



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, 50 (2), pp.258-273. <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 CC BY 4.0 - Attribution - International License

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

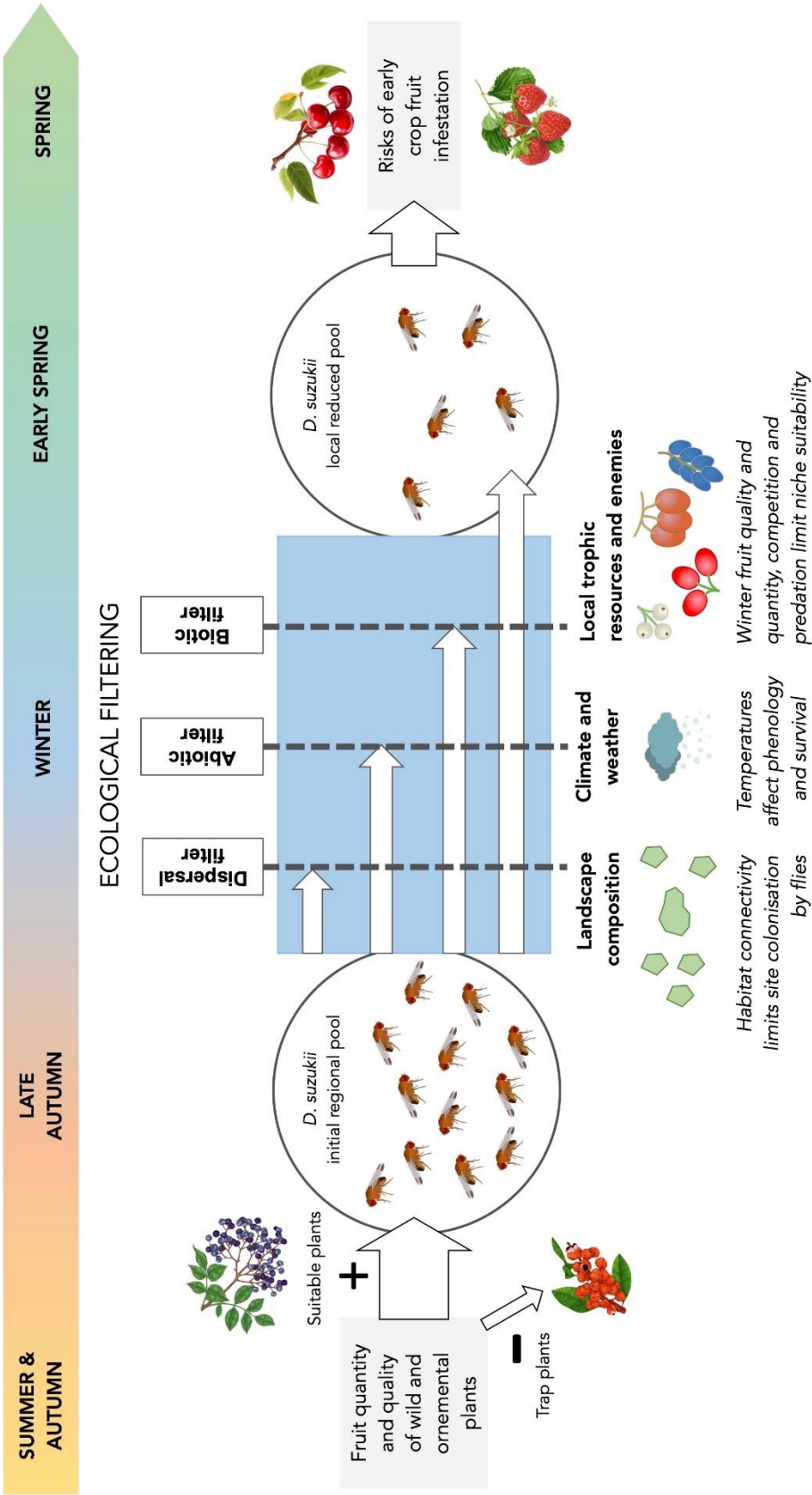
Gwenaëlle Deconninck¹, Méghan Boulembert², Patrice Eslin², Aude Couty², Françoise Dubois², Emilie Gallet-Moron², Sylvain Pincebourde¹, Olivier Chabrerie²

¹Institut de Recherche sur la Biologie de l’Insecte, IRBI UMR7261, CNRS - Université de Tours, Tours, France

²EDYSAN, Ecologie et Dynamique des Systèmes Anthropisés, UMR 7058 CNRS, Université de Picardie Jules Verne, Amiens, France

*: Corresponding author: olivier.chabrerie@u-picardie.fr

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



Authors' ORCID:

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

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

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

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

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

Running title

Winter fruit infested by Drosophila suzukii

Abstract (247 words)

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

Keywords

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

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-

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

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

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

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

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

Materials and Methods

Study area

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

Sampling design

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

Traits of host plant species and fruit

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

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

Environmental variables

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

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

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

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

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

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

Emergence of Drosophila species

After collection, the fruit sampled from each plant were placed on wet cotton wool in cylindrical plastic transparent containers (diameter = 118 mm, height = 135 mm, volume = 1,476 cm³), covered with a nylon mesh, and maintained in a temperature-controlled room at 20°C under a 16:8 L:D regime. Adult flies emerging from the fruit were placed in 70% ethanol. They were identified to species level using Bächli et al. (2004) and specific criteria published for *D. suzukii* (Withers and Allemand 2012). Individuals of each species were sexed and counted using a Leica M205C stereomicroscope equipped with a Leica MC170 HD camera and the Leica Application Suite software.

Infestation variables

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

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

Statistical analyses

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

Results

Availability of fruit resources across winter and spring

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

Host plant fruit infestation

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

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

Seasonality in host plant fruit infestation

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

Environmental variables correlating with fruit infestation

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

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

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

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

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

Discussion

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

Climate and weather effects on fruit infestation

Several climatic variables correlated with *D. suzukii* infestation. These variables acted at different temporal scales (cumulative climate of the year *versus* weather in the weeks immediately preceding sampling) and spatial scales (regional macroclimate *versus* sub-canopy microclimate). Cumulative precipitation and the number of frost hours locally measured under the canopy of the host plants in the week preceding sampling had an overall negative correlation with infestation. Rain is known to limit the flight ability of flies (Dickerson et al. 2014) and frost may have induced mortality (Ryan et al. 2016). The association between climatic variables and *D. suzukii* infestation differed between plant species. *Aucuba japonica* and *M. japonica* infestations were less associated with climatic variables than with the other environment features (i.e., by landscape composition or local conditions). These ornamental species are often planted in gardens close to houses and parks in an urbanised environment, which may have protected them from extreme low temperatures through the “heat island effect” (Oke 1973; Meineke et al. 2017), making climatic variations a secondary factor in the explanation of the FIR. *Elaeagnus ×submacrophylla* infestation was negatively correlated with frost in the 14 days preceding sampling and with rain in the previous week. Fruit of *E. ×submacrophylla* are soft and very sensitive to rot (pers. obs. reported in an experimental study: Larges et al. 2023); the alternation of frost followed by rain may have caused damage to fruit (Ladaniya 2015), thereby accelerating the rotting process (Rodrigo 2000) and reducing fruit suitability for *D. suzukii*, which prefers ripening and ripe fruit (Walsh et al. 2011; Atallah et al. 2014). Surprisingly, precipitation had contrasting effects on *D. suzukii* infestation between *E. ×submacrophylla* and *V. album* fruit. Precipitation in the previous week (i.e., on a short-term scale) had a negative correlation with *D. suzukii* infestation in *E. ×submacrophylla* fruit, while cumulative precipitation from the beginning of the year to the sampling date (i.e., on a long-term scale for an insect) positively correlated with *D. suzukii* infestation in *V. album* fruit. The first precipitation variable (RAIN7J; see Table 3), reflecting the most recent weather conditions, besides limiting the fly’s flight ability, may also favour the rot of *E. ×submacrophylla* fruit, as noted above. Conversely, the second precipitation variable (RAIN_01012022; see Table 5) reflects the regional climate and/or the progression of seasons; at this longer temporal scale, rain would have had a positive impact on plant phenology, growth and fruit production (Vergotti et al. 2019), increasing the number of ripe fruit available for *D. suzukii* on *V. album* plants. These contrasting correlations of climatic variables with infestation over different timescales also means that single-scale climatic models are insufficient to predict infestation rates, and that other variables related to the ecology of the focal insect and of the host plant identity need to be considered. Finally, it is notable that recent weather conditions were more associated with infestation than the cumulative climate experienced from the start of the year, as also shown by Wiman et al. (2016). This suggests that the end of the winter reproductive diapause in flies could be triggered more strongly by short-term spring heat peaks than by the accumulation of heat since the beginning of the year, in contrast to that of plants (Zavalloni et al. 2006). This also highlights an ongoing need to identify the true cues, and their timing, controlling *Drosophila* entry into and exit from diapause (Numata and Shintani 2023). The use of macroclimate alone in predictive models would tend

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Ecological filtering of Drosophila suzukii populations throughout winter

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

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

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

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

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

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

References

- Abdalla, T.E. (2019) Some wild *Elaeagnus* species: Overview, description, biochemistry, and utilization. In *Wild Fruits: Composition, Nutritional Value and Products* (ed. by Mariod, A.A.), Ghibaish, Sudan, pp. 507–522.
- Abe, T. (2001) Flowering phenology, display size, and fruit set in an understory dioecious shrub, *Aucuba japonica* (Cornaceae). *American Journal of Botany*, **88**, 455–461.
- Aitchison, C.W. (2001) The effect of snow cover on small animals. In *Snow Ecology: An Interdisciplinary Examination of Snow Covered Ecosystems* (ed. by Jones, H.G., Pomeroy, J.W., Walker, D.A., and Hoham, R.W.). Cambridge, UK: Cambridge University Press.
- Argañaraz, C.I., Rubio, G.D. & Gleiser, R.M. (2018) Spider communities in urban green patches and their relation to local and landscape traits. *Biodiversity and Conservation*, **27**, 981–1009.
- Aslan, C. & Rejmanek, M. (2012) Native fruit traits may mediate dispersal competition between native and non-native plants. *NeoBiota*, **12**, 1–24.
- Asplen, M.K. (2018) Dispersal strategies in terrestrial insects. *Current Opinion in Insect Science*, **27**, 16–20.
- Asplen, M.K., Anfora, G., Biondi, A., Choi, D.S., Chu, D., Daane, K.M., *et al.* (2015) Invasion biology of spotted wing *Drosophila* (*Drosophila suzukii*): a global perspective and future priorities. *Journal of Pest Science*, **88**, 469–494.
- Atallah, J., Teixeira, L., Salazar, R., Zaragoza, G. & Kopp, A. (2014) The making of a pest: The evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132840.
- Bächli, G., Vilela, C.R., Escher, S.A. & Saura, A. (2005) *The Drosophilidae Diptera of Fennoscandia and Denmark*. Leiden.
- Bale, J.S. & Hayward, S.A.L. (2010) Insect overwintering in a changing climate. *Journal of Experimental Biology*, **213**, 980–994.
- Ballard, J.W.O., Melvin, R.G. & Simpson, S.J. (2008) Starvation resistance is positively correlated with body lipid proportion in five wild caught *Drosophila simulans* populations. *Journal of Insect Physiology*, **54**, 1371–1376.
- Barney, C.W., Hawksworth, F.G. & Geils, B.W. (1998) Hosts of *Viscum album*. *European Journal of 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 to
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. & Kehrli, 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 ¹⁵N. *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.), 5th 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., Chabrerie, 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. & Blanus, 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., Kehrl, 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-doccupation-des-sols-de-la-france-](https://www.theia-land.fr/product/carte-doccupation-des-sols-de-la-france-metropolitaine/)
894 [metropolitaine/](https://www.theia-land.fr/product/carte-doccupation-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.

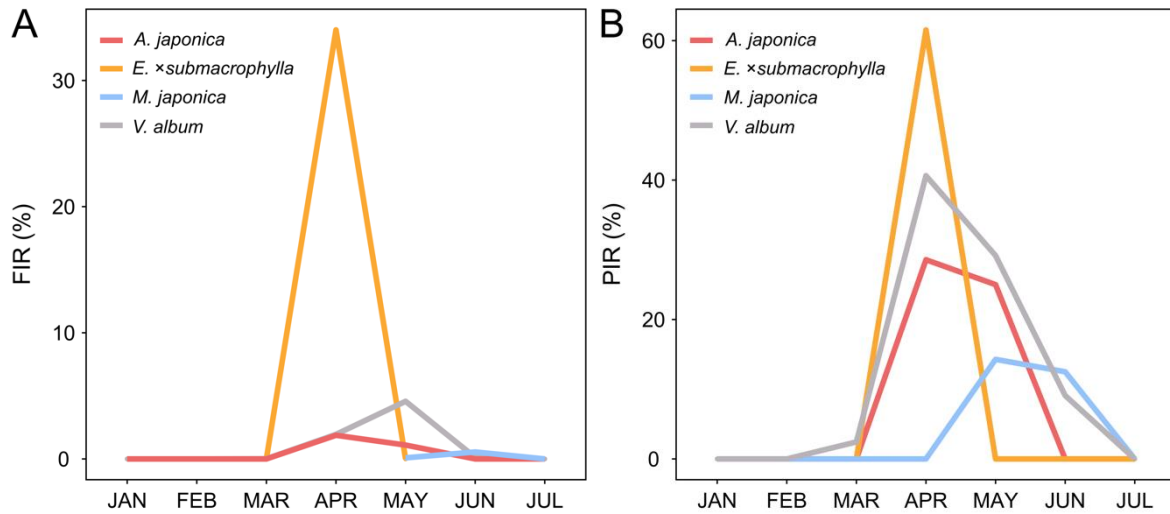
907 Ulmer, R., Couty, A., Eslin, P., Catterou, M., Baliteau, L., Bonis, A., *et al.* (2022) Macroecological
908 patterns of fruit infestation rates by the invasive fly *Drosophila suzukii* in the wild reservoir host
909 plant *Sambucus nigra*. *Agricultural and Forest Entomology*, **24**, 548–563.

910 Ulmer, R., Couty, A., Eslin, P. & Chabrierie, 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 & Chabrierie 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. & Chabrierie, 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.



953

954 **Figure 1** Variation of fruit infestation rate (FIR) (A) and plant infestation rate (PIR) (B) of *Aucuba*
955 *japonica*, *Elaeagnus ×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 $\text{plant individuals in the same month}$.

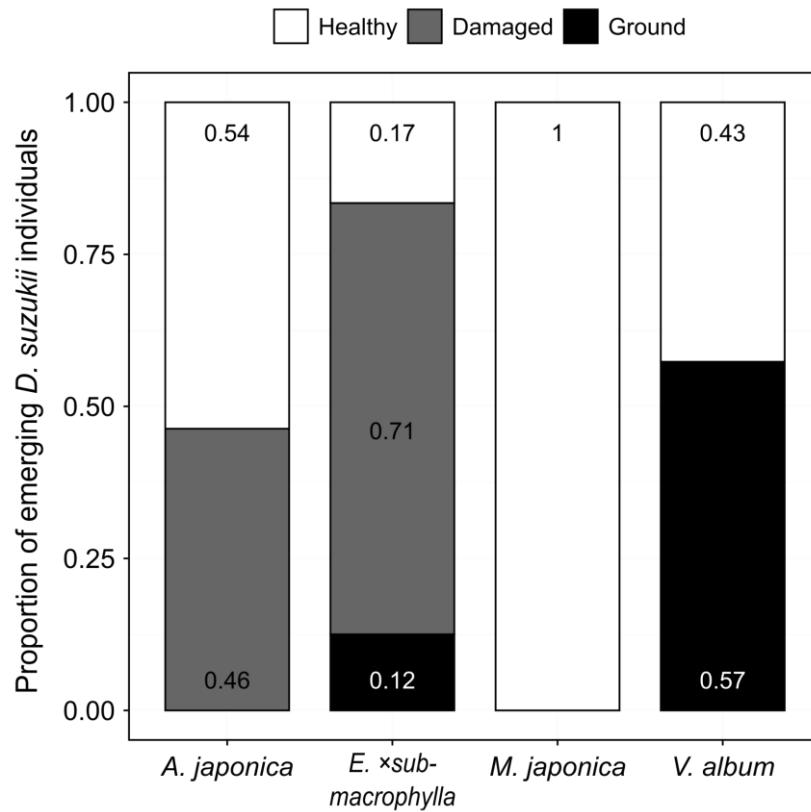
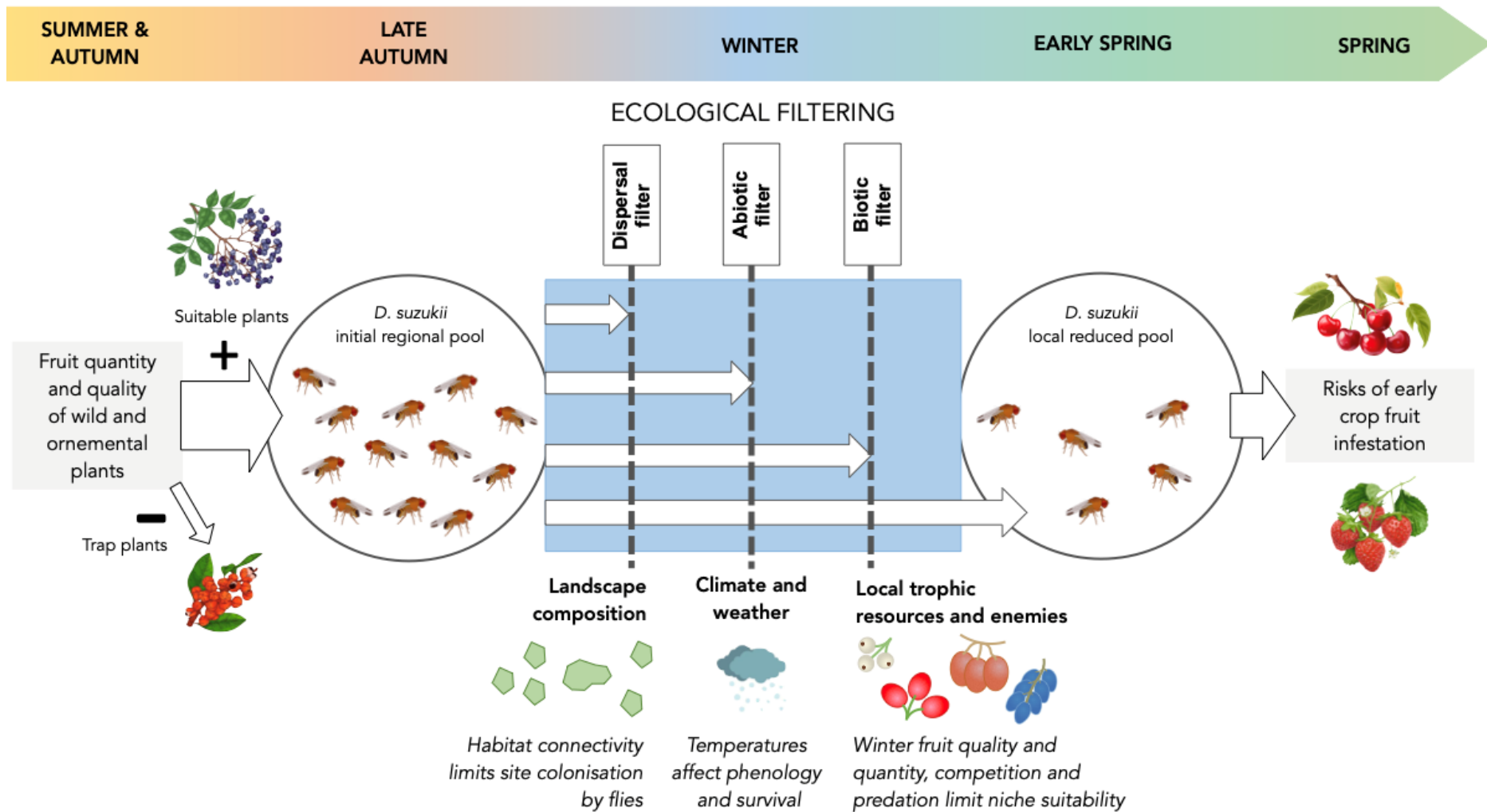


Figure 2 Proportion of *Drosophila suzukii* individuals emerging from the different fruit categories of *Aucuba japonica* (n = 1385), *Elaeagnus xsubmacrophylla* (n = 1357), *Mahonia japonica* (n = 2280) and *Viscum album* (n = 16,232) between January and July 2022, in relation to their position and health status: healthy on the plant (Healthy), damaged on the plant (Damaged) or fallen on the ground (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 (cm³) and per skin area (cm²) of fruit, mean $\pm$ SE and max FIR and PIR. Fruit
985 Infestation Rate: FIR = 100 $\times$ 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 $\times$ number of infested plant individuals in the study area / number of sampled plant individuals in the study
987 area.

Plant species	No plant	No fruit	No emerged	No emerged per fruit	No emerged per volume (cm ³) of fruit	No emerged per area (cm ²) of fruit	Mean FIR $\pm$ SE (%)	Max FIR (%)	PIR (%)
<i>Aucuba japonica</i>	43	1385	24	0.0173	0.0121	0.0028	0.81 $\pm$ 2.32	10.00	13.95
<i>Elaeagnus</i> $\times$ <i>submacrophylla</i>	25	1357	392	0.2889	0.3646	0.0683	17.68 $\pm$ 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 $\pm$ 1.07	4.41	11.76
<i>Viscum album</i>	119	16232	216	0.0133	0.0323	0.005	1.46 $\pm$ 5.87	42.55	18.49
Total	212	21944	636	0.029	0.045	0.0084	3.09 $\pm$ 14.83		

988

Table 2 Fruit seasonality of winter and spring host plant species of *D. suzukii* in the study area in 2022. Filled and empty bars correspond to months when adult flies emerged from fruit and to months 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>							
<i>Elaeagnus</i> × <i>submacrophylla</i>							
<i>Aucuba japonica</i>							
<i>Mahonia japonica</i>							
<i>Mahonia aquifolium</i>							

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

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.

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

Dependent variables	Explanatory variable	Model parameters					
		Wald χ^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 × 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	
	ROAD250	7.019	0.290	0.1095	21	0.008	
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.

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

Dependent variables	Explanatory variable	Model parameters						
		<i>F</i>	Estimates	SE	d.f.	<i>t</i>	<i>p</i>	AICC
Fruit Infestation Rate (FIR) of <i>Viscum album</i> by <i>D. suzukii</i> (log ₁₀ +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.

Supplementary Material

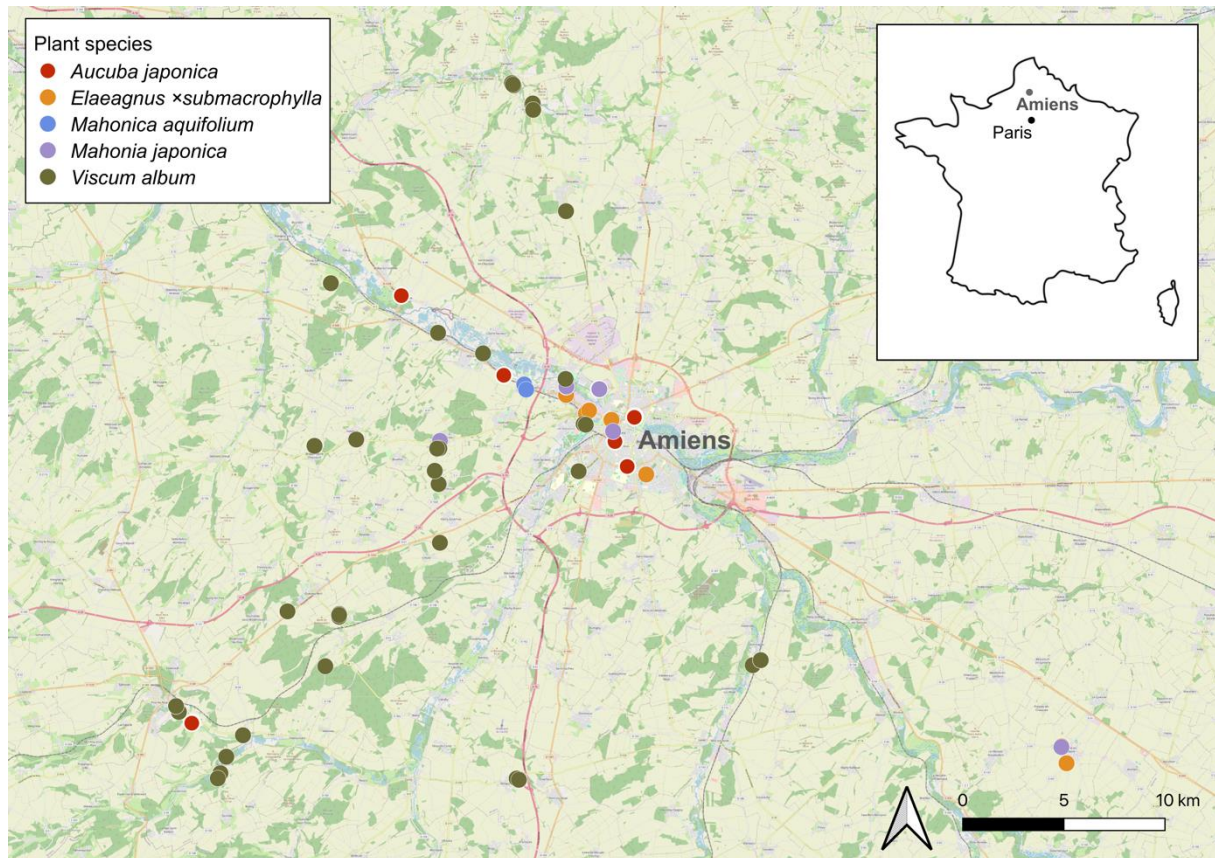


Figure S1 Map of the sampling locations of host plants of *Drosophila suzukii* in Amiens region in the north of France. Made with QGIS using OpenStreetMap base map.

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
DROSOPHILIDAE SPECIES					
INFESTATION INDICES	FIR	Fruit Infestation Rate = $100 \times \text{number of emerged } Drosophila \text{ individuals from fruit collected from target species individual} / \text{total number of fruit collected from the same target species individual}$	%		
	PIR	Plant Infestation Rate = $100 \times \text{number of infested target species individuals in a region or month} / \text{total number of target species individuals sampled in the same region or month}$	%		
FRUIT CATEGORIES					
NUMBER	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	+
PERCENTAGE	%HEALPLA	$100 \times \text{HEAFRUIT} / \text{PLAFRUIT}$	%	Resource quality	+
	%DAMAPLA	$100 \times \text{DAMFRUIT} / \text{PLAFRUIT}$	%	Resource quality	+
	%HEALTOT	$100 \times \text{HEAFRUIT} / \text{TOTFRUIT}$	%	Resource quality	+
	%DAMATOT	$100 \times \text{DAMFRUIT} / \text{TOTFRUIT}$	%	Resource quality	+
	%FPLANT	$100 \times \text{PLAFRUIT} / \text{TOTFRUIT}$	%	Resource quality	+
	%GROUTOT	$100 \times \text{GROFRUIT} / \text{TOTFRUIT}$	%	Resource quality	-
LIFE TRAITS OF THE <i>D. SUZUKII</i>'S HOST PLANT INDIVIDUALS					
FRUIT TRAITS	MFWIDTH	Mean fruit diameter (n = 5 fruit measured per plant individual)	cm	Resource quantity	+
	MFVOL	Mean fruit volume ($4/3 \times \pi \times \text{mean radius}^3$) (n = 5 fruit measured)	cm ³	Resource quantity	+

	MFSURF	Mean fruit skin area ($4 \times \pi \times \text{mean radius}^2$) (n = 5 fruit measured)	cm ²	Resource quantity	+
LEAVE TRAITS	MLLENGTH	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 ²	Protection against weather disturbances	+
INDIVIDUAL MORPHOLGY	LENGTH	Maximum diameter of the target species individual	m	Attractiveness / shelter	+
	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	+/-
MISTLETOE HOST TREE					
MISTLETOE HOST TREE	HOSTSPE	<i>Viscum album</i> host species	Species		
	HHEIGHT	Height of the host tree	m	Attractiveness / resource accessibility	+/-
	HLENGTH	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	+
SITE AND LANDSCAPE CHARACTERISTICS					
LOCAL ENVIRONMENT (in a 5 m radius around the sampled plant)	ALTM	Site altitude	m		+/-
	SLOM	Site slope	Degree		+/-
	CTREE	Cover of tree layer (height > 8 m)	%	Shelter	+

	CSHRUB	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	+/-
LOCAL HABITATS (in a 20 m radius around the sampled plant)	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	+
	CROP%	Cover of conventional agriculture crop	%	Resourced reservoir / pesticide risk	+/-
LANDSCAPE COMPOSITION (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)	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	-
METEOROLOGY					
HOURLY METEOROLOGY (hour scale, from h: HOBO data)	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 (≤ 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	+
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)	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 (≤ 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					

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

Geographic area	Station city	Station city coordinates	Label city	Label city coordinates	Mean distance (m)
Amiens	80260_Flesselles	50.0 N, 2.25 E	80600_Doullens	50.15724 N, 2.34019 E	16,288
	80160_Essertaux	49.75 N, 2.25 E	80000_Amiens	49.894067 N, 2.295753 E	17,516
	80890_Condé-Folie	50.017 N, 2.017 E	80420_Flixecourt	50.01465 N, 2.08095 E	22,404
	80300_Albert	50.0 N, 2.65 E	80300_Albert	50.00091 N, 2.65096 E	28,868
	80140_Doudelainville	50.0 N, 1.767 E	80100_Abbeville	50.105467 N, 1.836833 E	30,264
	60130_Angivillers	49.5 N, 2.5 E	80500_Montdidier	49.65 N, 2.56667 E	29,046

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.

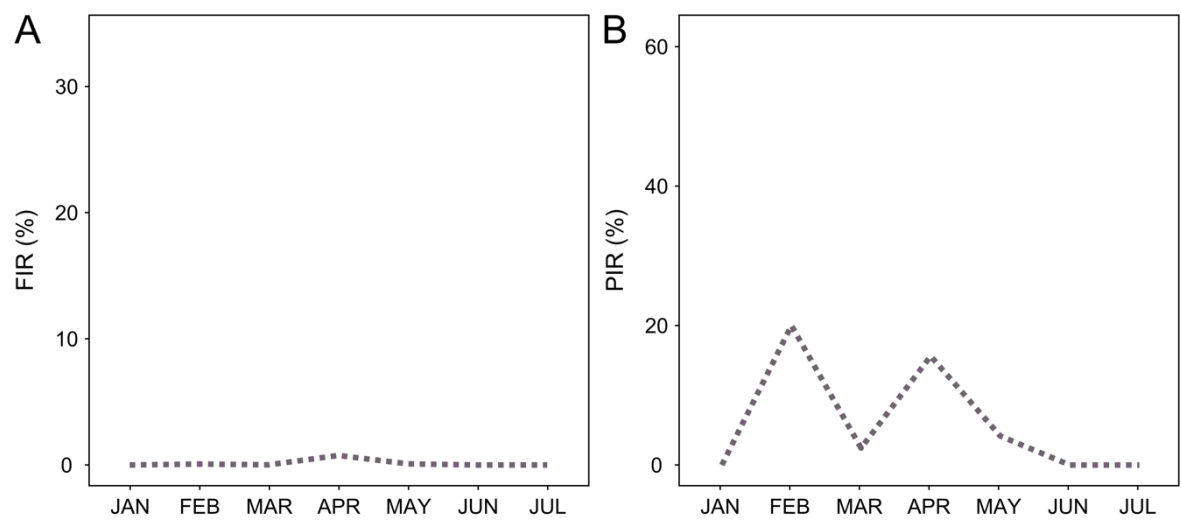
Plant species	No plant	No fruit	<i>D. subobscura</i>				<i>D. repleta</i>
			No emerged	Mean FIR $\pm$ SE (%)	Max FIR (%)	PIR (%)	No emerged
<i>Aucuba japonica</i>	43	1385	0	0.00	0.00	0.00	0
<i>Elaeagnus</i> $\times$ <i>submacrophylla</i>	25	1357	0	0.00	0.00	0.00	0
<i>Mahonia aquifolium</i>	8	690	0	0.00	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
Total	212	21944	27	0.13 $\pm$ 1.19			1

1033

Table S4 Fruit seasonality of winter and spring host plant species of *D. subobscura* in the study area in 2022. Filled and empty bars correspond to months when adult flies emerged from fruit and to months 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>							
<i>Elaeagnus</i> × <i>submacrophylla</i>							
<i>Aucuba japonica</i>							
<i>Mahonia japonica</i>							
<i>Mahonia aquifolium</i>							

1039



1040

1041

1042

1043

1044

1045

1046

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

Table S5 Effect of environmental variables on fruit infestation rate (FIR) by *D. subobscura* in *Viscum album* analysed by GLMM. Host tree species parasitised by *Viscum album* was used as a random factor (see Table S6 and Figure S3 for details on mistletoe host tree species). Fruit Infestation Rate: FIR = 100 × number of emerged individuals from all fruit collected from a *Viscum album* individual / number of 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 ₁₀ +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.

Discussion of *Drosophila subobscura* infestation results

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

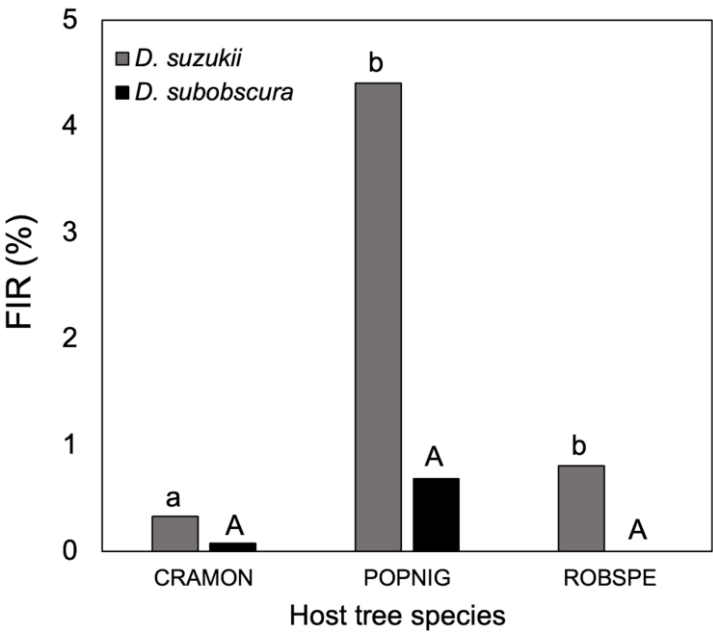
Species	Code	Number	%	Dsuz mean FIR $\pm$ SE (%)	Dsub mean FIR $\pm$ SE (%)
<i>Acer campestre</i>	ACECAM	6	5.0%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Acer</i> sp.	ACER	3	2.5%	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00
<i>Crataegus monogyna</i>	CRAMON	59	49.6%	0.33 $\pm$ 0.15	0.08 $\pm$ 0.04
<i>Malus domestica</i>	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
TOTAL		119	100.0%	1.46 $\pm$ 0.54	0.23 $\pm$ 0.15

1073

1074

1075

1076



1077

1078

1079

1080

1081

1082

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

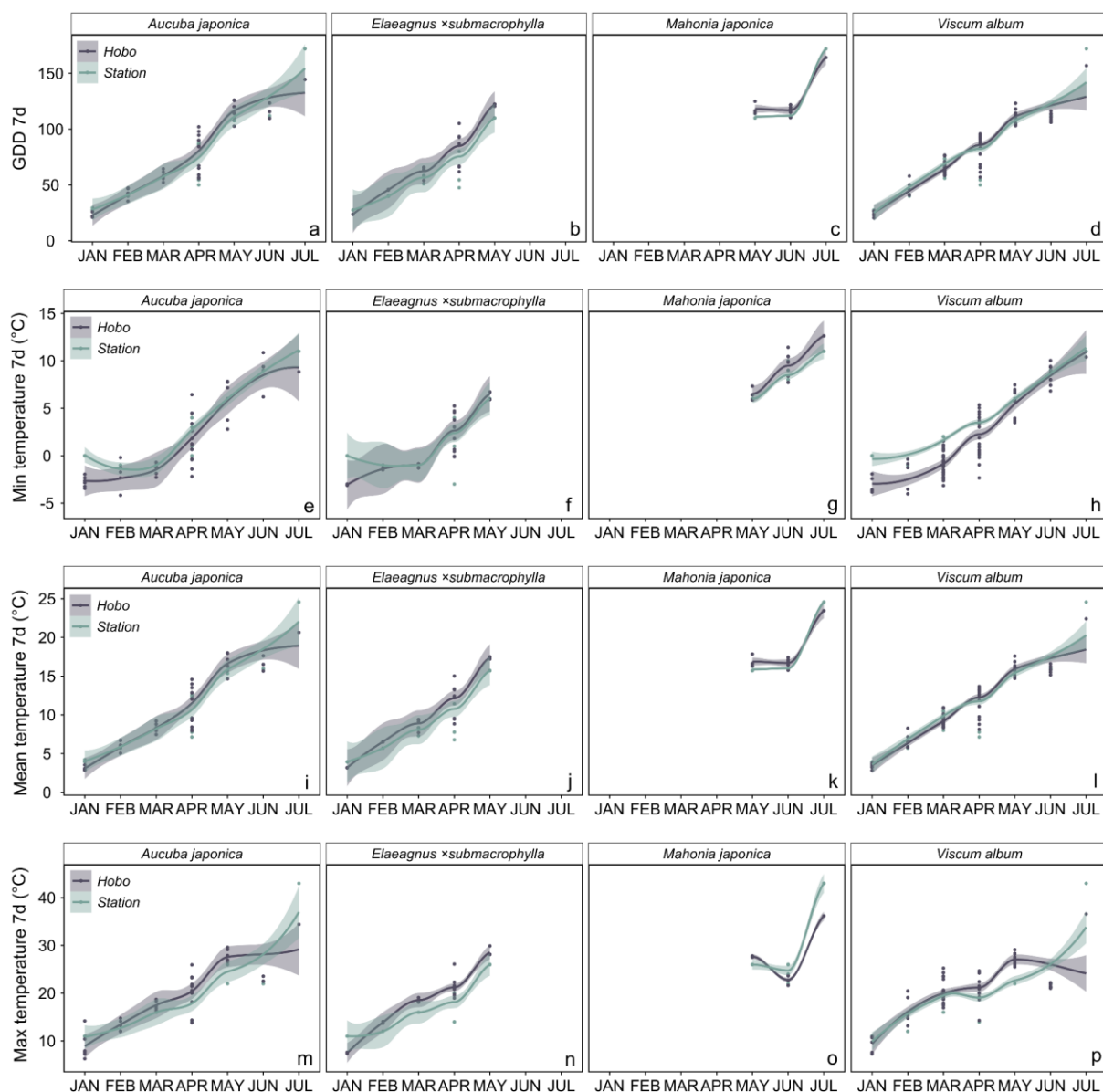


Figure S4 Difference in Growth Degree Days (a-d), minimum (e-h), mean (i-l) and maximum (m-p) temperatures (°C) of the last 7 days preceding fruit sampling between regional weather stations ('Station'; macroclimate) and local dataloggers under plant canopy ('Hobo'; microclimate) throughout the months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