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ORIGINAL PAPER

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

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Abstract

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

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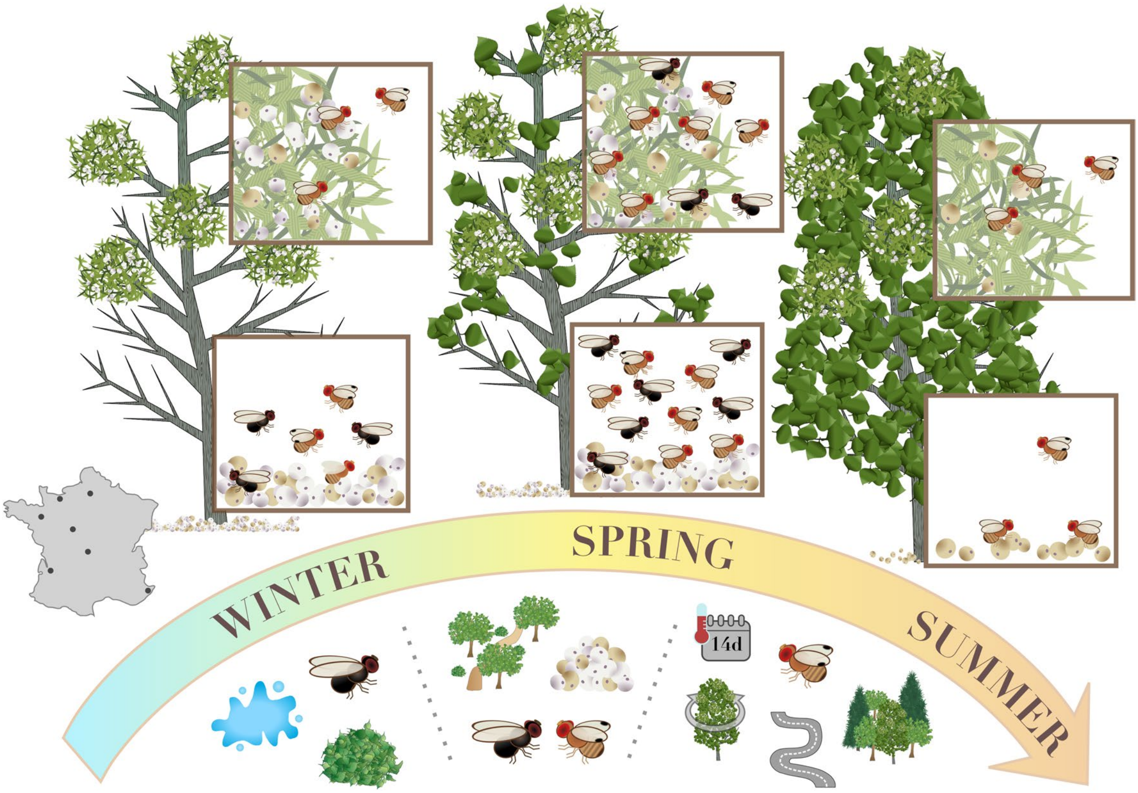
Graphical Abstract



Keywords Insect pest · Biological invasion · Mistletoe · *Viscum album* · Non-crop host plants · *Drosophila suzukii* · *Drosophila subobscura* · Landscape

Introduction

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

Drosophila suzukii (Matsumara 1931) is a globally important invasive fly and a fruit pest (Asplen et al. 2015). Contrasting with other *Drosophila* species, *D. suzukii* is able to oviposit and develop in unripe and ripening fruit, causing important economic losses (Walsh et al. 2011; Tait et al. 2021). This fly is highly polyphagous and uses wild as well as cultivated fruit (Lee et al. 2015; Poyet et al. 2015; Kenis et al. 2016; Ulmer et al. 2022), including fruit of invasive plants (Poyet et al. 2014). Winter is a demographic bottleneck period for *D. suzukii*, mainly because the low temperatures and the lack of trophic resources reduce the population pool (Asplen et al. 2015; Hamby et al. 2016; Stockton et al. 2019). Even if remaining *D. suzukii* individuals are active during winter (e.g., foraging, displacement; Ulmer et al. 2024), so that they do not have a diapause sensu stricto, cold temperatures cause an ephemeral reproductive diapause (quiescence), which is reversible when climatic conditions become more favorable (Toxopeus et al. 2016; Wallingford et al. 2018). A major challenge for the fly is thus to find suitable hosts (usually wild fruit in natural habitats) both to provide food to allow populations that developed in the previous year to persist between winter and late spring and to initiate the establishment of new generations (Poyet et al. 2015; Panel et al. 2018) before cultivated fruit become available as hosts. Among the few plant species bearing fruit in winter and early spring, *Viscum album* (mistletoe) is expected to be an important resource for *D. suzukii* since the fly can develop in the berries it produces (Panel et al. 2018; Poyet et al. 2015; Kenis et al. 2016) and because *V. album* and closely related species are widely distributed and often abundant across temperate regions worldwide (Watson 2001).

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

Viscum album is widely distributed across the area invaded by *D. suzukii* in Europe (Hultén and Fries 1986) and occurs in woodlands and hedges (Briggs 2021; Thomas et al. 2023) where *D. suzukii* overwinters (Rossi-Stacconi et al. 2016; Briem et al. 2018; Santoiemma et al. 2019). The relationship between *V. album* and *D. suzukii* has been explored using field monitoring of infestation at the end of winter (Briem et al. 2016; Panel et al. 2018; Delbac et al. 2020a) and in laboratory experiments assessing the ability of *D. suzukii* to infest *V. album* berries (Poyet et al. 2015; Briem et al. 2016; Wolf et al. 2020). Its ability to utilize the fruit suggests that *D. suzukii* is able to overcome the toxicity of *V. album* berries (Gaidamashvili et al. 2012), as has been shown with other toxic fruit (Poyet et al. 2015, 2017). In winter and early spring, mistletoe fruit also constitutes a food resource for adult *D. suzukii* females that are active but with underdeveloped oocytes in ovaries (Briem et al. 2016). As the fly's reproductive diapause ends and the female's oocytes mature, the mistletoe fruit may provide suitable breeding sites at a time when other commercial fruit are not yet available (Poyet et al. 2015; Briem et al. 2016; Panel et al. 2018; Delbac et al. 2020a). Seed populations of *D. suzukii* in these fruit could therefore catalyze the development of new generations in spring.

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

To date, the influence of environmental factors on *V. album* infestation rate has not been explored, although they are expected to act at multiple scales. Global warming, resulting in mild winter temperatures, may promote early winter fruit infestation, including those of *V. album*, by shortening the reproductive diapause period of *D. suzukii*. Thus, among climatic variables, those related to temperature may be important predictors of *V. album* infestation by *D. suzukii*. Landscape variables are also expected to influence fruit infestation. As wintering *D. suzukii* find shelter in hedges and woodland (Briem et al. 2018; Rossi-Stacconi et al. 2016; Ulmer et al. 2022), *V. album* individuals close to forest habitats are therefore likely to have a higher risk of infestation. Local variables such as the quantity and quality of berries are also likely to influence infestation levels (Ulmer et al. 2022). Conversely, bird foraging can reduce the availability of *V. album* fruit, especially when temperatures are low and alternative resources are scarce (Briggs 2021). There is, therefore, a risk that *D. suzukii* may face a lack of this key resource in late winter, before the fly's eggs mature in early spring. In general, *D. suzukii* prefers to oviposit in ripening and ripe fruits (Walsh et al. 2011; Atallah et al. 2014). In laboratory assays, flies laid more eggs in artificially damaged than in undamaged berries (Briem et al. 2016). Damaged fruits are commonly observed in the field after the birds have foraged or after a storm event, but the distribution of *D. suzukii* between damaged or undamaged mistletoe berries in the field remains unknown.

This study aimed to disentangle the relative roles of climatic, landscape, and local factors that could affect infestation rates of a wild host plant by *D. suzukii*. We focused on

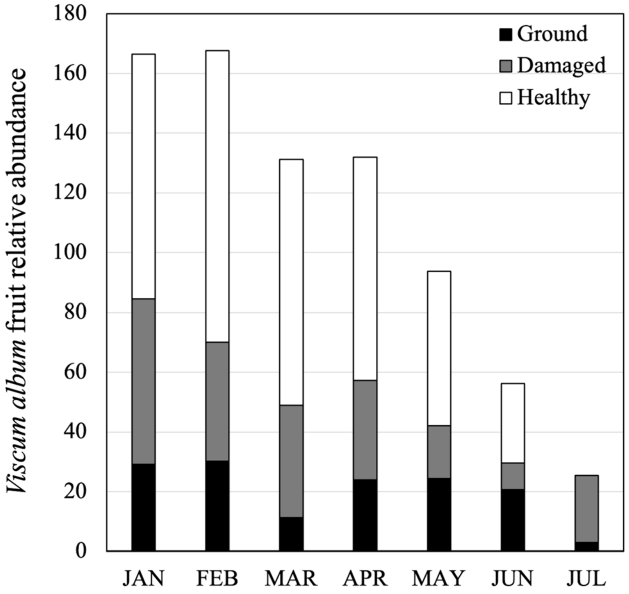


Fig. 1 Variation in *Viscum album* fruit relative abundance (number of collected fruits divided by the number of plants sampled) between January and July 2022, in relation to their position and status: on the ground (Ground), on the tree damaged (Damaged) or healthy (Healthy)

the mistletoe *V. album* because this major host plant is one of the few species bearing fruit in winter and early spring. This non-crop host plant could also support overwinter seed populations of *D. suzukii*, catalyzing the development of new generations in spring in advance of the availability of the first commercial fruit crops such as cherries, strawberries, or raspberries. We hypothesized that (i) *D. suzukii* presence in *V. album* would be positively associated with the abundance of natural habitats such as woodland, which provide winter refuge for *Drosophila* species (Basden 1954) and particularly for *D. suzukii* (Ulmer et al. 2024); and, (ii) *D. suzukii* infestation of *V. album* fruit would facilitate infestation by other *Drosophila* species such as *D. subobscura* (Poyet et al. 2014; Deconninck et al. 2024) or *D. melanogaster* (Rombaut et al. 2017; Deconninck et al. 2024). We determined the infestation rates across a large geographical area spanning 1000 km in France and including a large range of climatic conditions. At each sampling location, we also measured several local (e.g., mistletoe host tree and mistletoe traits) and landscape variables (e.g., vegetation cover, proportion of habitats) to identify the environmental drivers of mistletoe infestations.

Methods

Sampling design

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

Traits of mistletoe and host trees

Collected fruits were separated into three subsets to monitor *Drosophila* emergence: undamaged ('healthy') and damaged fruit collected on the plant and fruit collected

Table 1 Main features of the studied regions from north to south of France

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

Latitude and longitude are the mean values of geographic coordinates (WGS84 projection system) of the sampling locations in each region. Mean daily T°C and rainfall (mm): mean daily temperatures and cumulative rainfall calculated with daily data from meteorological stations in 2022 on the ground (if present). Several traits of the sampled mistletoe individuals and their host trees were measured to characterize the local resources available for the flies and the microhabitat. The following reproductive and vegetative traits were measured: the maximum and minimum diameter of the mistletoe individual sampled, and an estimate of the number of fruits present. For each sampled mistletoe individual, five berries were randomly selected to measure their length and width and calculate their volume ($4/3 \times \pi \times$ mean radius^3) and fruit skin area ($4 \times \pi \times$ mean radius^2). Five leaves were also taken; their length and width were measured and the leaf surface index (length × width; Ulmer et al. 2022) was calculated. The height of the mistletoe individual on the host tree (from the ground) was also recorded. The tree species hosting the mistletoe was identified (Table S1) and its height, crown diameter, and trunk circumference were measured. The number of mistletoe individuals on the host tree was recorded. Variables, units, and codes are listed in Table S2.

Environmental variables

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

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

The landscape composition around each sampled mistletoe was then characterized. A geographic database was created using a Geographic Information System (GIS; ArcGIS Pro v.2.5, ESRI). The sampled host trees 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, heartland, grassland, road, urban area, orchard, industrial zone) were extracted from the OSO 2022 database (THEIA, 2023) and updated using aerial photographs and field observations (in buffers < 100 m).

Macroclimatic conditions were characterized for each sampling site using regional measurements. The daily meteorological data were retrieved from the three nearest meteorological stations to each site, from January 1st 2022 to each day of sampling (https://www.historique-meteo.net/france/, details in Table S3). 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 S3). Accumulated degree days ("Growing Degree Days", GDD) were calculated using a lower threshold of 0 °C between January 1st, 2022, and the day of sampling (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). It was also chosen because 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 ; Ulmer et al. 2022) and because mistletoe fruit can undergo freeze–thaw cycles before ripening ends. From daily precipitation values, we also calculated mean daily and cumulative precipitation between January 1st, 2022, and the day of sampling and within the 7- or 14-day periods before each fruit sampling day.

Emergence of *Drosophila* species

After collection, the mistletoe fruits were individually placed on wet cotton wool in cylindrical plastic transparent containers (diameter = 118 mm, height = 135 mm, volume = 1476 cm^3), 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 fruits were placed in 70% ethanol. They were identified to species level using Bächli et al. (2005) and Withers and Allemand (2012). Individuals of the two major species found (*D. suzukii* and *D. subobscura*) 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 where either centered on the fruit (Fruit Infestation Rate: FIR = 100 × number of emerged *Drosophila* individuals from fruit collected from a given *V. album* individual / total number of fruit collected from the same *V. album* individual) or on the plant (Plant Infestation Rate: PIR = 100 × number of infested *V. album* individuals in a region or month / total number of *V. album* individuals sampled in the same region or month). A high FIR indicates that the majority of fruit on the plant are infested by the fly and a high PIR indicates that the majority of the plants in a region are infested by the flies. These variables can be interpreted as follows: a high FIR reflects the plant auto-contamination by the flies while a high PIR reflects fly dispersal (e.g., when the FIR and PIR are both high, there is both auto-contamination of the plant and dispersal of the flies; 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 contamination and dispersal). These infestation variables were also calculated for each fruit category (healthy or damaged fruit on the plant and fruit on the ground, following Deconninck et al. (2024)).

Statistical analyses

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

Table 2 Number of mistletoe individuals sampled in all studied regions between January and July 2022 with number of fruit sampled, total number of emerged *Drosophila* species, mean ± SE, and maximum fruit infestation rate

Region (main city)	No. mistletoes	No. fruit	*D. suzukii*				*D. subobscura*				*D. repleta*
			No. emerged	Mean FIR ± SE (%)	Max FIR (%)	PIR (%)	No. emerged	Mean FIR ± SE (%)	Max FIR (%)	PIR (%)	No emerged
Amiens	126	16,723	341	2.15 ± 0.77	72.86	20.63	33	0.31 ± 0.15	16.67	7.94	1
Caen	19	1870	16	2.66 ± 2.63	50.00	10.53	0	0.00	0.00	0.00	0
Rennes	30	3211	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0
Tours	22	3526	43	1.11 ± 0.61	11.63	31.82	8	0.26 ± 0.23	4.96	9.09	0
Clermont-Ferrand	15	1550	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0
Bordeaux	46	5673	335	6.11 ± 1.83	53.00	39.13	12	0.19 ± 0.07	1.96	15.22	0
Nice	6	983	0	0.00	0.00	0.00	0	0.00	0.00	0.00	0
Total	264	33,536	735	2.37 ± 0.53	72.86	20.08	53	0.20 ± 0.08	16.67	7.20	1

Regions are listed from north to south of France. Fruit Infestation Rate: FIR = 100 × number of emerged *Drosophila* sp. from all fruits collected from a *Viscum album* individual / number of fruit collected from the same *V. album* individual. Plant Infestation Rate: PIR = 100 × number of infested *V. album* individuals in a month / number of sampled *V. album* individuals in the same month

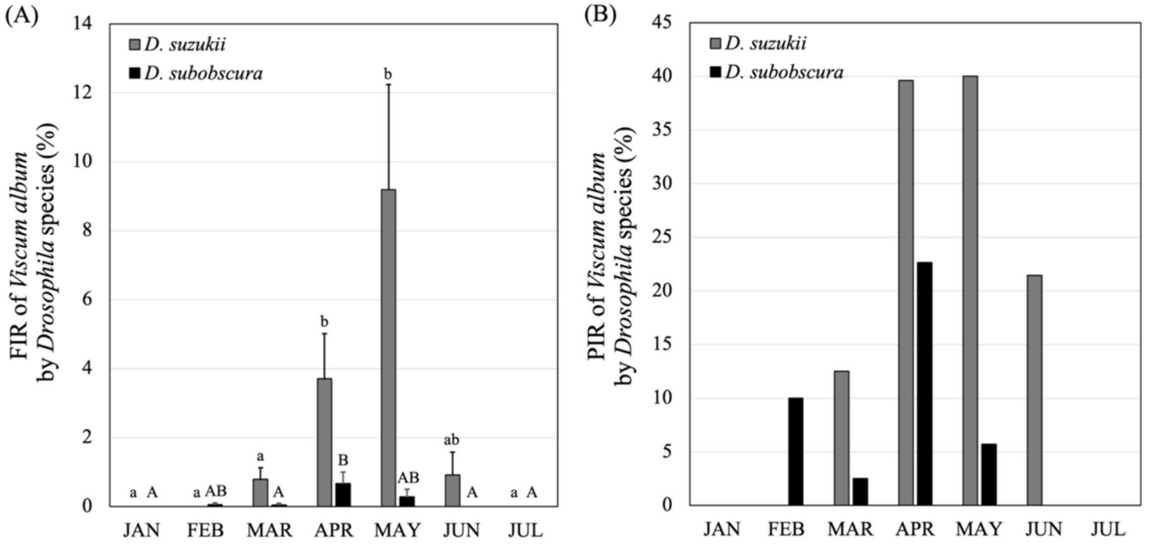


Fig. 2 Variation in FIR (**A**) and PIR (**B**) of *Viscum album* by *Drosophila suzukii* and *D. subobscura* between January and July 2022. Fruit Infestation Rate: FIR = 100 × number of emerged *Drosophila* sp. from all fruits collected from a *Viscum album* individual / number of fruits collected from the same *V. album* individual. Plant Infestation Rate: PIR = 100 × number of infested *V. album* individuals in a month / number of sampled *V. album* individuals in the same month. Significance of differences between months is represented by different lowercase and capital letters for *D. suzukii* and *D. subobscura*, respectively.

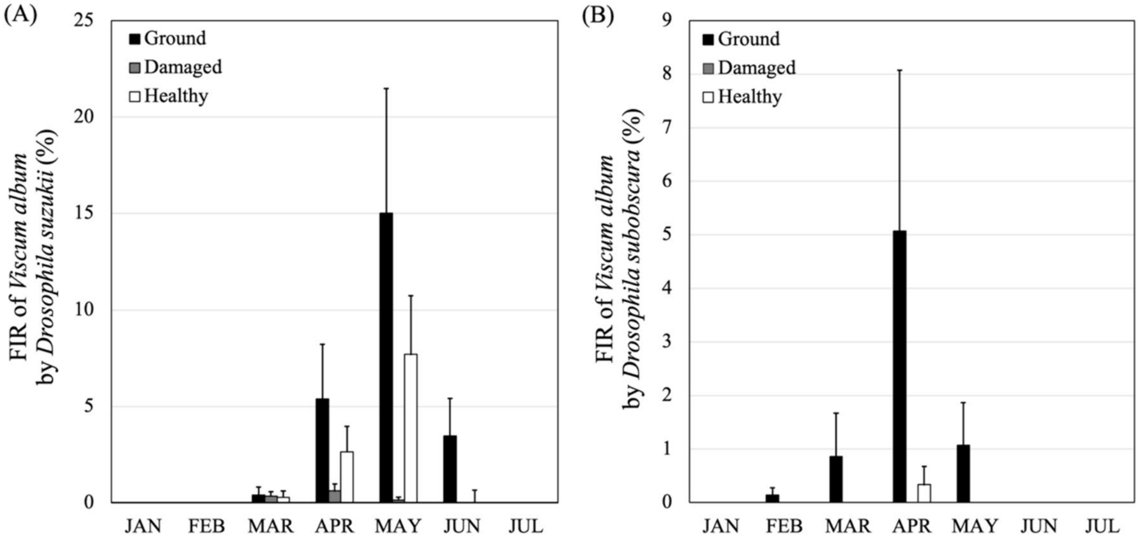


Fig. 3 Variation in FIR of *Viscum album* by *Drosophila suzukii* (**A**) and *D. subobscura* (**B**) between January and July 2022, in relation to their position and status: on the ground (Ground), on the tree damaged (Damaged), or healthy (Healthy). Fruit Infestation Rate: FIR = 100 × number of emerged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

Results

Dynamics of *Viscum album* fruit resource

A total of 33,536 fruits from 264 mistletoe individuals were sampled across all regions between January and July 2022 (Table 2). The number of fruit decreased progressively over the study period, from an average of 167 collected per mistletoe in January to an average of only 26 in July (Fig. 1). From January to June, the majority of fruit were healthy on the plant (47–63%) and the proportion of damaged fruit on the plant progressively declined from 33 to 16% over the

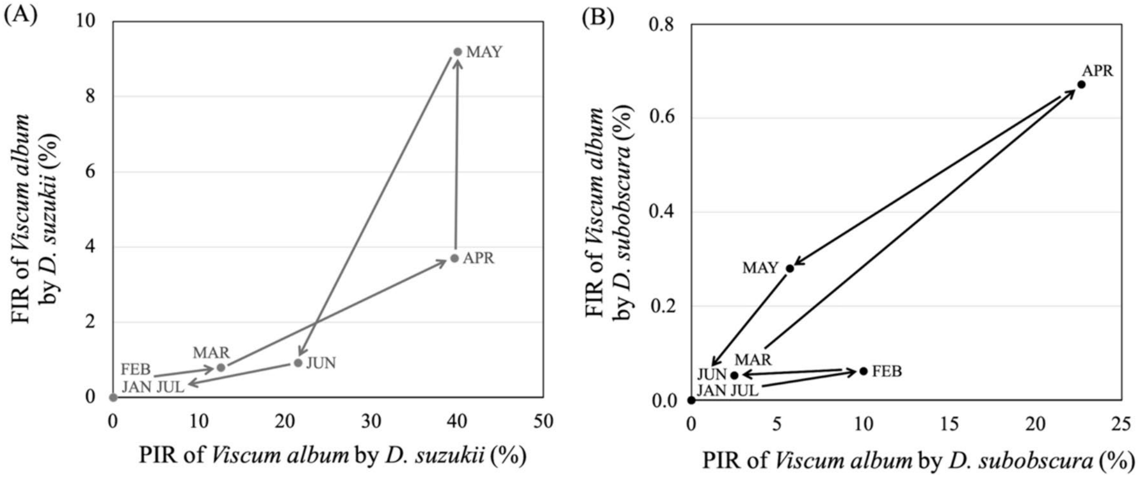


Fig. 4 Mean fruit infestation rate (FIR) in relation to plant infestation rate (PIR) of *Viscum album* according to months between January and July 2022 for (**A**) *Drosophila suzukii* and (**B**) *D. subobscura*. Interpretation: high FIR + high PIR = dispersion + auto-contamination; high FIR + low PIR = auto-contamination; low FIR + high PIR = dispersion; low FIR + low PIR = low auto-contamination / dispersion. Dispersal and auto-contamination are maximized in May for *D. suzukii* and in April for *D. subobscura*

same period. The proportion of fruit on the ground initially decreased from 18 to 9% between February and March, then increased by June to reach 37%. In July, no healthy fruit remained on the plants and most fruits were either damaged (88%) or on the ground (12%).

Regional infestation of *Viscum album*

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

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

Seasonality of *Viscum album* infestation

Drosophila subobscura was the earliest fly species to emerge from *V. album* fruits, emerging from fruits sampled in February in Amiens and Tours (Fig. 2A, B). In February, its FIR was low (0.06 ± 0.04%) then increased significantly in April and May to reach 0.67 ± 0.33% and 0.28 ± 0.23%, respectively (Kruskal–Wallis test, $\chi^2 = 26.145$, $p < 0.001$; Fig. 2A). This species did not emerge from fruits collected after May and was mostly found in fruits collected on the ground (95% of individuals), with only two individuals emerging from healthy fruits sampled on the plant (Fig. 3B). The sex ratio of emerging *D. subobscura* flies was unbiased (chi-squared test: $\chi^2 = 0.647$, $p = 0.42$), with 30 females against 23 males.

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

In February, 10% of *V. album* individuals were infested by *D. subobscura*, which decreased to 3% in March, then increased to 23% in April, and finally decreased to 6% in May (Fig. 2B). In March, 13% of *V. album* individuals were

Table 3 Effect of environmental variables on *Viscum album* fruit infestation rate (FIR) by *Drosophila suzukii* and *D. subobscura* analyzed using GLMMs

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

GROUTOT: % fruit collected on the ground, HLENGH: Canopy width of the host tree (m), PATH: Path cover (in a 5 m radius), GARDEN20: Garden cover (in a 20 m radius), FOREST20: Forest cover (in a 20 m radius), GDDMC14J: Growing Degree Days (of the last 14 days), WATE20: Water cover (in a 20 m radius), HEDGE20: Hedgerow cover (in a 20 m radius), PARK20: Urban park cover (in a 20 m radius)

infested by *D. suzukii*, increasing to 39% and 40% in April and May, respectively, and then decreasing in June to reach 22%.

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

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

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

Discussion

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

Local and landscape drivers of fruit infestation

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

Landscape features affected the two *Drosophila* species differently. Garden and forest cover in the area of the sampling locations positively influenced the levels of infestation by *D. suzukii*, while the cover of water, hedgerow, and urban park positively influenced those of *D. subobscura*. Semi-natural habitats including woodland, grassland, hedgerow, and shrubs are known to positively affect the abundance of Drosophilidae species by providing food resources, breeding sites, and shelters with beneficial microclimatic conditions (Santoiemma et al. 2018; Delbac et al. 2020b). The differences between the semi-natural habitats affecting each species may be due to their diet and breeding preferences, as *D. suzukii* is mostly frugivorous (Walsh et al. 2011; Poyet et al. 2015; but see Stockton et al. 2019 for alternative resources), while *D. subobscura* is both frugivorous and fungivorous (Begon 1975; Delbac et al. 2020b). The food and breeding resources the flies are seeking may not be found in the same semi-natural habitats. Similarly, the canopy width of the host tree only affected *D. suzukii*, which has a strong preference for the canopy layer (Tanabe 2002).

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

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

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

The fruit infestation rate (FIR) was quite low in our data, but the plant infestation rate (PIR) was very high (up to 40%). This discrepancy between the two metrics may be explained by a combination of the low survival rate of *D. suzukii* at the end of winter and by the high quantity of fruit on each plant, diluting the overall infestation rate. Nonetheless, a host tree bearing numerous mistletoe individuals (e.g., a maximum of 110 mistletoe individuals was counted in a single poplar tree in this study) will generate a high number of flies even if its mean FIR is low. Therefore, commercial fruit fields surrounded by trees bearing mistletoe individuals may be exposed to a wave of *D. suzukii* around mid-April once the first crop fruit mature sufficiently to attract these flies, although this effect will depend on the location.

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

Potential impact of *D. suzukii* on ecosystem functioning

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

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

Considerations about pest management strategies

The data obtained in this study suggest that the use of mistletoe fruit by *D. suzukii* could catalyze an increase in fly populations available to infest early maturing cultivated fruit in spring. Developing integrated pest management strategies is essential (Tait et al. 2021) and the consideration of winter processes in these will become increasingly important. Better understanding of *D. suzukii* overwintering strategies is required in order to identify the potential avenues for the development of pest management strategies applicable in winter (Panel et al. 2018). *Viscum album* fruit being an important trophic resource not only for *D. suzukii* but also for birds and mammals; it is not viable or acceptable to eradicate mistletoe generally. However, removal could be considered from trees adjacent to certain fruit crop production areas (e.g., cherry, strawberry, raspberry, etc.), which could help reduce or delay the initial crop infestation. Notably, *V. album* host tree species influenced the fruit infestation rate:

mistletoe on poplars were most heavily infested compared to those on hawthorn, apple, or black locust which were eight, two and 0.33 times less infested, respectively. Pest management strategies should initially focus on the most heavily infested host plant species.

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

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