  
366 preceding sampling) and spatial scales (regional macroclimate *versus* sub-canopy microclimate).  
367 Cumulative precipitation and the number of frost hours locally measured under the canopy of the host  
368 plants in the week preceding sampling had an overall negative correlation with infestation. Rain is  
369 known to limit the flight ability of flies (Dickerson et al. 2014) and frost may have induced mortality  
370 (Ryan et al. 2016). The association between climatic variables and *D. suzukii* infestation differed  
371 between plant species. *Aucuba japonica* and *M. japonica* infestations were less associated with climatic  
372 variables than with the other environment features (i.e., by landscape composition or local conditions).  
373 These ornamental species are often planted in gardens close to houses and parks in an urbanised  
374 environment, which may have protected them from extreme low temperatures through the “heat island  
375 effect” (Oke 1973; Meineke et al. 2017), making climatic variations a secondary factor in the  
376 explanation of the FIR. *Elaeagnus ×submacrophylla* infestation was negatively correlated with frost in  
377 the 14 days preceding sampling and with rain in the previous week. Fruit of *E. ×submacrophylla* are soft  
378 and very sensitive to rot (pers. obs. reported in an experimental study: Larges et al. 2023); the alternation  
379 of frost followed by rain may have caused damage to fruit (Ladaniya 2015), thereby accelerating the  
380 rotting process (Rodrigo 2000) and reducing fruit suitability for *D. suzukii*, which prefers ripening and  
381 ripe fruit (Walsh et al. 2011; Atallah et al. 2014). Surprisingly, precipitation had contrasting effects on  
382 *D. suzukii* infestation between *E. ×submacrophylla* and *V. album* fruit. Precipitation in the previous week  
383 (i.e., on a short-term scale) had a negative correlation with *D. suzukii* infestation in *E. ×submacrophylla*  
384 fruit, while cumulative precipitation from the beginning of the year to the sampling date (i.e., on a long-  
385 term scale for an insect) positively correlated with *D. suzukii* infestation in *V. album* fruit. The first  
386 precipitation variable (RAIN7J; see Table 3), reflecting the most recent weather conditions, besides  
387 limiting the fly’s flight ability, may also favour the rot of *E. ×submacrophylla* fruit, as noted above.  
388 Conversely, the second precipitation variable (RAIN\_01012022; see Table 5) reflects the regional  
389 climate and/or the progression of seasons; at this longer temporal scale, rain would have had a positive  
390 impact on plant phenology, growth and fruit production (Vergotti et al. 2019), increasing the number of  
391 ripe fruit available for *D. suzukii* on *V. album* plants. These contrasting correlations of climatic variables  
392 with infestation over different timescales also means that single-scale climatic models are insufficient  
393 to predict infestation rates, and that other variables related to the ecology of the focal insect and of the  
394 host plant identity need to be considered. Finally, it is notable that recent weather conditions were more  
395 associated with infestation than the cumulative climate experienced from the start of the year, as also  
396 shown by Wiman et al. (2016). This suggests that the end of the winter reproductive diapause in flies  
397 could be triggered more strongly by short-term spring heat peaks than by the accumulation of heat since  
398 the beginning of the year, in contrast to that of plants (Zavalloni et al. 2006). This also highlights an  
399 ongoing need to identify the true cues, and their timing, controlling *Drosophila* entry into and exit from  
400 diapause (Numata and Shintani 2023). The use of macroclimate alone in predictive models would tend

401 to mask the reality of microclimate and weather variations, potentially explaining the discrepancies  
402 between predictions and actual population densities. Thus, annual measures of temperature variation  
403 may be more appropriate to model the infestation of summer fruit (Dalton et al. 2011; Kamiyama et al.  
404 2020), but we suggest that winter fruit infestation may be better predicted by shorter timescale warming  
405 events occurring between winter and spring.

#### 406 *Association between landscape and local factors and infestation differ according to host plant species*

407 Habitats and landscape elements that correlated with overall *D. suzukii* infestations were the  
408 grassland, water and shrubland covers. Local grass cover (in a 20 m radius) negatively correlated with  
409 the infestations. This result is consistent with those of Santoiemma et al. (2019) showing that during  
410 winter, at lower temperatures, *D. suzukii* had a greater density in forest than in grassland. The presence  
411 of mown grassland under or near the fruiting plants, frequently observed in our sites, was also identified  
412 as an efficient management tool reducing infestation (Santoiemma et al. 2020). Grasslands also host  
413 predatory species, including macroarthropods such as spiders, centipedes or ants (Ulmer et al. 2021),  
414 which may control *D. suzukii* overwintering populations (Ulmer et al. 2021; Perrot et al. 2023).  
415 Surprisingly, the cover of shrubland at a large spatial scale (in a 3 km radius) also negatively correlated  
416 with infestations. Shrubland is an excellent overwintering area for *D. suzukii* as it includes several  
417 fruiting shrubs which provide both food resources and shelter (Panel et al. 2018; Tait et al. 2021; Ulmer  
418 et al. 2024). Thus, the presence of large shrub patches in the landscape mosaic may cause a dilution  
419 effect on the fly's density. Shrubland and other wooded habitats are used as a winter refuge by the flies  
420 and represent sink-habitats for their population during the cold season (Santoiemma et al. 2019; Ulmer  
421 et al. 2024). They may thus compete in terms of attractiveness to flies with our sampling sites, reducing  
422 the numbers present in the latter (see Ulmer et al. 2024 showing changes in the fly distribution between  
423 preferred habitats during the cold seasons). Finally, the area of water within a 100 m radius was  
424 positively correlated with infestation. This may be an indirect consequence of water provisioning for the  
425 preferred host plants of *D. suzukii* (Predieri et al. 2003), further illustrating the influence of landscape  
426 structure on infestation.

427 The association between landscape elements and infestation was also modulated by the plant  
428 species. *Aucuba japonica* infestations were more strongly correlated with local variables than with  
429 landscape variables: the cover of bare soil in a 10 m radius and the richness of fleshy-fruited plant species  
430 in a radius of 20 m positively correlated with *D. suzukii* infestation of this species, while the cover of  
431 grass in a 20 m radius and water area in a 250 m radius were negatively correlated with infestation. Bare  
432 soil, primarily a result of local trampling or even ploughing, is an indicator of anthropogenic impacts  
433 (Previati et al. 2007). *Aucuba japonica* is mainly found in gardens where soil is frequently and  
434 intensively disturbed by owners for the management of their ornamental plants. Our findings are  
435 consistent with those of Rossi-Stacconi et al. (2016), confirming the affinity of *D. suzukii* for

436 anthropogenic habitats. Here, fleshy-fruited species around the sampled plant may have provided a food  
437 resource and shelter for *D. suzukii*, increasing its population in the sampling area and inducing greater  
438 infestation of *A. japonica* fruit. Begon (1975) similarly showed that the density of berries of several wild  
439 plant species in an area increased the success of breeding in *D. subobscura*. Ulmer et al. (2024) also  
440 demonstrated that the local diversity in fruit-bearing plant species promoted *D. suzukii* populations. The  
441 negative association between infestation and grass cover in this instance may be analogous to that  
442 described above for overall *D. suzukii* infestation, suggesting that flies avoid open areas and short  
443 vegetation in winter. However, the negative association between water area and *A. japonica* infestation  
444 contrasts with its overall positive association with infestation across all plant species, demonstrating that  
445 the same environmental factor may have divergent effects on different plant species. *Aucuba japonica*  
446 is commonly planted taking advantage of its very high resistance to drought (Percival and Sheriffs 2002)  
447 and it is negatively impacted by fluvial flooding in its natural range (Kamisako et al. 2007). Thus,  
448 excessive water in its environment (from the Somme valley in our study) contrasts with its natural  
449 ecological niche and performance, including fruit production. Water is also commonly associated with  
450 fog in our study area, particularly in the Somme valley. This may, in turn, have been associated with  
451 higher humidity and colder temperatures which could negatively impact *D. suzukii*, as fog alters flight  
452 abilities in insects with thin wings (Dickerson et al. 2015). Furthermore, increased water area within the  
453 landscape area inevitably results in decreased vegetation cover, which may reduce the spatial  
454 opportunities for *D. suzukii* to find resources as shown by Ulmer et al. (2024).

455 In *E. ×submacrophylla*, *D. suzukii* infestation was positively associated with the road area in a  
456 250 m radius. Roads are an indicator of urbanisation and *D. suzukii* is known to be an anthropogenically-  
457 associated species whose occurrence has been correlated with the local area of buildings (Deconninck  
458 et al. 2024b) and presence of artificial habitats (Rossi-Staconi et al. 2016). In *V. album*, the presence of  
459 poplar plantations and hedges in a 20 m radius positively correlated with infestation. As an important  
460 mistletoe host tree species (Briggs 2021), and the most heavily infested by *D. suzukii* (Deconninck et al.  
461 2024a; see also Table S6 and Figure S3), the presence of surrounding poplars increases the density of  
462 available fruit for *D. suzukii*, increasing the chances of breeding by the flies as shown by Begon (1975).  
463 Finally, *M. japonica* infestation by *D. suzukii* were not associated with landscape elements, but  
464 exclusively and negatively correlated with the sampled plant trunk circumference. When young, *M.*  
465 *japonica* plants are bushy, compact and close to the ground but, as they age and if they are not pruned,  
466 the stems become larger, erect and their foliage becomes much sparser basally (Silver 2023). This  
467 architecture of older *Mahonia* plants would be unfavourable for *D. suzukii*, which relies on shelter within  
468 the shrub canopy close to the ground (Evans et al. 2017).

469 In *V. album*, the percentage of fruit collected on the ground and the mean leaf area were  
470 positively associated with *D. suzukii* infestation. The former measure has already been reported to  
471 positively correlated both with *D. suzukii* and *D. subobscura* infestation in *V. album* at a larger national



472 scale (Deconninck et al. 2024a). In addition, the combination of low FIR and high PIR for *V. album*  
473 highlights the importance of dispersal over auto-contamination, suggesting that this resource attracts  
474 flies from a distance. The leaf surface area of a *V. album* individual is a proxy for the compactness of  
475 the mistletoe individual, which forms a more or less dense ball of evergreen leaves and branches. This  
476 compactness varies considerably over climatic gradients and with mistletoe age, and inter-individual  
477 differences can be important within a region. The denser an individual (i.e., greater leaf surface area),  
478 the more it is protected from wind influence, even if the host tree itself is bare. This may create a  
479 favourable microhabitat for *D. suzukii*, explaining the positive correlation of this plant trait with  
480 infestations. *Viscum album* provides both a food resource and shelter for *D. suzukii*, as do the dense  
481 evergreen leaves of *Hedera helix* (ivy) in winter (Ulmer et al. 2024). Future research should explore the  
482 role of plant architecture in the maintenance of winter *D. suzukii* populations, as has previously been  
483 surveyed in blackberry field for summer *D. suzukii* infestations (Diepenbrock and Burrack 2016), or  
484 even in more details for other species (e.g., see Pincebourde et al. 2007). Overall, the role of plant  
485 architecture on plant-insect interactions during winter remains understudied.

#### 486 *Trade-off between auto-contamination and dispersal depending on the host plant*

487 The FIR (autocontamination) / PIR (dispersal) ratio differed between host plant species. This  
488 ratio represents the trade-off between intra- and inter-individual host plant infestation within a plant  
489 species. When  $FIR > PIR$  (i.e., mean fruit infestation rate of a host plant species is higher than the  
490 infestation rate of the individuals within a population of this same host plant species), the fly could be  
491 opting for a strategy of auto-contaminating the fruit within a host plant individual, rather than dispersing  
492 to new sites to infest other host plant individuals, as observed in *D. suzukii* infesting *E. ×submacrophylla*  
493 and *V. album* (Max  $FIR > PIR$ ; Table 1). In contrast, a  $FIR < PIR$  (i.e., infestation rate of individuals  
494 within a population of a host plant species is higher than the mean fruit infestation rate of this same host  
495 plant) can suggest that flies disperse between individuals of the same plant species, rather than auto-  
496 contaminating a single plant individual, as observed in *D. suzukii* infesting *A. japonica* and *M. japonica*.  
497 These contrasts between host plants could result from varying fruit quality and indicate a modulation of  
498 the fly's choices to adapt to the variable developmental success of its offspring in these fruit. *Elaeagnus*  
499 *×submacrophylla* and *V. album* exhibited a high FIR / PIR ratio and *D. suzukii* is known to perform well  
500 in these species in terms of larval development (Poyet et al. 2015; Panel et al. 2018; Deconninck et al.  
501 2024a). However, when developing on *A. japonica*, *D. suzukii* shows higher mortality and a longer  
502 developmental time compared to the previous two species (Panel et al. 2018; Poyet et al. 2018). No data  
503 are available on *M. japonica* utilisation by *D. suzukii* but a similar pattern to that of *A. japonica* could  
504 be expected because of similar fruit characteristics.

505 Our findings suggest that dispersal is favoured by the flies when the host plant is of low quality.  
506 Dispersal is well-known in insects (Clobert et al. 2009), allowing avoidance of environmental stressors

507 and access to seasonally-available habitats (Asplen 2018) or ephemeral resources (Butterworth et al.  
508 2023). In the case of *D. suzukii*, dispersal allows the exploitation of spatially and temporally variable  
509 fruit resources. However, increased levels of mobility also impose costs in terms of survival and/or  
510 reproductive success (Chapman et al. 2015). Therefore, we suggest that *D. suzukii* individuals will tend  
511 to leave their fruit/host plants (i.e., Max FIR < PIR) only when their quality is low (illustrated by the  
512 case of *A. japonica* in our study). The fruit quality could also be assessed by measuring the fruit  
513 penetration force, which may influence the fruit susceptibility to *D. suzukii* (Burrack et al. 2013). At a  
514 daily scale, flies are able to move between neighbouring habitats, driven by temperature, humidity and  
515 the availability of alternative hosts (Tait et al. 2020), limited to distances below 100 m (experimental  
516 measures from Vacas et al. (2019)). However, long-distance dispersal at a regional scale of up to 9,000  
517 m has also been recorded (Tait et al. 2018), while passive dispersal over multiple generations of the  
518 species over more than 1,400 km in one year has been documented (Vacas et al. 2019). In the current  
519 study, landscape influenced *D. suzukii* infestation within a radius of up to 250 m, consistent with  
520 previous research. *Drosophila suzukii* dispersal ability is hard to evaluate, mainly because of the  
521 difficulty to follow individuals in nature (Klick et al. 2016), even if marking-recapture techniques were  
522 successfully applied (Klick et al. 2015, 2016; Clymans et al. 2020). However, studying the role of  
523 climate and landscape features (e.g., barriers) on active flight performance, as well as passive dispersal,  
524 could improve our understanding of the fly's use of resources and its potential for range expansion.

#### 525 *Ornamental and wild plants as catalysts of rapid population expansion of D. suzukii in spring?*

526 In recent years, the ecological impacts of the ornamental plant trade, its important economic  
527 value (Oxford Economics 2018), have received much less attention than the impacts of the commodity  
528 exchange (Hinsley et al. 2023). Ornamental horticulture is a major pathway for plant invasions, but also  
529 co-transport associated exotic microbes and invertebrate species, including pests (Hu et al. 2023). These  
530 already serious biosecurity risks are further exacerbated by contemporary climate change (Tubby and  
531 Webber 2010; Hinsley et al. 2023). For instance, in Portugal, 13 alien species were discovered associated  
532 with allochthonous ornamental plants, including several pest species (Bella 2013). Most of the species  
533 reported by Bella (2013) were specialists, limiting the risk of their further successful dispersal, but this  
534 limitation may not apply or be so stringent in the case of generalist species such as *D. suzukii*. Notably,  
535 most species in our study, with the exception of *V. album*, are ornamental plants. The only plant species  
536 not infested by *D. suzukii* in our study was *M. aquifolium* (but see Poyet et al. (2015), who reported low  
537 levels of infestation in this species) and we provide the first record of infestation in *M. japonica*. The  
538 highest infestation rate was observed in *E. ×submacrophylla*, whose fruit availability takes over from  
539 *V. album* and *A. japonica* fruit in April and, in turn, are succeeded by commercial strawberries and  
540 cherries. We suggest that the presence of *E. ×submacrophylla* in the vicinity of commercial crop sites  
541 gives this plant species a pivotal role in the early initiation of *D. suzukii* infestation in cultivated fruit.

542 To limit the risk of *D. suzukii* infestation in spring, pruning of *E. ×submacrophylla* could be carried out  
543 after flowering in the autumn (Edwards 2017), which would reduce the amount of fruit formed.

#### 544 *Ecological filtering of Drosophila suzukii populations throughout winter*

545 Figure 3 illustrates a global summary of the successive challenges that *D. suzukii* must face over  
546 the seasonal cycle and which, in particular, shape the dynamics of its populations subjected to winter  
547 conditions. Based on existing conceptual studies of species assembly rules in plant communities linked  
548 to environmental filtering (Grime 1998; Rahel 2002; Lortie et al. 2004; Lake et al. 2007; Kraft et al.  
549 2015; Germain et al. 2018), this theoretical framework is adapted here to insects at the population scale.  
550 It summarises the hierarchy of ecological filters identified as influencing fruit infestation by *D. suzukii*  
551 in the present study and in other relevant studies (Poyet et al. 2014, 2015; Ulmer et al. 2020, 2021, 2022,  
552 2024; Deconninck et al. 2024b). Here, environmental filtering refers to ecological factors that prevent  
553 the establishment and/or persistence of *D. suzukii* individuals in a particular location. The large set of  
554 influencing factors are grouped into three types of ecological filter (i.e., dispersal, abiotic and biotic  
555 filters; Rahel 2002; Lortie et al. 2004) that act at different spatial and temporal scales and may affect the  
556 fly's migration, activity, fitness and survival. The scheme is centred on the winter season bottleneck but  
557 also integrates the upstream processes of population formation in autumn and the downstream  
558 consequences of winter processes on the first cultivated fruit that mature in spring.

559 Regional *D. suzukii* populations increase throughout the summer months, reaching a maximum  
560 in late autumn (Ulmer et al. 2024) coincident with the peak in diversity and abundance of fruit that are  
561 compatible with the fly's physiological requirements (peak in October in temperate regions; Poyet et al.  
562 2014, 2015; Ulmer et al. 2022). In nature, about half of fruit bearing plants produce fruit that can be  
563 utilised by *D. suzukii* (Poyet et al. 2015). However, some usually rare fruit in which the fly's  
564 development is impaired, named dead-end trap fruit (Ulmer et al. 2020), may reduce its population in  
565 autumn (Ulmer et al. 2020; Fragnière et al. 2024). *Drosophila suzukii* may also suffer from competition  
566 with other Drosophilidae in late cultivated fruit, such as apples (Deconninck et al. 2024b). Nevertheless,  
567 globally, autumn-maturing fruit generate a large population of *D. suzukii* (Poyet et al. 2014), primarily  
568 winter morphs (Panel et al. 2018; Ulmer et al. 2024) that are ready to face the winter season. This initial  
569 large pool of overwintering adult flies is then subjected to three ecological filters during winter before  
570 the first commercial fruit ripen in late spring or early summer. First, only a portion reaches locations  
571 harbouring suitable winter-available fruit. This first "dispersal filter" immediately reduces the number  
572 of arriving *D. suzukii* individuals, depending on landscape variables favouring or limiting access to fruit  
573 sites and affecting connectivity between semi-natural habitats –that provide winter shelters (e.g., forests,  
574 hedges, anthropogenic habitats; Rossi-Stacconi et al. 2016)– and sites that provide spring fruit. The risk  
575 of fruit infestation increases with the extent of wooded habitats available in the surrounding landscape

576 (Pelton et al. 2016; Urbaneja-Bernat et al. 2020; Ulmer et al. 2022). For individuals that successfully  
577 pass this first filter, they then face two other ecological filters, abiotic and biotic.

578         During winter and the immediate post-winter period, the abiotic filter preventing fruit  
579 infestation by *D. suzukii*, is primarily composed of macroclimatic and microclimatic variables.  
580 Macroclimatic variables, as measured by free-air meteorological stations at a regional scale over several  
581 months from the beginning of the year, determine the female's ability to start producing eggs and  
582 oviposit. Female *D. suzukii* experience a reproductive diapause in winter (Rossi-Stacconi et al. 2016)  
583 when their ovaries become atrophied (Zerulla et al. 2015; Langille et al. 2016; Toxopeus et al. 2016;  
584 Wiman et al. 2016). The timing or cues for the end of this diapause period in nature are unclear.  
585 However, post-diapause, the ovaries become mature as early as March in our study area (Ulmer 2022),  
586 so that fruit attacks by flies can start at the very end of winter. Local microclimatic conditions differ  
587 from those of the regional macroclimate (Suggitt et al. 2011) because of the shading and transpiration  
588 provided by trees and shrubs (Geiger et al. 2003). Beneath the tree and shrub canopy, temperature  
589 extremes are moderated, with higher minimum and lower maximum air temperatures (Gril et al. 2023b),  
590 as shown in Figure S4. Conversely, air temperature extremes can be amplified near the ground in open  
591 or sparse vegetation (with lower minima and higher maxima; Gril et al. 2023a), as shown in Figure S4.  
592 Soil/litter surface temperatures can be amplified to an even greater extent (Pincebourde and Salle 2020).  
593 Thus, during winter, the phenology of flies and fruit in open areas can be delayed by the microclimatic  
594 amplification of cold, while it can be advanced in warmer sites protected by a forest canopy (Pelton et  
595 al. 2016).

596         Finally, local biotic filters must be surpassed. In particular, predation must be avoided (Siffert  
597 et al. 2021; Ulmer et al. 2021), most likely through habitat choice, as suggested by the influence of the  
598 grass cover in a radius of 20 m for *D. suzukii*. They may also face competition for available fruit  
599 resources with birds (Briggs 2011). Having overcome these filters, infestation success will then depend  
600 on the quantity and quality of suitable fruit (Figure 2), which varies depending on the plant species.

601         This integrated and multiscale approach to the study of *D. suzukii* winter ecology highlights the  
602 importance of understanding the winter season for the development and early application of effective  
603 pest management strategies. The identification and quantification in time and space of winter host plants  
604 in regions of commercial production of early maturing fruit will provide an important first step in the  
605 control of this pest. Avoiding the inclusion of specific non-native ornamental plants in local hedgerows  
606 and garden/shrub areas in the vicinity of fruit farms will also provide a benefit to producers. We further  
607 recommend pruning these exotic fruit sources in autumn after flowering. Beyond the direct economic  
608 benefits this would achieve for fruit producers, such actions could also limit bird dispersal competition  
609 between native and non-native plants (Aslan and Rejmanek 2012).

610

611 **References**

- 612 Abdalla, T.E. (2019) Some wild *Elaeagnus* species: Overview, description, biochemistry, and  
613 utilization. In *Wild Fruits: Composition, Nutritional Value and Products* (ed. by Mariod, A.A.).  
614 Ghibaish, Sudan, pp. 507–522.
- 615 Abe, T. (2001) Flowering phenology, display size, and fruit set in an understory dioecious shrub, *Aucuba*  
616 *japonica* (Cornaceae). *American Journal of Botany*, **88**, 455–461.
- 617 Aitchison, C.W. (2001) The effect of snow cover on small animals. In *Snow Ecology: An*  
618 *Interdisciplinary Examination of Snow Covered Ecosystems* (ed. by Jones, H.G., Pomeroy, J.W.,  
619 Walker, D.A., and Hoham, R.W.). Cambridge, UK: Cambridge University Press.
- 620 Argañaraz, C.I., Rubio, G.D. & Gleiser, R.M. (2018) Spider communities in urban green patches and  
621 their relation to local and landscape traits. *Biodiversity and Conservation*, **27**, 981–1009.
- 622 Aslan, C. & Rejmanek, M. (2012) Native fruit traits may mediate dispersal competition between native  
623 and non-native plants. *NeoBiota*, **12**, 1–24.
- 624 Asplen, M.K. (2018) Dispersal strategies in terrestrial insects. *Current Opinion in Insect Science*, **27**,  
625 16–20.
- 626 Asplen, M.K., Anfora, G., Biondi, A., Choi, D.S., Chu, D., Daane, K.M., *et al.* (2015) Invasion biology  
627 of spotted wing *Drosophila* (*Drosophila suzukii*): a global perspective and future priorities. *Journal*  
628 *of Pest Science*, **88**, 469–494.
- 629 Atallah, J., Teixeira, L., Salazar, R., Zaragoza, G. & Kopp, A. (2014) The making of a pest: The  
630 evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species. *Proceedings of*  
631 *the Royal Society B: Biological Sciences*, **281**, 20132840.
- 632 Bächli, G., Vilela, C.R., Escher, S.A. & Saura, A. (2005) *The Drosophilidae Diptera of Fennoscandia*  
633 *and Denmark*. Leiden.
- 634 Bale, J.S. & Hayward, S.A.L. (2010) Insect overwintering in a changing climate. *Journal of*  
635 *Experimental Biology*, **213**, 980–994.
- 636 Ballard, J.W.O., Melvin, R.G. & Simpson, S.J. (2008) Starvation resistance is positively correlated with  
637 body lipid proportion in five wild caught *Drosophila simulans* populations. *Journal of Insect*  
638 *Physiology*, **54**, 1371–1376.
- 639 Barney, C.W., Hawksworth, F.G. & Geils, B.W. (1998) Hosts of *Viscum album*. *European Journal of*  
640 *Forest Pathology*, **28**, 187–208.

- 641 Basden, E.B. (1954) The distribution and biology of Drosophilidae (Diptera) in Scotland, including a  
642 new species of *Drosophila*. *Transactions of the Royal Society of Edinburgh*, **62**, 603–654.
- 643 Baskerville, G.L. & Emin, P. (1969) Rapid estimation of heat accumulation from maximum and  
644 minimum temperatures. *Ecology*, **50**, 514–517.
- 645 Bayton, R.P. (2017) The identity of *Mahonia japonica*. *The Plantsman*, **December**, 244–248.
- 646 Begon, M. (1975) Population densities in *Drosophila obscura* Fallén and *D. subobscura* Collin on  
647 naturally-occurring fruits. *Oecologia*, **20**, 255–277.
- 648 Bella, S. (2013) New alien insect pests to Portugal on urban ornamental plants and additional data on  
649 recently introduced species. *Annales de la Societe Entomologique de France*, **49**, 374–382.
- 650 Benavidez, A., Ordano, M. & Schliserman, P. (2021) What is the level of fruit infestation by pulp-  
651 feeding insects? An overview of their meaning and measurement. *European Journal of Horticultural*  
652 *Science*, **86**, 520–531.
- 653 Blanuša, T., Qadir, Z.J., Kaur, A., Hadley, J. & Gush, M.B. (2020) Evaluating the effectiveness of urban  
654 hedges as air pollution barriers: Importance of sampling method, species characteristics and site  
655 location. *Environments - MDPI*, **7**, 1–21.
- 656 Briggs, J. (2011) Mistletoe (*Viscum album*): a brief review of its local status with recent observations  
657 on its insect associations and conservation problems. *Proceedings of the Cotteswold Naturalists’*  
658 *Field Club*, **XLV (II)**, 181–193.
- 659 Briggs, J. (2021) Mistletoe, *Viscum album* (Santalaceae), in Britain and Ireland; a discussion and review  
660 of current status and trends. *British & Irish Botany*, **3**, 419–454.
- 661 Burrack, H.J., Fernandez, G.E., Spivey, T. & Kraus, D.A. (2013) Variation in selection and utilization  
662 of host crops in the field and laboratory by *Drosophila suzukii* Matsumura (Diptera: Drosophilidae),  
663 an invasive frugivore. *Pest Management Science*, **69**, 1173–1180.
- 664 Butterworth, N.J., Benbow, M.E. & Barton, P.S. (2023) The ephemeral resource patch concept.  
665 *Biological Reviews*, **98**, 697–726.
- 666 Chapman, J.W., Reynolds, D.R. & Wilson, K. (2015) Long-range seasonal migration in insects:  
667 Mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters*, **18**, 287–302.
- 668 Cini, A., Ioriatti, C. & Anfora, G. (2012) A review of the invasion of *Drosophila suzukii* in Europe and  
669 a draft research agenda for integrated pest management. *Bulletin of Insectology*, **65**, 149–160.

670 Clobert, J., Galliard, J.F. Le, Cote, J., Meylan, S. & Massot, M. (2009) Informed dispersal, heterogeneity  
671 in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*,  
672 **12**, 197–209.

673 Clymans, R., Kerckvoorde, V. Van, Beliën, T., Bylemans, D. & Clercq, P. De. (2020) Marking  
674 *Drosophila suzukii* (Diptera: Drosophilidae) with fluorescent dusts. *Insects*, **11**, 152.

675 Coklar, H. & Akbulut, M. (2017) Anthocyanins and phenolic compounds of *Mahonia aquifolium* berries  
676 and their contributions to antioxidant activity. *Journal of Functional Foods*, **35**, 166–174.

677 Cuff, J.P., Gajski, D., Michalko, R., Kosulic, O. & Pekár, S. (2024) Biomonitoring of biocontrol across  
678 the full annual cycle in temperate climates: post-harvest, winter and early-season interaction data and  
679 methodological considerations for its collection. *OSF Preprints*.

680 Dalton, D.T., Walton, V.M., Shearer, P.W., Walsh, D.B., Caprile, J. & Isaacs, R. (2011) Laboratory  
681 survival of *Drosophila suzukii* under simulated winter conditions of the Pacific Northwest and  
682 seasonal field trapping in five primary regions of small and stone fruit production in the United  
683 States. *Pest Management Science*, **67**, 1368–1374.

684 Dam, D., Molitor, D. & Beyer, M. (2019) Natural compounds for controlling *Drosophila suzukii*. A  
685 review. *Agronomy for Sustainable Development*, **39**, 53.

686 Danks, H. V. (1978) Modes of seasonal adaptation in the insects: I. Winter survival. *The Canadian*  
687 *Entomologist*, **110**, 1167–1205.

688 David, J.R., Gibert, P., Moreteau, B., Gilchrist, G.W. & Huey, R.B. (2003) The fly that came in from  
689 the cold: Geographic variation of recovery time from low-temperature exposure in *Drosophila*  
690 *subobscura*. *Functional Ecology*, **17**, 425–430.

691 Deconninck, G., Boulembert, M., Eslin, P., Couty, A., Bonis, A., Dubois, F., *et al.* (2024a)  
692 Environmental factors driving infestations of a keystone winter fruit by an invasive and a native fruit  
693 fly. *Arthropod-Plant Interactions*. <https://doi.org/10.1007/s11829-024-10073-6>

694 Deconninck, G., Boulembert, M., Eslin, P., Couty, A., Dubois, F., Gallet-Moron, E., *et al.* (2024b) Fallen  
695 fruit: A backup resource during winter shaping fruit fly communities. *Agricultural and Forest*  
696 *Entomology*, **26**, 232–248.

697 Delbac, L., Rusch, A., Binet, D. & Thiéry, D. (2020) Seasonal variation of Drosophilidae communities  
698 in viticultural landscapes. *Basic and Applied Ecology*, **48**, 83–91.

699 Dickerson, A.K., Liu, X., Zhu, T. & Hu, D.L. (2015) Fog spontaneously folds mosquito wings. *Physics*  
700 *of Fluids*, **27**, 021901.

- 701 Dickerson, A.K., Shankles, P.G. & Hu, D.L. (2014) Raindrops push and splash flying insects. *Physics*  
702 *of Fluids*, **26**, 027104.
- 703 Diepenbrock, L.M. & Burrack, H.J. (2017) Variation of within-crop microhabitat use by *Drosophila*  
704 *suzukii* (Diptera: Drosophilidae) in blackberry. *Journal of Applied Entomology*, **141**, 1–7.
- 705 Edwards, D. (2017) A new name for an *Elaeagnus* hybrid. *The Plantsman*, **16**, 222–223.
- 706 Evans, R.K., Toews, M.D. & Sial, A.A. (2017) Diel periodicity of *Drosophila suzukii* (Diptera:  
707 Drosophilidae) under field conditions. *PLoS ONE*, **12**, 1–20.
- 708 Fragnière, A.L., Bacher, S. & Kehrlı, P. (2024) Identifying candidate host plants for trap cropping  
709 against *Drosophila suzukii* in vineyards. *Journal of Pest Science*.
- 710 Francis, J.K. (2004) *Mahonia aquifolium* (Pursh) Nutt. In *Wildland Shrubs of the United States and Its*  
711 *Territories: Thamnic Descriptions* (ed. by Francis, J.K.). San Juan, PR, US, pp. 461–463.
- 712 Gajski, D., Mifková, T., Košulič, O., Michálek, O., Serbina, L.Š., Michalko, R., *et al.* (2023) Brace  
713 yourselves, winter is coming: the winter activity, natural diet, and prey preference of winter-active  
714 spiders on pear trees. *Journal of Pest Science*, **97**, 113–126.
- 715 Geiger, R., Aron, R.H. & Todhunter, P. (2003) *The Climate Near the Ground*. Rowman & Littlefield.
- 716 Germain, R.M., Mayfield, M.M. & Gilbert, B. (2018) The ‘filtering’ metaphor revisited: Competition  
717 and environment jointly structure invasibility and coexistence. *Biology Letters*, **14**.
- 718 Gill, H.K., Goyal, G. & Chahil, G. (2017) Insect diapause: A review. *Journal of Agricultural Science*  
719 *and Technology A*, **7**, 454–473.
- 720 Grassi, A., Gottardello, A., Dalton, D.T., Tait, G., Rendon, D., Ioriatti, C., *et al.* (2018) Seasonal  
721 reproductive biology of *Drosophila suzukii* (Diptera: Drosophilidae) in temperate climates.  
722 *Environmental Entomology*, **47**, 166–174.
- 723 Gril, E., Laslier, M., Gallet-Moron, E., Durrieu, S., Spicher, F., Roux, V. Le, *et al.* (2023a) Using  
724 airborne LiDAR to map forest microclimate temperature buffering or amplification. *Remote Sensing*  
725 *of Environment*, **298**.
- 726 Gril, E., Spicher, F., Greiser, C., Ashcroft, M.B., Pincebourde, S., Durrieu, S., *et al.* (2023b) Slope and  
727 equilibrium: A parsimonious and flexible approach to model microclimate. *Methods in Ecology and*  
728 *Evolution*, **14**, 885–897.
- 729 Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects.  
730 *Journal of Ecology*, **86**, 902–910.



- 731 Hamby, K.A., E. Bellamy, D., Chiu, J.C., Lee, J.C., Walton, V.M., Wiman, N.G., *et al.* (2016) Biotic  
732 and abiotic factors impacting development, behavior, phenology, and reproductive biology of  
733 *Drosophila suzukii*. *Journal of Pest Science*, **89**, 605–619.
- 734 Henry, Y., Overgaard, J. & Colinet, H. (2020) Dietary nutrient balance shapes phenotypic traits of  
735 *Drosophila melanogaster* in interaction with gut microbiota. *Comparative Biochemistry and*  
736 *Physiology -Part A: Molecular and Integrative Physiology*, **241**, 110626.
- 737 Hinsley, A., Hughes, A.C., Valkenburg, J. van, Stark, T., Delft, J. van, Sutherland, W., *et al.* (2023) The  
738 true cost of the global ornamental plant trade. *Preprints*.
- 739 Hu, S., Jin, C., Liao, R., Huang, L., Zhou, L., Long, Y., *et al.* (2023) Herbaceous ornamental plants with  
740 conspicuous aesthetic traits contribute to plant invasion risk in subtropical urban parks. *Journal of*  
741 *Environmental Management*, **347**, 119059.
- 742 Hurvich, C.M. & Tsai, C.-L. (1989) Regression and time series model selection in small samples.  
743 *Biometrika*, **76**, 297–307.
- 744 Iacovone, A., Girod, P., Ris, N., Weydert, C., Gibert, P., Poirié, M., *et al.* (2015) Worldwide invasion  
745 by *Drosophila suzukii*: Does being the “cousin” of a model organism really help setting up biological  
746 control? Hopes, disenchantments and new perspectives. *Revue d’Ecologie, Terre et Vie*, **70**, 207–  
747 214.
- 748 Iler, A.M., Inouye, D.W., Høye, T.T., Miller-Rushing, A.J., Burkle, L.A. & Johnston, E.B. (2013)  
749 Maintenance of temporal synchrony between syrphid flies and floral resources despite differential  
750 phenological responses to climate. *Global Change Biology*, **19**, 2348–2359.
- 751 Jiménez-Padilla, Y., Ferguson, L. V. & Sinclair, B.J. (2020) Comparing apples and oranges (and  
752 blueberries and grapes): Fruit type affects development and cold susceptibility of immature  
753 *Drosophila suzukii* (Diptera: Drosophilidae). *Canadian Entomologist*, **152**, 532–545.
- 754 Kamisako, M., Sannoh, K. & Kamitani, T. (2007) Does understory vegetation reflect the history of  
755 fluvial disturbance in a riparian forest? *Ecological Research*, **22**, 67–74.
- 756 Kamiyama, M.T., Bradford, B.Z., Groves, R.L. & Guédot, C. (2020) Degree day models to forecast the  
757 seasonal phenology of *Drosophila suzukii* in tart cherry orchards in the Midwest U.S. *PLoS ONE*,  
758 **15**, 1–13.
- 759 Kenis, M., Tonina, L., Eschen, R., Sluis, B. van der, Sancassani, M., Mori, N., *et al.* (2016) Non-crop  
760 plants used as hosts by *Drosophila suzukii* in Europe. *Journal of Pest Science*, **89**, 735–748.
- 761 Kennedy, G.G. & Storer, N.P. (2000) Life systems of polyphagous arthropod pests in temporally  
762 unstable cropping systems. *Annual Review of Entomology*, **45**, 467–493.

- 763 Klick, J., Yang, W.Q., Walton, V.M., Dalton, D.T., Hagler, J.R., Dreves, A.J., *et al.* (2016) Distribution  
764 and activity of *Drosophila suzukii* in cultivated raspberry and surrounding vegetation. *Journal of*  
765 *Applied Entomology*, **140**, 37–46.
- 766 Klick, J., Yang, W.Q. & Bruck, D.J. (2015) Marking *Drosophila suzukii* (Diptera: Drosophilidae) with  
767 Rubidium or <sup>15</sup>N. *Journal of Economic Entomology*, **108**, 1447–1451.
- 768 Košťál, V., Šimek, P., Zahradníčková, H., Cimlová, J. & Štětina, T. (2012) Conversion of the chill  
769 susceptible fruit fly larva (*Drosophila melanogaster*) to a freeze tolerant organism. *Proceedings of*  
770 *the National Academy of Sciences of the United States of America*, **109**, 3270–3274.
- 771 Košťál, V., Korbelová, J., Poupardin, R., Moos, M. & Šimek, P. (2016) Arginine and proline applied as  
772 food additives stimulate high freeze tolerance in larvae of *Drosophila melanogaster*. *Journal of*  
773 *Experimental Biology*, **219**, 2358–2367.
- 774 Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2015) Community  
775 assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, **29**, 592–599.
- 776 Ladaniya, M.S. (2015) Climate change effects on fruit quality and post-harvest management practices.  
777 In *Climate Dynamics in Horticultural Science, Volume One: The Principles and Applications* (ed.  
778 by Choudhary, M.L., Patel, V.B., Siddiqui, M.W. & Mahdl, S.S.). Apple Academic Press, p. 263.
- 779 Lake, P.S., Bond, N. & Reich, P. (2007) Linking ecological theory with stream restoration. *Freshwater*  
780 *Biology*, **52**, 597–615.
- 781 Langille, A.B., Arteca, E.M., Ryan, G.D., Emiljanowicz, L.M. & Newman, J.A. (2016) North American  
782 invasion of spotted-wing drosophila (*Drosophila suzukii*): A mechanistic model of population  
783 dynamics. *Ecological Modelling*, **336**, 70–81.
- 784 Larges, J., Ulmer, R., Eslin, P., Chabrierie, O. & Couty, A. (2023) Winter is ending: how does the  
785 invasive pest *Drosophila suzukii* develop and survive in winter fruits? (Virtual Poster #160423). In:  
786 J. van Baaren (Ed.), 5<sup>th</sup> Annual Virtual Symposium hosted by the International Branch of the  
787 Entomological Society of America, April 24-26, 2023. Entomological Society of America (ESA) -  
788 International Branch: <https://entsoc.org/membership/branches/international/virtual-symposium>
- 789 Lee, J.C., Dreves, A.J., Cave, A.M., Kawai, S., Isaacs, R., Miller, J.C., *et al.* (2015) Infestation of wild  
790 and ornamental noncrop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). *Annals of the*  
791 *Entomological Society of America*, **108**, 117–129.
- 792 Lee, K.P., Simpson, S.J. & Wilson, K. (2008) Dietary protein-quality influences melanization and  
793 immune function in an insect. *Functional Ecology*, **22**, 1052–1061.

- 794 Lehmann, P., Bijl, W. Van Der, Nylin, S., Wheat, C.W. & Gotthard, K. (2017) Timing of diapause  
795 termination in relation to variation in winter climate. *Physiological Entomology*, **42**, 232–238.
- 796 Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I., *et al.* (2004)  
797 Rethinking plant community theory. *Oikos*, **107**, 433–438.
- 798 McNeil, D.J., McCormick, E., Heimann, A.C., Kammerer, M., Douglas, M.R., Goslee, S.C., *et al.*  
799 (2020) Bumble bees in landscapes with abundant floral resources have lower pathogen loads.  
800 *Scientific Reports*, **10**, 1–12.
- 801 Meineke, E.K., Holmquist, A.J., Wimp, G.M. & Frank, S.D. (2017) Changes in spider community  
802 composition are associated with urban temperature, not herbivore abundance. *Journal of Urban*  
803 *Ecology*, **3**, 1–8.
- 804 Moore, M. V. & Lee, R.E. (1991) Surviving the big chill: Overwintering strategies of aquatic and  
805 terrestrial insects. *American Entomologist*, **37**, 111–118.
- 806 Numata, H. & Shintani, Y. (2023) Diapause in univoltine and semivoltine life cycles. *Annual Review of*  
807 *Entomology*, **68**, 257–276.
- 808 Oke, T.R. (1973) City size and the urban heat island. *Atmospheric Environment (1967)*, **7**, 769–779.
- 809 Oxford Economics. (2018) The Economic Impact of Ornamental Horticulture and Landscaping in the  
810 UK a Report for the Ornamental Horticulture Round Table Group. Available online:  
811 <https://www.rhs.org.uk/science/pdf/The-economic-impact-of-ornamental-horticulture-and.pdf>  
812 (accessed on February 2024).
- 813 Panel, A.D.C., Pen, I., Pannebakker, B.A., Helsen, H.H.M. & Wertheim, B. (2020) Seasonal  
814 morphotypes of *Drosophila suzukii* differ in key life-history traits during and after a prolonged period  
815 of cold exposure. *Ecology and Evolution*, **10**, 9085–9099.
- 816 Panel, A.D.C., Zeeman, L., Sluis, B.J. van der, Elk, P. van, Pannebakker, B.A., Wertheim, B., *et al.*  
817 (2018) Overwintered *Drosophila suzukii* are the main source for infestations of the first fruit crops  
818 of the season. *Insects*, **9**, 145.
- 819 Pauli, J.N., Zuckerberg, B., Whiteman, J.P. & Porter, W. (2013) The subnivium: A deteriorating  
820 seasonal refugium. *Frontiers in Ecology and the Environment*, **11**, 260–267.
- 821 Pelton, E., Gratton, C., Isaacs, R., Timmeren, S. Van, Blanton, A. & Guédot, C. (2016) Earlier activity  
822 of *Drosophila suzukii* in high woodland landscapes but relative abundance is unaffected. *Journal of*  
823 *Pest Science*, **89**, 725–733.
- 824 Percival, G.C. & Sheriffs, C.N. (2002) Identification of drought-tolerant woody perennials using  
825 chlorophyll fluorescence. *Journal of Arboriculture*, **28**, 215–223.

- 826 Perrot, T., Rusch, A., Gaba, S. & Bretagnolle, V. (2023) Both long-term grasslands and crop diversity  
827 are needed to limit pest and weed infestations in agricultural landscapes. *Proceedings of the National*  
828 *Academy of Sciences*, **120**.
- 829 Pincebourde, S. & Salle, A. (2020) On the importance of getting fine-scale temperature records near any  
830 surface. *Global Change Biology*, **26**, 6025–6027.
- 831 Pincebourde, S., Sinoquet, H., Combes, D. & Casas, J. (2007) Regional climate modulates the canopy  
832 mosaic of favourable and risky microclimates for insects. *Journal of Animal Ecology*, **76**, 424–438.
- 833 Poyet, M., Eslin, P., Chabrierie, O., Prud’Homme, S.M., Desouhant, E. & Gibert, P. (2017) The invasive  
834 pest *Drosophila suzukii* uses trans-generational medication to resist parasitoid attack. *Scientific*  
835 *Reports*, **7**, 1–8.
- 836 Poyet, M., Eslin, P., Héraude, M., Roux, V. Le, Prévost, G., Gibert, P., *et al.* (2014) Invasive host for  
837 invasive pest: When the Asiatic cherry fly (*Drosophila suzukii*) meets the American black cherry  
838 (*Prunus serotina*) in Europe. *Agricultural and Forest Entomology*, **16**, 251–259.
- 839 Poyet, M., Roux, V. Le, Gibert, P., Meirland, A., Prévost, G., Eslin, P., *et al.* (2015) The wide potential  
840 trophic niche of the asiatic fruit fly *Drosophila suzukii*: The key of its invasion success in temperate  
841 Europe? *PLoS ONE*, **10**.
- 842 Predieri, S., Dris, R., Sekse, L. & Rapparini, F. (2003) Influence of environmental factors and orchard  
843 management on yield and quality of sweet. *Journal of Food Agriculture & Environment*, **1**, 263–266.
- 844 Previati, E., Anna Fano, E. & Leis, M. (2007) Arthropods biodiversity in agricultural landscapes: effects  
845 of land use and Anthropization. *Italian Journal of Agronomy*, **2**, 135.
- 846 Prior, W.D. (1881) *Hardy shrubs*. Oxford.
- 847 Qadir, Z.J., Hadley, J., Breeze, T. & Blanusa, T. (2021) Potential of urban roadside hedges for particulate  
848 matter removal – importance of species choice, and its economic impact. *Acta Horticulturae*, 139–  
849 144.
- 850 Rahel, F.J. (2002) Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics*,  
851 **33**, 291–315.
- 852 Rodrigo, J. (2000) Spring frosts in deciduous fruit trees. Morphological damage and flower hardiness.  
853 *Scientia Horticulturae*, **85**, 155–173.
- 854 Rombaut, A., Guilhot, R., Xuéreb, A., Benoit, L., Chapuis, M.P., Gibert, P., *et al.* (2017) Invasive  
855 *Drosophila suzukii* facilitates *Drosophila melanogaster* infestation and sour rot outbreaks in the  
856 vineyards. *Royal Society Open Science*, **4**, 170117.

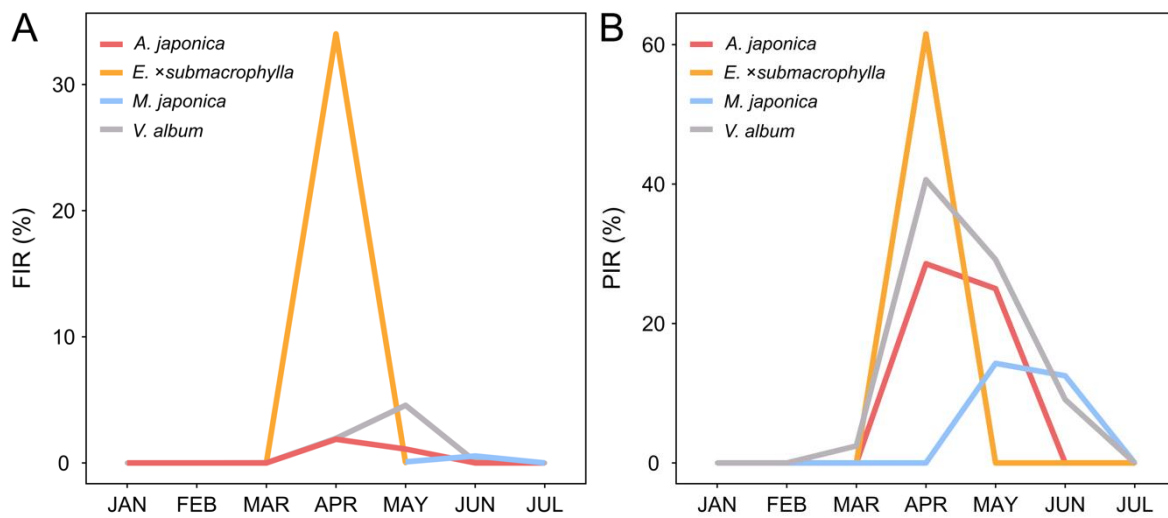
- 857 Rombouts, J.E. & Links, J. (1954) The chemical nature of the antibacterial substance present in *Aucuba*  
858 *japonica* Thunbg. *Experientia*, **XII**, 78–80.
- 859 Rossi-Stacconi, M.V., Kaur, R., Mazzoni, V., Ometto, L., Grassi, A., Gottardello, A., *et al.* (2016)  
860 Multiple lines of evidence for reproductive winter diapause in the invasive pest *Drosophila suzukii*:  
861 useful clues for control strategies. *Journal of Pest Science*, **89**, 689–700.
- 862 Ryan, G.D., Emiljanowicz, L., Wilkinson, F., Kornya, M. & Newman, J.A. (2016) Thermal tolerances  
863 of the spotted-wing drosophila *Drosophila suzukii* (Diptera: Drosophilidae). *Journal of Economic*  
864 *Entomology*, **109**, 746–752.
- 865 Santoiemma, G., Trivellato, F., Caloi, V., Mori, N. & Marini, L. (2019) Habitat preference of *Drosophila*  
866 *suzukii* across heterogeneous landscapes. *Journal of Pest Science*, **92**, 485–494.
- 867 Santoiemma, G., Tonina, L., Marini, L., Duso, C. & Mori, N. (2020) Integrated management of  
868 *Drosophila suzukii* in sweet cherry orchards. *Entomologia Generalis*, **40**, 297–305.
- 869 Shaw, B., Fountain, M. & Wijnen, H. (2019) Control of daily locomotor activity patterns in *Drosophila*  
870 *suzukii* by the circadian clock, light, temperature and social interactions. *Journal of Biological*  
871 *Rhythms*, **34**, 463–481.
- 872 Siffert, A., Cahenzli, F., Kehrli, P., Daniel, C., Dekumbis, V., Egger, B., *et al.* (2021) Predation on  
873 *Drosophila suzukii* within hedges in the agricultural landscape. *Insects*, **12**, 1–12.
- 874 Silver, H. (2023) How to grow the colourful, scented winter shrub Mahonia [WWW Document]. URL  
875 <https://www.houseandgarden.co.uk/article/mahonia-grow-guide> [accessed on 2024].
- 876 Sinclair, B.J. (2015) Linking energetics and overwintering in temperate insects. *Journal of Thermal*  
877 *Biology*, **54**, 5–11.
- 878 Stockton, D.G., Brown, R. & Loeb, G.M. (2019) Not berry hungry? Discovering the hidden food sources  
879 of a small fruit specialist, *Drosophila suzukii*. *Ecological Entomology*, **44**, 810–822.
- 880 Storey, K.B. & Storey, J.M. (2012) Insect cold hardiness: metabolic, gene, and protein adaptation.  
881 *Canadian Journal of Zoology*, **90**, 456–475.
- 882 Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., *et al.* (2011) Habitat  
883 microclimates drive fine-scale variation in extreme temperatures. *Oikos*, **120**, 1–8.
- 884 Tait, G., Cabianca, A., Grassi, A., Pfab, F., Oppedisano, T., Puppato, S., *et al.* (2020) *Drosophila suzukii*  
885 daily dispersal between distinctly different habitats. *Entomologia Generalis*, **40**, 25–37.
- 886 Tait, G., Grassi, A., Pfab, F., Crava, C.M., Dalton, D.T., Magarey, R., *et al.* (2018) Large-scale spatial  
887 dynamics of *Drosophila suzukii* in Trentino, Italy. *Journal of Pest Science*, **91**, 1213–1224.

- 888 Tait, G., Mermer, S., Stockton, D., Lee, J., Avosani, S., Abrieux, A., *et al.* (2021) *Drosophila suzukii*  
889 (Diptera: Drosophilidae): A decade of research towards a sustainable integrated pest management  
890 program. *Journal of Economic Entomology*, **114**, 1950–1974.
- 891 THEIA (2023) OSO 2022 database: product “OSO\_20220101\_VECTOR\_departement\_80”, Somme  
892 department, France, 1/01/2022, Centre d’Expertise Scientifique (CES) “Occupation des sols”,  
893 published: 2023-07-06; [https://www.theia-land.fr/product/carte-occupation-des-sols-de-la-france-](https://www.theia-land.fr/product/carte-occupation-des-sols-de-la-france-metropolitaine/)  
894 [metropolitaine/](https://www.theia-land.fr/product/carte-occupation-des-sols-de-la-france-metropolitaine/)
- 895 Terabayashi, S. (1978) Studies in the morphology and systematics of Berberidaceae II. Floral anatomy  
896 of *Mahonia japonica* (Thunb.) DC. and *Berberis thunbergii* DC. *Acta Phytotaxonomica et*  
897 *Geobotanica*, **XXIX**, 106–118.
- 898 Thomas, P.A., Dering, M., Giertych, M.J., Iszkuło, G., Tomaszewski, D. & Briggs, J. (2023) Biological  
899 Flora of Britain and Ireland: *Viscum album*: No. 303. *Journal of Ecology*, **111**, 701–739.
- 900 Toxopeus, J., Jakobs, R., Ferguson, L. V., Garipey, T.D. & Sinclair, B.J. (2016) Reproductive arrest and  
901 stress resistance in winter-acclimated *Drosophila suzukii*. *Journal of Insect Physiology*, **89**, 37–51.
- 902 Tubby, K. V. & Webber, J.F. (2010) Pests and diseases threatening urban trees under a changing climate.  
903 *Forestry*, **83**, 451–459.
- 904 Ulmer, R. (2022) *Déterminants environnementaux locaux, paysagers et macroclimatiques des relations*  
905 *plante-insecte dans les agrosystèmes : le cas de la drosophile envahissante Drosophila suzukii et des*  
906 *plantes à fruits charnus*. Thesis. Université de Picardie Jules Verne (UPJV), Amiens, France.
- 907 Ulmer, R., Couty, A., Eslin, P., Catterou, M., Baliteau, L., Bonis, A., *et al.* (2022) Macroecological  
908 patterns of fruit infestation rates by the invasive fly *Drosophila suzukii* in the wild reservoir host  
909 plant *Sambucus nigra*. *Agricultural and Forest Entomology*, **24**, 548–563.
- 910 Ulmer, R., Couty, A., Eslin, P. & Chabrerie, O. (2021) Effect of macroarthropods on *Drosophila suzukii*  
911 peri-oviposition events: an experimental screening. *Entomologia Experimentalis et Applicata*, **169**,  
912 519–530.
- 913 Ulmer R., Couty A., Eslin P., Dubois F., Gallet-Moron E., Lamotte N., Pavis J., Samama A., Spicher F.  
914 & Chabrerie O. (2024). Urban ecology of *Drosophila suzukii*. *Urban Ecosystems*.  
915 <https://doi.org/10.1007/s11252-024-01554-w>
- 916 Ulmer, R., Couty, A., Eslin, P., Gabola, F. & Chabrerie, O. (2020) The firethorn (*Pyracantha coccinea*),  
917 a promising dead-end trap plant for the biological control of the spotted-wing drosophila (*Drosophila*  
918 *suzukii*). *Biological Control*, **150**, 104345.

- 919 Urbaneja-Bernat, P., Polk, D., Sanchez-Pedraza, F., Benrey, B., Salamanca, J. & Rodriguez-Saona, C.  
920 (2020) Non-crop habitats serve as a potential source of spotted-wing drosophila (Diptera:  
921 Drosophilidae) to adjacent cultivated highbush blueberries (Ericaceae). *Canadian Entomologist*, **152**,  
922 474–489.
- 923 Vacas, S., Primo, J., Manclús, J.J., Montoya, Á. & Navarro-Llopis, V. (2019) Survey on *Drosophila*  
924 *suzukii* natural short-term dispersal capacities using the mark-release-recapture technique. *Insects*,  
925 **10**, 268.
- 926 Vergotti, M.J., Fernández-Martínez, M., Kefauver, S.C., Janssens, I.A. & Peñuelas, J. (2019) Weather  
927 and trade-offs between growth and reproduction regulate fruit production in European forests.  
928 *Agricultural and Forest Meteorology*, **279**, 107711.
- 929 Wallingford, A.K., Lee, J.C. & Loeb, G.M. (2016) The influence of temperature and photoperiod on the  
930 reproductive diapause and cold tolerance of spotted-wing drosophila, *Drosophila suzukii*.  
931 *Entomologia Experimentalis et Applicata*, **159**, 327–337.
- 932 Walsh, D.B., Bolda, M.P., Goodhue, R.E., Dreves, A.J., Lee, J., Bruck, D.J., *et al.* (2011) *Drosophila*  
933 *suzukii* (Diptera: Drosophilidae): Invasive pest of ripening soft fruit expanding its geographic range  
934 and damage potential. *Journal of Integrated Pest Management*, **2**, 3–9.
- 935 Wharton, D.A. (2011) Cold tolerance of New Zealand alpine insects. *Journal of Insect Physiology*, **57**,  
936 1090–1095.
- 937 White, S.N., Boyd, N.S. & Acker, R.C. van. (2012) Growing degree-day models for predicting lowbush  
938 blueberry (*Vaccinium angustifolium* Ait.) ramet emergence, tip dieback, and flowering in Nova  
939 Scotia, Canada. *HortScience*, **47**, 1014–1021.
- 940 Wiman, N.G., Dalton, D.T., Anfora, G., Biondi, A., Chiu, J.C., Daane, K.M., *et al.* (2016) *Drosophila*  
941 *suzukii* population response to environment and management strategies. *Journal of Pest Science*, **89**,  
942 653–665.
- 943 Withers, P. & Allemand, R. (2012) Les Drosophiles de la région Rhône-Alpes (Diptera, Drosophilidae).  
944 *Bulletin de la Société entomologique de France*, **117**, 473–482.
- 945 Zavalloni, C., Andresen, J.A. & Flore, J.A. (2006) Phenological models of flower bud stages and fruit  
946 growth of “Montmorency” sour cherry based on growing degree-day accumulation. *Journal of the*  
947 *American Society for Horticultural Science*, **131**, 601–607.
- 948 Zerulla, F.N., Schmidt, S., Streitberger, M., Zebitz, C.P.W. & Zelger, R. (2015) On the overwintering  
949 ability of *Drosophila suzukii* in South Tyrol. *Journal of Berry Research*, **5**, 41–48.
- 950 Zuber, D. (2004) Biological flora of Central Europe: *Viscum album* L. *Flora*, **199**, 181–203.

951 **Tables and Figures**

952



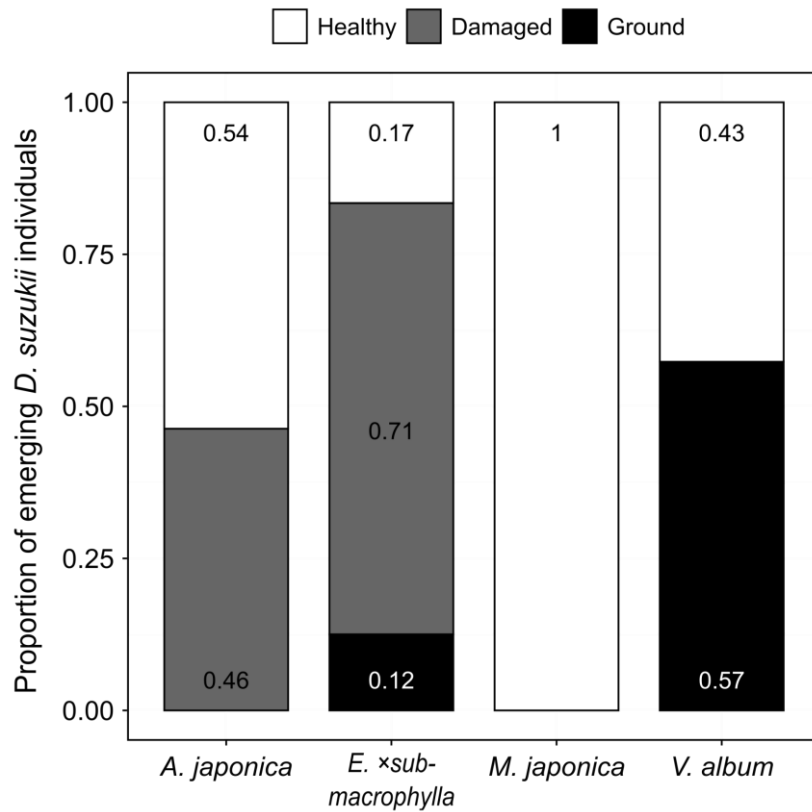
953

954 **Figure 1** Variation of fruit infestation rate (FIR) (A) and plant infestation rate (PIR) (B) of *Aucuba*  
955 *japonica*, *Elaeagnus x submacrophylla*, *Mahonia japonica* and *Viscum album* by *Drosophila suzukii*  
956 between January and July 2022. Fruit Infestation Rate:  $FIR = 100 \times \text{number of emerged individuals}$   
957  $\text{from all fruit collected from a plant individual} / \text{number of fruit collected from the same plant individual}$ .  
958 Plant Infestation Rate:  $PIR = 100 \times \text{number of infested plant individuals in a month} / \text{number of sampled}$   
959  $\text{plant individuals in the same month}$ .

960

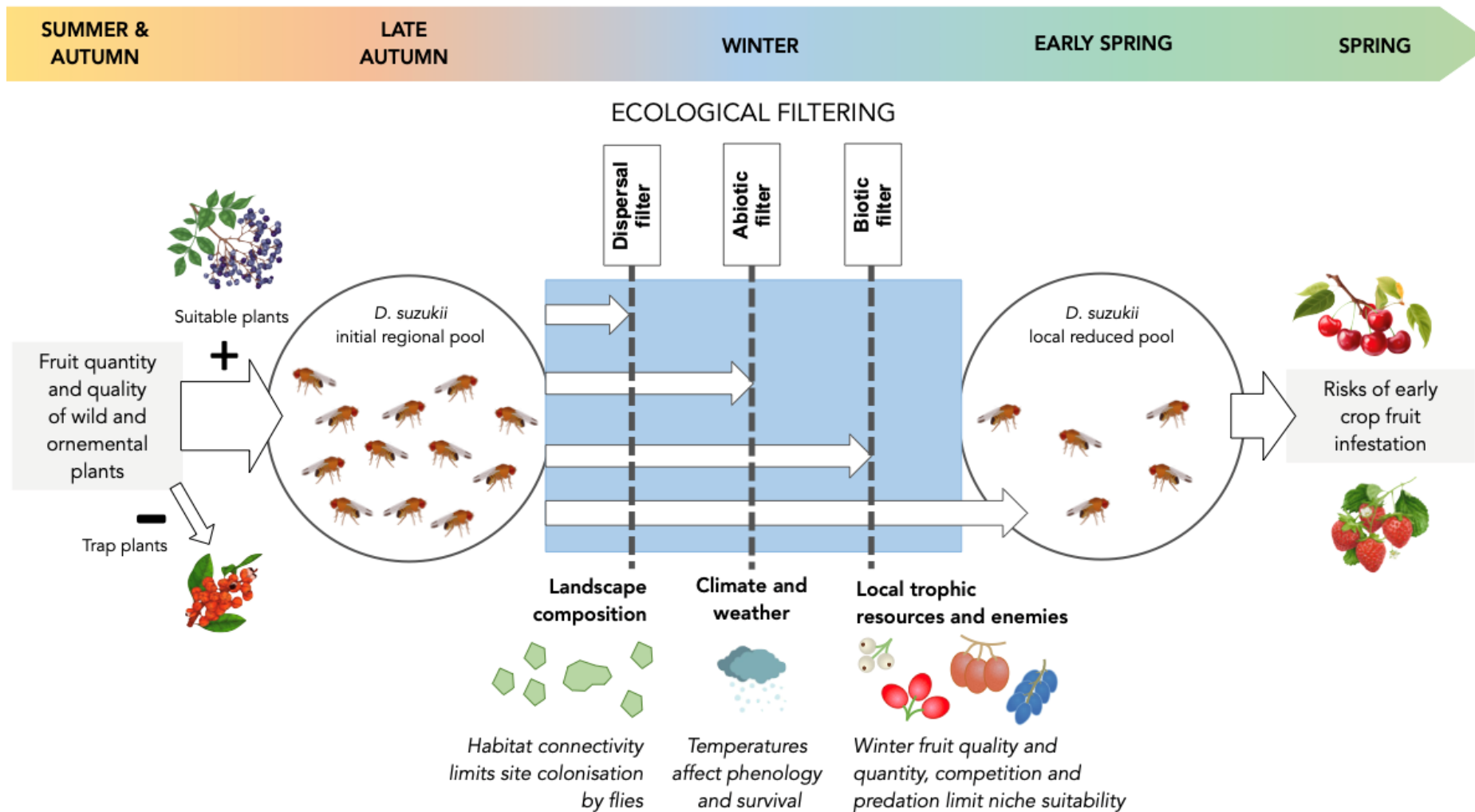
961





962

963 **Figure 2** Proportion of *Drosophila suzukii* individuals emerging from the different fruit categories of  
 964 *Aucuba japonica* (n = 1385), *Elaeagnus xsubmacrophylla* (n = 1357), *Mahonia japonica* (n = 2280)  
 965 and *Viscum album* (n = 16,232) between January and July 2022, in relation to their position and health  
 966 status: healthy on the plant (Healthy), damaged on the plant (Damaged) or fallen on the ground  
 967 (Ground).



968

969 **Figure 3** Conceptual summary of the successive ecological challenges that *Drosophila suzukii* must face over the seasonal cycle and which, in particular, shape  
 970 the dynamics of populations subjected to winter conditions. It provides an organised view of the hierarchy of ecological filters (“environmental filtering”,

971 adapted from theories in plant ecology: Lake et al. 2007; Lortie et al. 2004; Rahel 2002) influencing vernal fruit infestations by *D. suzukii* and preceding the  
972 arrival of the earliest commercial fruit (e.g., strawberries, cherries). First, in autumn, an initial large pool of *D. suzukii* individuals is produced as the result of  
973 emergences from a high diversity of summer and autumnal fruit (Poyet et al. 2015) present in various habitats of the region (even if some of the fruit are not  
974 favourable to the fly, Ulmer et al. 2020). Second, a dispersal filter determines the sub-pool of *D. suzukii* individuals (among the autumnal regional pool) which  
975 arrives at a particular site, depending principally on the abundance of semi-natural (forests and hedgerows) or anthropic habitats in the surrounding landscape  
976 (Deconninck et al. 2024a). Third, abiotic factors, mainly climatic conditions (e.g., frost, cumulative temperature, microclimatic refuges, recent rain events...),  
977 affect flies's activity (e.g., end of winter diapause, flight and oviposition) and survival in each local site. Fourth, biotic filtering can occur when a fly arrives at  
978 a focal site but fails to lay eggs, produce offspring and persist, depending on biotic interactions with local plant (i.e., types of fruit, their availability and  
979 suitability) and animal diversity (e.g., potential presence of enemies such as predators (Ulmer et al. 2021) or competitors (Deconninck et al. 2024b)). Finally,  
980 the legacy of these multiscale ecological filters results in a reduced pool of *D. suzukii* at the end of winter (Ulmer et al. 2024). This spring fly population emerging  
981 from vernal fruit (*Elaeagnus × submacrophylla*, *Viscum album*, *Aucuba japonica*, *Mahonia japonica*) is the main source for infestations of the first fruit crops  
982 (Panel et al. 2018).

983 **Table 1** Number of plant individuals sampled in the study area between January and July 2022 with number of fruit sampled, total number of emerged *D. suzukii*  
 984 individuals, number of emerged *D. suzukii* individuals per fruit, per volume (cm<sup>3</sup>) and per skin area (cm<sup>2</sup>) of fruit, mean ± SE and max FIR and PIR. Fruit  
 985 Infestation Rate: FIR = 100 × number of emerged individuals from all fruit collected from a given plant individual / number of fruit collected from the same  
 986 plant individual. Plant Infestation Rate: PIR = 100 × number of infested plant individuals in the study area / number of sampled plant individuals in the study  
 987 area.

<b>Plant species</b>	<b>No plant</b>	<b>No fruit</b>	<b>No emerged</b>	<b>No emerged per fruit</b>	<b>No emerged per volume (cm<sup>3</sup>) of fruit</b>	<b>No emerged per area (cm<sup>2</sup>) of fruit</b>	<b>Mean FIR ± SE (%)</b>	<b>Max FIR (%)</b>	<b>PIR (%)</b>
<i>Aucuba japonica</i>	43	1385	24	0.0173	0.0121	0.0028	0.81 ± 2.32	10.00	13.95
<i>Elaeagnus ×submacrophylla</i>	25	1357	392	0.2889	0.3646	0.0683	17.68 ± 38.74	146.97	32.00
<i>Mahonia aquifolium</i>	8	690	0	0	0	0	0.00	0.00	0.00
<i>Mahonia japonica</i>	17	2280	4	0.0018	0.0071	0.0009	0.30 ± 1.07	4.41	11.76
<i>Viscum album</i>	119	16232	216	0.0133	0.0323	0.005	1.46 ± 5.87	42.55	18.49
<b>Total</b>	<b>212</b>	<b>21944</b>	<b>636</b>	<b>0.029</b>	<b>0.045</b>	<b>0.0084</b>	<b>3.09 ± 14.83</b>		

988

989 **Table 2** Fruit seasonality of winter and spring host plant species of *D. suzukii* in the study area in 2022.  
 990 Filled and empty bars correspond to months when adult flies emerged from fruit and to months when  
 991 ripe fruit were present and sampled but no flies emerged, respectively.

Plant species	JAN	FEB	MAR	APR	MAY	JUN	JUL
<i>Viscum album</i>	Empty		Filled				Empty
<i>Elaeagnus ×submacrophylla</i>	Empty			Filled	Empty	Empty	
<i>Aucuba japonica</i>	Empty			Filled		Empty	
<i>Mahonia japonica</i>	Empty				Filled		Empty
<i>Mahonia aquifolium</i>	Empty				Empty		

992

993 **Table 3** Effect of environmental variables on fruit infestation rate (FIR) by *Drosophila suzukii* analysed  
 994 by GLMM. Host plant species were used as a random factor. Fruit Infestation Rate:  $FIR = 100 \times$  number  
 995 of emerged *Drosophila suzukii* individuals from all fruit collected from a host plant individual / number  
 996 of fruit collected from the same host plant individual.

Dependent variables	Explanatory variable	Model parameters						
		F	Estimates	SE	d.f.	t	p	AICC
Fruit Infestation Rate (FIR) by <i>D. suzukii</i> ( $\log_{10}+1$ , n = 204 plants individual sampled, random factor = plant species)	Model constant	54.061	0.4729	0.0643	198.00	7.353	<0.001	206.97
	RAIN7J	11.574	-0.0524	0.0154	198.00	-3.402	0.001	
	NFH7Jh	12.890	-0.0109	0.0030	198.00	-3.590	<0.001	
	GRASS20	9.282	-0.0033	0.0011	198.00	-3.047	0.003	
	WATE100	17.461	0.0265	0.0063	198.00	4.179	<0.001	
	HETH3000	13.896	-5.8668	1.5738	198.00	-3.728	<0.001	

Note: RAIN7J: cumulative precipitation in the last 7 days, NFH7Jh: number of frost hours in the last 7 days, GRASS20: cover of grassland in a radius of 20 m, WATE100: cover of water in a radius of 100 m, HETH3000: cover of shrub land in a 3 km radius.

997

998

999 **Table 4** Effect of environmental variables on fruit infestation rate (FIR) of each host plant species  
 1000 (*Aucuba japonica*, *Elaeagnus*  $\times$  *submacrophylla*, *Mahonia japonica* and *Viscum album*) by *Drosophila*  
 1001 *suzukii* analysed by GLMs.

Dependent variables	Explanatory variable	Model parameters					
		Wald $\chi^2$	Estimates	SE	d.f.	p	AICC
Fruit Infestation Rate (FIR) of <i>Aucuba japonica</i> by <i>D. suzukii</i> ( $\log_{10}+1$ , n = 43 plant individuals sampled)	Model constant	0.385	0.058	0.0929	38	0.535	-11.539
	SOIL	17.247	0.011	0.0027	38	<0.001	
	GRASS20	23.771	-0.009	0.0019	38	<0.001	
	RP_FC	26.718	0.320	0.0619	38	<0.001	
	WATE250	14.152	-0.151	0.0401	38	<0.001	
Fruit Infestation Rate (FIR) of <i>Elaeagnus</i> $\times$ <i>submacrophylla</i> by <i>D. suzukii</i> ( $\log_{10}+1$ , n = 25 plant individuals sampled)	Model constant	50.310	1.141	0.1608	21	<0.001	35.000
	NFD14Js	19.659	-0.190	0.0428	21	<0.001	
	RAIN7J	45.122	-0.327	0.0487	21	<0.001	
Fruit Infestation Rate (FIR) of <i>Mahonia japonica</i> by <i>D. suzukii</i> ( $\log_{10}+1$ , n = 17 plant individuals sampled)	Model constant	5.802	0.752	0.3122	15	0.016	-7.337
	STRUNK	5.053	-0.051	0.0228	15	0.025	

Note: SOIL: cover of bare soil in a radius of 10 m, GRASS20: cover of grassland in a radius of 20 m, RP\_FC: richness of fleshy-fruited plant species in a radius of 20 m, WATE250: cover of water in a radius of 250 m, NFD14Js: number of frost days in the last 14 days, RAIN7J: cumulative precipitation in the last 7 days, ROAD250: cover of road in a radius of 250 m, STRUNK: trunk circumference.

1002

1003

1004 **Table 5** Effect of environmental variables on fruit infestation rate (FIR) by *Drosophila suzukii* in *Viscum*  
 1005 *album* analysed by GLMM. Host tree species parasitised by *Viscum album* was used as a random factor  
 1006 (see Table S6 and Figure S3 for details on mistletoe host tree species). Fruit Infestation Rate:  $FIR = 100$   
 1007  $\times$  number of emerged individuals from all fruit collected from a *Viscum album* individual / number of  
 1008 fruit collected from the same *Viscum album* individual.

Dependent variables	Explanatory variable	Model parameters						
		F	Estimates	SE	d.f.	t	p	AICC
Fruit Infestation Rate (FIR) of <i>Viscum album</i> by <i>D. suzukii</i> (log <sub>10</sub> +1, n = 119 host plants)	Model constant	28.678	-0.601	0.1123	20.676	-5.355	<0.001	58.013
	GROUTOT	18.794	0.006	0.0015	113.961	4.335	<0.001	
	MLSURF	20.111	0.050	0.0112	13.968	4.485	0.001	
	RAIN_010122	20.844	0.007	0.0016	111.239	4.566	<0.001	

Note: GROUTOT: % of fruit collected on the ground, MLSURF: mean leaf area index of *Viscum album*, RAIN\_010122: cumulative precipitation between 01/01/22 and the sampling date.

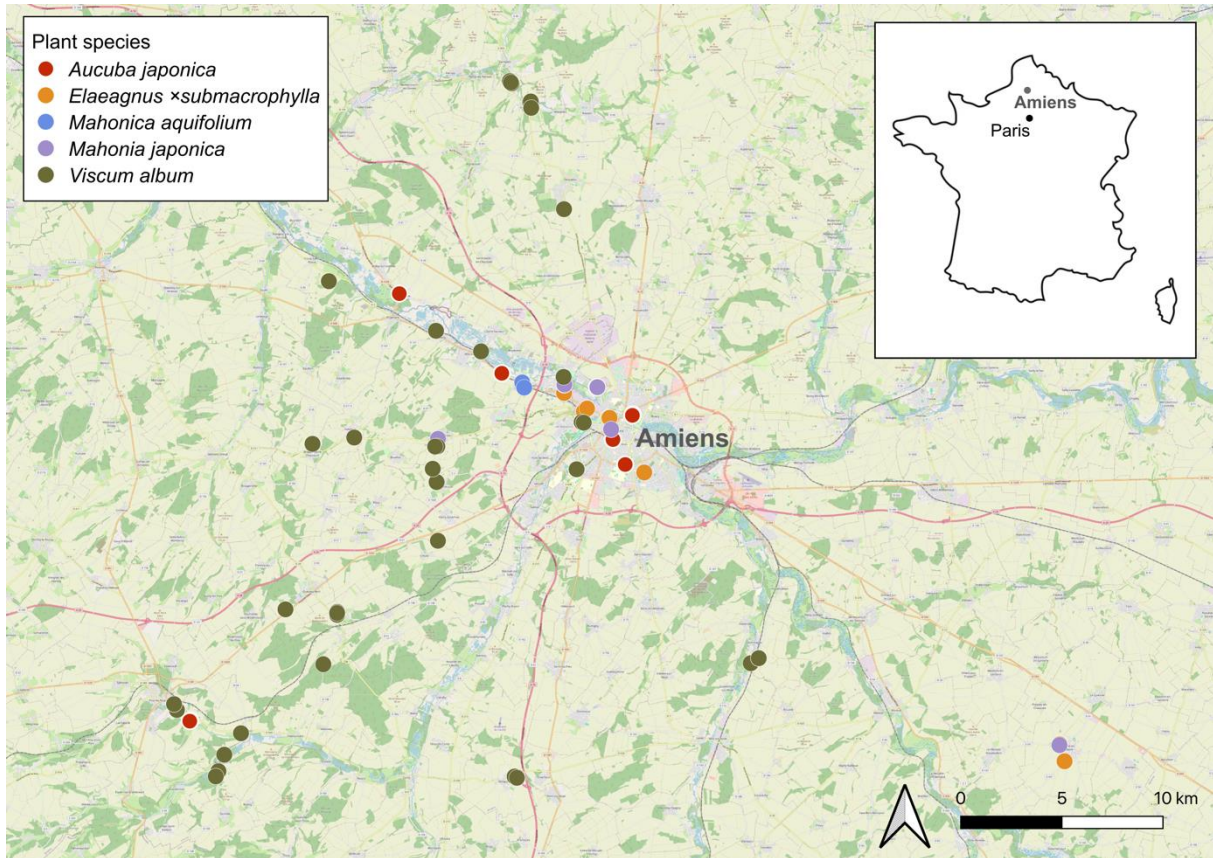
1009

## Supplementary Material

1010

1011

1012



1013

1014 **Figure S1** Map of the sampling locations of host plants of *Drosophila suzukii* in Amiens region in the  
1015 north of France. Made with QGIS using OpenStreetMap base map.



1016 **Table S1** List of the variables assessed in the study. Abbreviations: h: local air temperature measurement from HOBO, s: measurement from weather station, 7J  
 1017 and 14J: measurements taken 7 and 14 days before fruit collection. The columns ‘Ecological relevance’ and ‘Expected correlation’ give information about what  
 1018 was the expected link between the potential explanatory variables and the fruit infestation by *Drosophila suzukii*.

CATEGORY	CODE	DESCRIPTION	UNIT	ECOLOGICAL RELEVANCE	EXPECTED CORRELATION
<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 target species individual / total number of fruit collected from the same target species individual	%		
	PIR	Plant Infestation Rate = $100 \times$ number of infested target species individuals in a region or month / total number of target species individuals sampled in the same region or month	%		
<b>FRUIT CATEGORIES</b>					
<b>NUMBER</b>	HEAFRUIT	Number of healthy fruit collected on a plant individual	Number	Developmental substrate	+
	DAMFRUIT	Number of damaged fruit (rotten or with open skin) collected on a plant individual	Number	Developmental substrate	+
	PLAFRUIT	Sum of healthy and damaged fruit collected on a plant individual	Number	Developmental substrate	+
	GROFRUIT	Number of fruit collected on the ground under the canopy of a plant individual	Number	Developmental substrate	-
	TOTFRUIT	Sum of fruit collected on the canopy and on the ground of a plant individual	Number	Developmental substrate	+
<b>PERCENTAGE</b>	%HEALPLA	$100 \times$ HEAFRUIT / PLAFRUIT	%	Resource quality	+
	%DAMAPLA	$100 \times$ DAMFRUIT / PLAFRUIT	%	Resource quality	+
	%HEALTOT	$100 \times$ HEAFRUIT / TOTFRUIT	%	Resource quality	+
	%DAMATOT	$100 \times$ DAMFRUIT / TOTFRUIT	%	Resource quality	+
	%FPLANT	$100 \times$ PLAFRUIT / TOTFRUIT	%	Resource quality	+
	%GROUTOT	$100 \times$ GROFRUIT / TOTFRUIT	%	Resource quality	-
<b>LIFE TRAITS OF THE <i>D. SUZUKII</i>'S HOST PLANT INDIVIDUALS</b>					
<b>FRUIT TRAITS</b>	MFWIDTH	Mean fruit diameter (n = 5 fruit measured per plant individual)	cm	Resource quantity	+
	MFVOL	Mean fruit volume ( $4/3 \times \pi \times$ mean radius <sup>3</sup> ) (n = 5 fruit measured)	cm <sup>3</sup>	Resource quantity	+

	MFSURF	Mean fruit skin area ( $4 \times \pi \times \text{mean radius}^2$ ) (n = 5 fruit measured)	cm <sup>2</sup>	Resource quantity	+
<b>LEAVE TRAITS</b>	MLENGTH	Mean leaf length (from the basis of the petiole to the top/apex of the blade; n = 5 leaves measured per plant individual)	cm	Protection against weather disturbances	+
	MLWIDTH	Mean leaf width (n = 5 leaves measured)	cm	Protection against weather disturbances	+
	MLSURF	Mean leaf area index (area index = length $\times$ width; n = 5 leaves measured)	cm <sup>2</sup>	Protection against weather disturbances	+
	LENGTH	Maximum diameter of the target species individual	m	Attractiveness / shelter	+
<b>INDIVIDUAL MORPHOLGY</b>	WIDTH	Minimum diameter of the target species individual	m	Attractiveness / shelter	+
	STRUNK	Circumference of the largest trunk (not measured for <i>Viscum album</i> individuals)	cm	Attractiveness / resource permanence	+
	INDFRUIT	Total number of fruit present on a sampled target species individual	Number	Resource quantity	+
	HEIGHT	Height of <i>Viscum album</i> individual from the ground	m	Resource accessibility	+/-
<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	Attractiveness / resource accessibility	+/-
	HLENGH	Maximum diameter of the host tree canopy	m	Attractiveness / shelter	+
	HWIDTH	Minimum diameter of the host tree canopy	m	Attractiveness / shelter	+
	HTRUNK	Circumference of the host tree trunk	cm	Attractiveness / resource permanence	+
	HFRUIT	Number of fleshy fruit of the host tree	Number	Resource quantity	+
	HMISTLETOE	Number of <i>Viscum album</i> individuals on the host tree	Number	Resource quantity	+
	HMISTLETOE20	Number of <i>Viscum album</i> individuals in a 20 m radius around the host tree	Number	Resource quantity	+
SUMHMIST20	Sum of <i>Viscum album</i> individuals on the host tree and in a 20 m radius around the host tree	Number	Resource quantity	+	
<b>SITE AND LANDSCAPE CHARACTERISTICS</b>					
<b>LOCAL ENVIRONMENT (in a 5 m radius around the sampled plant)</b>	ALTM	Site altitude	m		+/-
	SLOM	Site slope	Degree		+/-
	CTREE	Cover of tree layer (height > 8 m)	%	Shelter	+

	CSTRUB	Cover of shrub layer (1-8 m)	%	Shelter or resource / predator reservoir	+/-
	CHERB	Cover of herb layer (< 1 m)	%	Shelter / predator reservoir	+/-
	HHERBMEAN	Height of herbaceous layer	cm	Shelter / predator reservoir	+/-
	HTREE / HSHRUB	Height of shrubs / trees	m	Shelter / predator reservoir	+/-
	COMP	Cover of biowaste composter	%	Resource	+
	SOIL	Cover of bare soil	%	Reduced presence of potential resource / anthropogenic disturbance indicator	-
	DWOOD	Cover of dead wood debris on the ground	%	Shelter	+
	TLITTER	Depth of leaf litter	cm	Shelter	+
	LITTER	Cover of leaf litter	%	Shelter	+
	RIVER	Cover of stream	%	Reduced presence of potential resource / water availability	+/-
	POND	Cover of pond	%	Reduced presence of potential resource / water availability	+/-
	PATH	Cover of (unpaved) pathway	%	Reduced presence of potential resource	-
	ROAD	Cover of road and paved surface	%	Reduced presence of potential resource	-
	BUILD	Cover of building	%	Shelter / anthropization	+/-
<b>LOCAL HABITATS (in a 20 m radius around the sampled plant)</b>	ORC20	Cover of orchard area (fruit trees and their associated grassland)	%	Resource reservoir	+
	FOREST20	Cover of woodland	%	Shelter / predator reservoir	+/-
	PASTURE20	Cover of grazed grassland	%	Shelter / predator reservoir	+/-
	MOW20	Cover of mown grassland	%	Shelter / predator reservoir	+/-
	GRASS20	Cover of grassland (PASTURE20+MOW20)	%	Shelter / predator reservoir	+/-
	SWAMP20	Cover of swamp	%	Reduced presence of potential resource	-
	CROP20	Cover of conventional agriculture crop	%	Resource reservoir / pesticide risk	+/-

	VEGGAR20	Cover of market garden	%	Shelter or resource reservoir	+
	GARDEN20	Cover of private garden	%	Shelter or resource reservoir	+
	SHRUB20	Cover of shrub	%	Shelter or resource / predator reservoir	+/-
	BUILD20	Cover of building	%	Shelter / anthropization	+/-
	HEDGE20	Cover of hedgerow	%	Shelter or resource / predator reservoir	+/-
	RIVER20	Cover of river	%	Reduced presence of potential resource / water availability	+/-
	POND20	Cover of pond	%	Reduced presence of potential resource / water availability	+/-
	POPLARP20	Cover of poplar plantation	%	Resource reservoir	+
	GREESP20	Cover of urban green space (small urban planted herbaceous or shrub strips)	%	Shelter or resource / predator reservoir	+/-
	PARK20	Cover of park	%	Shelter or resource / predator reservoir	+/-
	GGSP20	Total urban vegetated area (sum of garden, green space and park cover)	%	Shelter or resource / predator reservoir	+/-
	RP_FC	Fleshy-fruited plant species richness	Number	Resource reservoir	+
<b>LANDSCAPE COMPOSITION</b> (from OSO 2022 data basis; cover percentages calculated within the following radii around the sampled plant: 10 m, 20 m, 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	%	Resourced reservoir / pesticide risk	+/-
	WATE%	Cover of river and other water surfaces	%	Reduced presence of potential resource / water availability	+/-
	FORE%	Cover of woodland	%	Shelter or resource / predator reservoir	+/-
	HETH%	Cover of heathland	%	Shelter or resource / predator reservoir	+/-
	MOW%	Cover of grassland	%	Shelter or resource / predator reservoir	+/-
	ROAD%	Cover of road and paved surface	%	Anthropization	-
	URB%	Cover of urban area	%	Shelter / anthropization	+/-

	ORC%	Cover of orchard area (fruit trees and their associated grassland)	%	Resource	+
	INDU%	Cover of industrial area	%	Anthropization	-
<b>METEOROLOGY</b>					
<b>HOURLY METEOROLOGY (hour scale, from h: HOBO data)</b>	GDH7J	Sum of positive temperature hours (Growth Degree Hours) in the 7 days before sampling	°C	Larval development and adult activity	+
	SMTH7J	Sum of negative temperature hours in the 7 days before sampling	°C	Larval development and adult activity	+
	NFH7J	Number of hours with negative temperatures ( $\leq 0$ °C) (Number of freezing hours) in the 7 days before sampling	Number	Larval development and adult activity	-
	MINMINTH7J	Minimum temperature in the 7 days before sampling	°C	Larval development and adult activity	+
	MAXMAXTH7J	Maximum temperature in the 7 days before sampling	°C	Larval development and adult activity	+
	MEANTH7J	Mean temperature over the 7 days before sampling	°C	Larval development and adult activity	+
	<b>DAILY METEOROLOGY (day scale, from h: HOBO data, s: 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)</b>	GDDMC	Sum of daily positive temperature (Growth Degree Days) calculated from the mean temperatures of the 7 or 14 days before fruit sampling	°C	Larval development and adult activity
NFD		Number of days with negative temperature ( $\leq 0$ °C) during the 7 or 14 days before fruit sampling	Number	Larval development and adult activity	-
RAIN		Sum of daily precipitation in the 7 or 14 days before the fruit sampling	cm	Plant growth / adult activity	+/-
SNOW		Sum of daily snowfall in the 7 or 14 days before the fruit sampling	cm	Larval development and adult activity	-
MMIN		Mean minimum temperature during the 7 and 14 days before fruit sampling	°C	Larval development and adult activity	+
MMAX		Mean maximum temperature during the 7 days before fruit sampling	°C	Larval development and adult activity	+
MMEANCALC		Calculated mean of daily mean temperatures of the 7 or 14 days before the fruit sampling	°C	Larval development and adult activity	+
MINMIN		Lowest minimum temperature during the 7 or 14 days before fruit sampling	°C	Larval development and adult activity	+
MAXMAX		Highest maximum temperature during the 7 or 14 days before fruit sampling	°C	Larval development and adult activity	+
SUMT_010122		Sum of daily positive temperature (Growth Degree Days) between 01/01/2022 and the sampling date	°C	Plant growth, seasonal progression / adult activity	+

	RAIN_010122	Sum of rain precipitation between 01/01/2022 and the sampling date	cm	Plant growth, seasonal progression / adult activity	+/-
1019					
1020					
1021					

1022 **Table S2** Weather station information. Geographic area: city of the research laboratories, station city:  
 1023 postcode and the municipality name of the weather station location, Station coordinates: geographic  
 1024 location of the city where the weather station is located, Label city: postcode and municipality name  
 1025 according to Historique-Météo.net, Label city coordinates: geographic location of the label city, Mean  
 1026 distance: mean distance between the weather station and sampled sites (in kilometers). Geographic  
 1027 coordinate system: WGS 84.

<b>Geographic area</b>	<b>Station city</b>	<b>Station city coordinates</b>	<b>Label city</b>	<b>Label city coordinates</b>	<b>Mean distance (m)</b>
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

1028

1029 **Table S3** Number of plant individuals sampled in the study area between January and July 2022 with number of fruit sampled, total number of emerged *D.*  
 1030 *subobscura* and *D. repleta* individuals, mean  $\pm$  SE and max FIR and PIR. Fruit Infestation Rate: FIR =  $100 \times$  number of emerged individuals from all fruit  
 1031 collected from a given plant individual / number of fruit collected from the same plant individual. Plant Infestation Rate: PIR =  $100 \times$  number of infested plant  
 1032 individuals in the study area / number of sampled plant individuals in the study area.

Plant species	No plant	No fruit	<i>D. subobscura</i>				<i>D. repleta</i>
			No emerged	Mean FIR $\pm$ SE (%)	Max FIR (%)	PIR (%)	No emerged
<i>Aucuba japonica</i>	43	1385	0	0.00	0.00	0.00	0
<i>Elaeagnus</i> $\times$ <i>submacrophylla</i>	25	1357	0	0.00	0.00	0.00	0
<i>Mahonia aquifolium</i>	8	690	0	0.00	0.00	0.00	0
<i>Mahonia japonica</i>	17	2280	0	0.00	0.00	0.00	0
<i>Viscum album</i>	119	16232	27	0.23 $\pm$ 1.58	16.67	6.72	1
<b>Total</b>	<b>212</b>	<b>21944</b>	<b>27</b>	<b>0.13 <math>\pm</math> 1.19</b>			<b>1</b>

1033



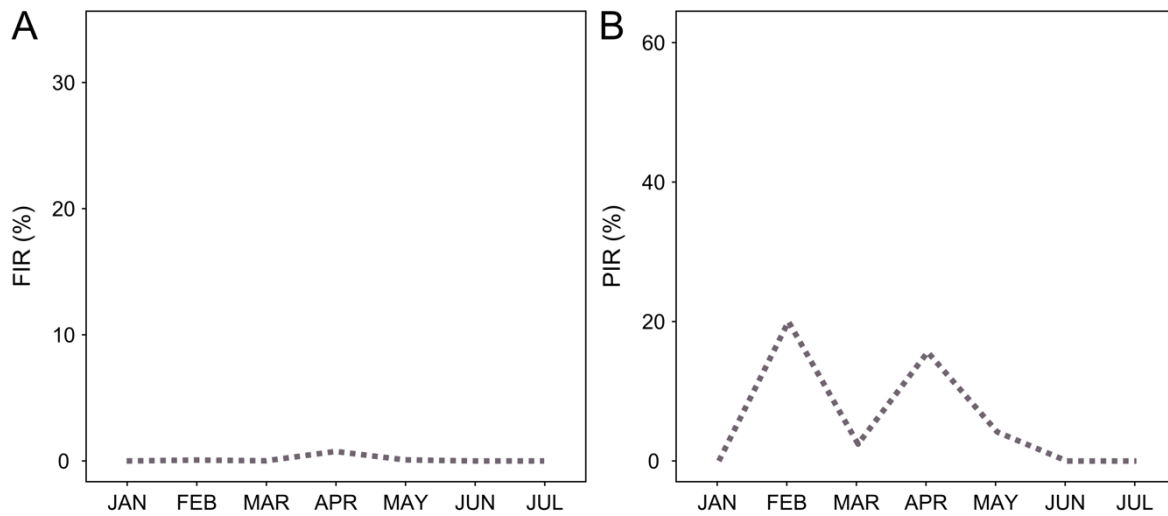
1034 **Table S4** Fruit seasonality of winter and spring host plant species of *D. subobscura* in the study area in  
 1035 2022. Filled and empty bars correspond to months when adult flies emerged from fruit and to months  
 1036 when ripe fruit were present and sampled but no flies emerged, respectively.

Plant species	JAN	FEB	MAR	APR	MAY	JUN	JUL
<i>Viscum album</i>	Empty	Filled	Filled	Filled	Filled	Empty	Empty
<i>Elaeagnus ×submacrophylla</i>	Empty	Empty	Empty	Empty	Empty	Empty	Empty
<i>Aucuba japonica</i>	Empty	Empty	Empty	Empty	Empty	Empty	Empty
<i>Mahonia japonica</i>	Empty	Empty	Empty	Empty	Empty	Empty	Empty
<i>Mahonia aquifolium</i>	Empty	Empty	Empty	Empty	Empty	Empty	Empty

1037

1038

1039



1040

1041 **Figure S2** Variation of fruit infestation rate (FIR) (A) and plant infestation rate (PIR) (B) of *Viscum*  
1042 *album* by *Drosophila subobscura* between January and July 2022. Fruit Infestation Rate:  $FIR = 100 \times$   
1043 number of emerged individuals from all fruit collected from a plant individual / number of fruit collected  
1044 from the same plant individual. Plant Infestation Rate:  $PIR = 100 \times$  number of infested plant individuals  
1045 in a month / number of sampled plant individuals in the same month.

1046

1047 **Table S5** Effect of environmental variables on fruit infestation rate (FIR) by *D. subobscura* in *Viscum*  
 1048 *album* analysed by GLMM. Host tree species parasitised by *Viscum album* was used as a random factor  
 1049 (see Table S6 and Figure S3 for details on mistletoe host tree species). Fruit Infestation Rate:  $FIR = 100$   
 1050  $\times$  number of emerged individuals from all fruit collected from a *Viscum album* individual / number of  
 1051 fruit collected from the same *Viscum album* individual.

Dependent variables	Explanatory variable	Model parameters						
		F	Estimates	SE	d.f.	t	p	AICC
Fruit Infestation Rate (FIR) of <i>Viscum album</i> by <i>D. subobscura</i> (log <sub>10</sub> +1, n = 119 host plants)	Model constant	4.422	0.059	0.028	115	2.103	0.038	-107.704
	HSHRUB	4.866	-0.015	0.007	115	-2.206	0.029	
	POPLARP20	4.986	0.003	0.002	115	2.233	0.027	
	SNOW14J	11.748	0.088	0.026	115	3.428	0.001	

Note: GROUTOT: % of fruit collected on the ground, MLSURF: mean leaf area index of *Viscum album*, RAIN\_010122: cumulative precipitation between 01/01/22 and the sampling date, HSHRUB: mean shrub height in a radius of 5 m, POPLARP20: % of poplar grove in a radius of 20 m, SNOW14J: cumulative snow precipitation in the last 14 days.

1052

### 1053 **Discussion of *Drosophila subobscura* infestation results**

1054 *Drosophila subobscura* infestation in *V. album* fruit was positively associated with the cover of  
 1055 poplar in a radius of 20 m and the cumulative snow precipitation in the preceding 14 days, and negatively  
 1056 associated with the mean shrub height in a 5 m radius (GLMM, Table S5; but see Table S6 and Figure  
 1057 S3 for poplar influence on infestations). The association with snow is consistent with *D. subobscura*  
 1058 ecology and phenology, given that it is a cold tolerant species and often found in winter (David et al.  
 1059 2003; Delbac et al. 2020), when it can even be dominant (Deconninck et al. 2024b). Snow may also  
 1060 provide an ephemeral shelter against freezing for the flies, as reported for some other arthropods  
 1061 (Aitchison 2001; Pauli et al. 2013). Concerning shrub height, Argañaraz et al. (2018) showed that a  
 1062 vertical structure of vegetation at least up to 1 m in height contributes to higher richness and abundance  
 1063 of insect predators in urban green areas, potentially explaining the negative association between  
 1064 vegetation height and *D. subobscura* infestation. As *D. subobscura* mainly infests fruit on the ground,  
 1065 this same feature of local vegetation architecture may have also masked the presence of small fallen  
 1066 fruit of *V. album* to the fly. Conversely, as *V. album* is frequently found on poplars (Briggs 2021), the  
 1067 cover of poplar plantation might indicate the size of the mistletoe reservoir available for *D. subobscura*,  
 1068 as this fly is known to overwinter in mistletoe (Deconninck et al. 2024a) and mistletoe on poplars are  
 1069 the most heavily infested by *D. subobscura* (Table S6 and Figure S3).

1070 **Table S6** Host trees of *Viscum album* individuals sampled in the study and mean FIR  $\pm$  SE (%) by *D.*  
 1071 *suzukii* (*Dsuz*) and *D. subobscura* (*Dsub*).

1072

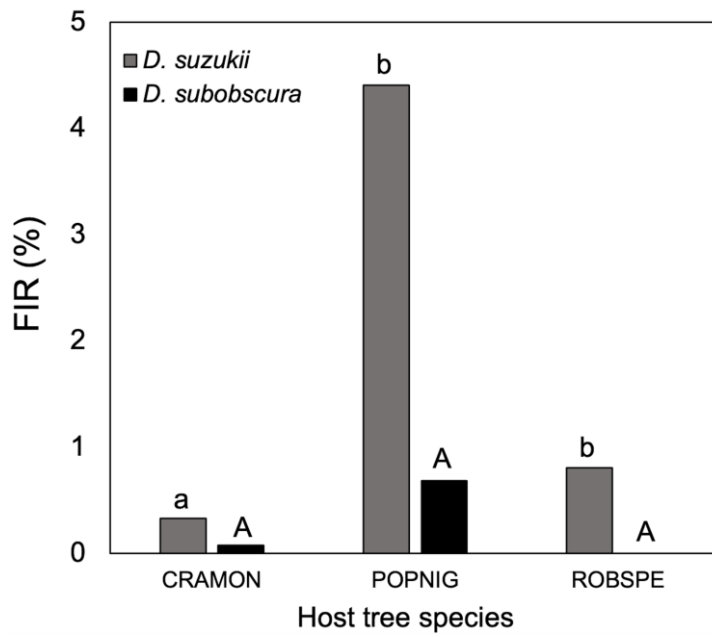
Species	Code	Number	%	<b>Dsuz mean FIR <math>\pm</math> SE (%)</b>	<b>Dsub mean FIR <math>\pm</math> SE (%)</b>
<i>Acer campestre</i>	ACECAM	6	5.0%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Acer</i> sp.	ACER	3	2.5%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Crataegus monogyna</i>	CRAMON	59	49.6%	0.33 $\pm$ 0.15	0.08 $\pm$ 0.04
<i>Malus domestica</i>	MALDOM	7	5.9%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Populus nigra</i>	POPNEG	33	27.7%	4.41 $\pm$ 1.83	0.69 $\pm$ 0.52
<i>Robinia pseudoacacia</i>	ROBSPE	11	9.2%	0.81 $\pm$ 0.74	0.00 $\pm$ 0.00
<b>TOTAL</b>		119	100.0%	1.46 $\pm$ 0.54	0.23 $\pm$ 0.15

1073

1074

1075

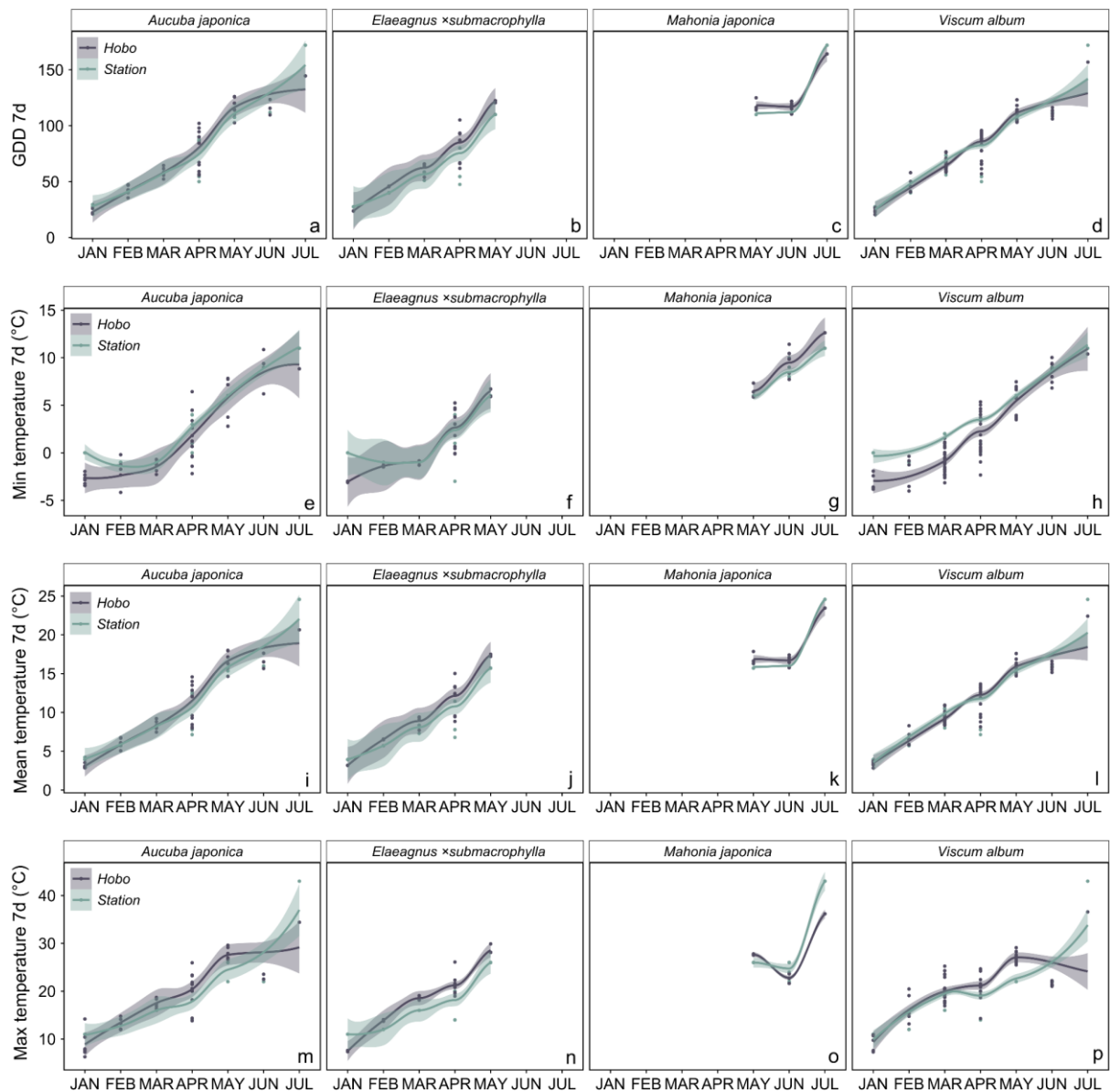
1076



1077

1078 **Figure S3** Mean FIR  $\pm$  SE (%) by *D. suzukii* and *D. subobscura* in *Viscum album* individuals according  
1079 to its major host tree species. CRAMON: *Crataegus monogyna*, POPNIG: *Populus nigra*, ROBSPE:  
1080 *Robinia pseudoacacia*. Significant differences ( $p < 0.05$ ) between months are represented by different  
1081 lowercase and capital letters for *D. suzukii* and *D. subobscura* respectively (Kruskal-Wallis tests).

1082



1083

1084 **Figure S4** Difference in Growth Degree Days (a-d), minimum (e-h), mean (i-l) and maximum (m-p)  
 1085 temperatures (°C) of the last 7 days preceding fruit sampling between regional weather stations  
 1086 ('Station'; macroclimate) and local dataloggers under plant canopy ('Hobo'; microclimate) throughout  
 1087 the months and according to plant species (*Aucuba japonica*: a, e, i, m; *Elaeagnus x submacrophylla*: b,  
 1088 f, j, n; *Mahonia japonica*: c, g, k, o; *Viscum album*: d, h, l, p).

1089