Agriculture, Ecosystems and Environment 399 (2026) 110184

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Forest habitats improve biological control of *Drosophila suzukii*

Giovanni Dal Zotto [a,*], Lorenzo Tonina [a,b], Silvia Ceroni [c], Nicola Mori [a], Lorenzo Marini [d]

[a] Department of Biotechnology – University of Verona, Strada Le Grazie 15, Verona 37134, Italy
[b] Technology Transfer Centre - Edmund Mach Foundation, Via Edmund Mach 1, San Michele All'Adige, TN 38098, Italy
[c] Plant Protection Service Veneto Region, Viale dell'Agricoltura 1, Buttapietra, Verona 37060, Italy
[d] Department of Agronomy, Food, Natural resources, Animals and Environment – University of Padova, Via dell' Università 16, Legnaro, PD 35020, Italy

ARTICLE INFO

Keywords:
Classical biological control
Ecosystem services
Habitat management
Semi-natural habitats
Spotted-wing Drosophila

ABSTRACT

To date, significant efforts have been made to promote the biological control of *Drosophila suzukii* outside its native range. Recently, classical biological control using exotic parasitoids, both intentionally and accidentally introduced, has attracted considerable interest. In particular, adventive populations of *Leptopilina japonica* have been rapidly expanding in Europe and North America. In this study, we assessed how *D. suzukii* density, host plant species, season, and landscape composition and configuration influence this exotic parasitoid. We sampled elderberry, wild blackberry, and pokeweed fruits over two years from 27 sites in northeastern Italy selected to represent statistically independent gradients of forest cover and forest patch density. *L. japonica* exhibited a strong host-density response at the local scale, enabling it to track the temporal and spatial distribution of *D. suzukii*. This led to higher parasitism rates in late summer and in landscapes with greater forest habitat cover. Parasitism rates observed in plant species associated with forest habitats were positively correlated with forest cover and high patch density, highlighting the pivotal role of these habitats in supporting the biological control of *D. suzukii*. Thus, preserving complex agricultural landscapes is crucial for promoting biological control of *D. suzukii* and for facilitating the establishment of viable populations of natural enemies in pesticide-free areas where natural pest-regulation processes can operate.

1. Introduction

The Spotted-wing Drosophila, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), since its first detection in 2008 in North America (Bolda et al., 2010) and Europe (Calabria et al., 2012), has rapidly become the most disruptive pest of soft and stone fruit cultivations worldwide (Asplen et al., 2015). As natural biocontrol effectively regulates *D. suzukii* populations in its native range (Girod et al., 2018a), there has been considerable interest in improving this key ecosystem service in invaded ranges. In the early stages of *D. suzukii* invasion, due to regulatory restrictions on classical biocontrol, research primarily focused on augmentative biological control using native parasitoids (Chabert et al., 2012; Wang et al., 2016; Rossi Stacconi et al., 2018, 2019; Colombari et al., 2020; Hogg et al., 2022). More recently, the focus has moved to classical biological control by exotic parasitoid species associated with *D. suzukii* in its native range (Wang et al., 2018). *Ganaspis kimorum* Buffington is the most frequently detected species in Japan and China (Girod et al., 2018a,b). Due to its high host specificity towards *D. suzukii* (Daane et al., 2021), releases in North America, where adventive populations have already been detected (Abram et al., 2020) and Italy (Fellin et al., 2023; Lisi et al., 2022) are currently ongoing (Stahl et al., 2024). *Leptopilina japonica* Novković & Kimura, is also a dominant species in Asia, but having a broader host range, which includes non-target species such as *D. melanogaster* and *D. simulans*, it has not been authorized for classical biological control programs (Daane et al., 2021; Rossi Stacconi et al., 2025). However, adventive populations of *L. japonica* were first reported in North America as early as 2016 (Abram et al., 2020) and in Europe in 2019 (Puppato et al., 2020). To date, the species has spread, becoming the most dominant parasitoid species in the invaded areas (Fellin et al., 2023, Gariepy et al., 2024, Rossi Stacconi et al., 2025). It is therefore crucial to identify the biotic and abiotic factors driving *L. japonica* population dynamics.

There are several factors that can regulate *L. japonica* populations. First, several studies in both native and invaded ranges (Daane et al.,

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* Corresponding author.
E-mail addresses: giovanni.dalzotto@univr.it (G. Dal Zotto), lorenzo.tonina@fmach.it (L. Tonina), silvia.ceroni@regione.veneto.it (S. Ceroni), nicola.mori@univr.it (N. Mori), lorenzo.marini@unipd.it (L. Marini).

https://doi.org/10.1016/j.agee.2025.110184
Received 18 August 2025; Received in revised form 10 December 2025; Accepted 18 December 2025
Available online 22 December 2025

2016, Girod et al., 2018a,b, Giorgini et al., 2019, Abram et al., 2022, Fellin et al., 2023, Rossi Stacconi et al., 2025, Van Timmeren et al., 2025) suggest that *L. japonica* does not exhibit a marked preference for any specific host plant species exploited by *D. suzukii*, suggesting a high plasticity in its host plant selection. *Drosophila suzukii* can exploit a wide range of cultivated, wild, and ornamental plants (Kenis et al., 2016; Lee et al., 2015; Poyet et al., 2015) and can use multiple plants across different habitats and altitudes (Santoiemma et al., 2019a; 2019b). Second, as a specialized parasitoid, *L. japonica* is expected to display a density-dependent response to *D. suzukii*, exhibiting a higher parasitism rate at high host infestation levels. Third, landscape composition and configuration, especially the presence of forest areas, represents another key factor shaping the population dynamics of *D. suzukii* (Santoiemma et al., 2018, 2019a) and its parasitoids (Haro-Barchin et al. (2018). Forest habitats are insecticide-free areas where *D. suzukii* can find alternative wild host plant (Kenis et al., 2016; Lee et al., 2015; Poyet et al., 2015), favourable microclimatic conditions during summer (Tochen et al., 2016), and suitable overwintering sites (Zerulla et al., 2015). Moreover, landscapes with complex configuration (e.g., high patch density) enhance *D. suzukii* activity favouring the exploitation of multiple hosts across different habitats (Santoiemma et al., 2019a). While in the early phase of *D. suzukii* invasions, semi-natural habitats were often associated with an increased *D. suzukii* infestation in neighbouring fruit orchards (Santoiemma et al., 2018; Tonina et al., 2018), they could also provide a valuable reservoir of Drosophilidae that can support exotic parasitoid populations (Bianchi et al., 2006). In particular, similar to the *D. suzukii* native range, the ecological interactions between host and the recently introduced exotic parasitoids are expected to be particularly strong in pesticide-free habitats, such as forest areas.

This study aimed to investigate how the exotic parasitoid *L. japonica* is affected by *D. suzukii* density, season and landscape structure in three wild host plant species occurring in semi-natural habitats adjacent to cherry orchards across two growing seasons. In particular, we hypothesize that biocontrol is favoured by an increase cover of forest and an increased forest patch density in the surrounding landscape and that the parasitoid exhibits a density-dependence response to *D. suzukii* density fluctuations.

2. Materials and methods

2.1. *Study area*

The study was conducted in areas dominated by cherry cultivation in the Veneto region, Northeast Italy. In these areas, the climate is temperate, with average annual rainfall ranging from 800 to 900 mm. The growing season is characterized by maximum temperatures of 25–30°C, with occasional heatwaves leading to higher temperatures, and minimum temperatures of 18–20°C.

2.2. *Experimental design*

Twenty-seven landscapes, characterized by independent gradients of forest cover and patch density and the presence of susceptible crops, primarily cherry orchards, were selected following a preliminary screening in Google Earth Pro. The elevation of the sites ranged between 20 and 830 m above sea level overlapping with the distribution of susceptible crops (Fig. 1). For each site, landscape composition data within a 500, 750 and 1000 m radius buffer were extracted using the CORINE Land Cover (CLC) database (© European Union, Copernicus Land Monitoring Service 2018, European Environment Agency) and geoprocessing tools in QGIS software (QGIS Development Team, 2020) (Table S1). We quantified the percentage of forest cover and forest patch density, defined as the number of patches per square kilometer. Each of the selected sites hosted at least one of the following wild host plant species of *D. suzukii*: elderberry (*Sambucus nigra* L.), wild blackberry (*Rubus fruticosus* L. aggr. spp.), and pokeweed (*Phytolacca americana* L.) (Table S2). The three species were selected because they are among the most common and heavily infested wild host plant of *D. suzukii* occurring in semi-natural habitats adjacent to cherry orchards in the study area (Kenis et al., 2016; Tonina et al., 2018). The mean forest cover around these sites was 28.5 ± 14.5 % (range: 1.8 – 57.5 %), 34.5 ± 16.1 % (6.3 – 57.5 %), and 24.5 ± 23.7 % (0.4 – 80.7 %), respectively. The average forest patch density was 12.0 ± 5.0 (1.7 – 19.8), 11.5 ± 5.1 (2.8 – 18.7), and 9.6 ± 7.4 (1.1 – 18.7) patches/km^2, respectively.

2.3. *Insect sampling*

In each landscape, fruits of elderberry, wild blackberry, and pokeweed were collected in 2022 and 2023, with one to five collections per season, depending on availability. On each sampling date, at least one sample of each target species present at the site was collected, with a maximum of three samples per species, depending on their abundance. A total of 241 fruit samples were collected across both years: 106 in 2022 and 135 in 2023. In 2022, elderberry was sampled from early July to early October, with the majority collected in August (45 samples), wild blackberry from early August to early October, with one late

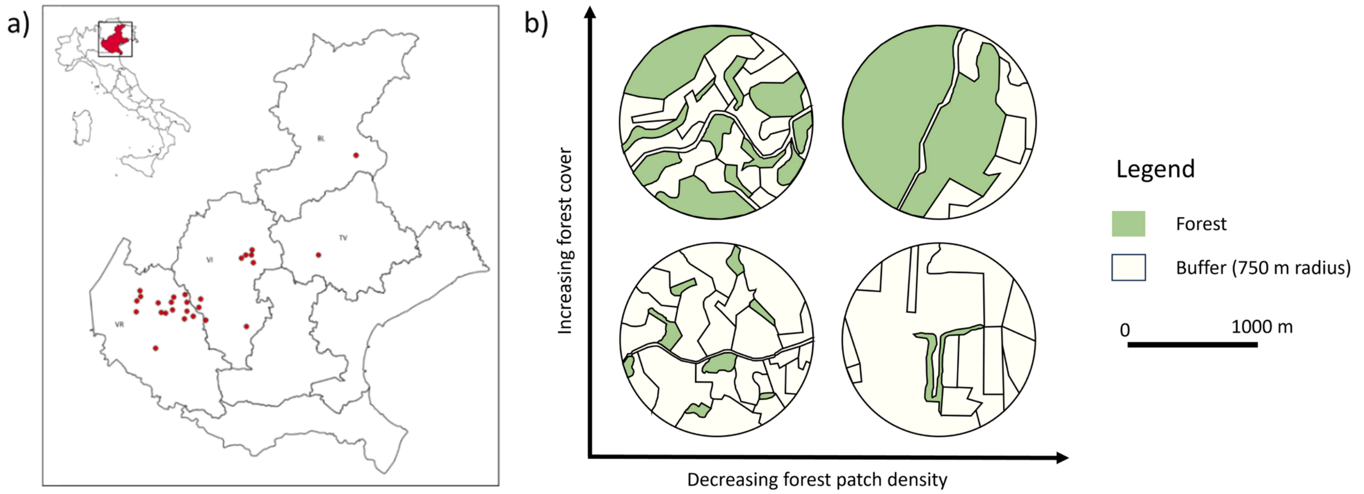

Fig. 1. a) Location of the sampling sites in the Veneto Region and b) representation of the sampling design keeping statistical independent gradient in landscape composition and configuration (forest cover and patch density).

sample in early November (24 samples), and pokeweed from early September to mid-October (37 samples). In 2023, elderberry was sampled from late June to late September (41 samples), wild blackberry from late August to late September (43 samples), and pokeweed from late August to early October (51 samples) (Fig. 2). The mean number of fruit clusters/berries collected per sample was 4.0 ± 1.5 for elderberry, 50.2 ± 18.1 for wild blackberry, and 7.3 ± 3.2 for pokeweed, corresponding to a mean weight of 52.4 ± 26.2 g, 44.1 ± 21.6 g, and 65.6 ± 25.8 g, respectively. The collected fruits were placed in plastic boxes with ventilated lids and absorbing paper on the bottom. For each sample, GPS coordinates were recorded.

After each sample collection, we assessed the local abundance of ripe and fresh fruits belonging to the sampled species within a 10-meter radius of the sampling point. The fruit abundance was categorized as follows: *Low*: 0 – 5 elderberry fruit clusters, 0 – 7 pokeweed fruit clusters, 0 – 20 wild blackberry berries; *Medium*: 6 – 15 elderberry fruit clusters, 8 – 20 pokeweed fruit clusters, 21 – 50 wild blackberry berries; *High*: > 15 elderberry fruit clusters, > 20 pokeweed fruit clusters, > 50 wild blackberry berries.

2.4. *Post-sampling laboratory procedures*

In the laboratory, each fruit sample was first inspected, and any undesired arthropods were removed. Then, the number of fruit clusters or berries was counted and weighed. Samples were stored in a climatic chamber at 22 ± 1°C and 75 ± 10 % relative humidity and were checked every 2–3 days during the first 15 days. Emerging *Drosophila* spp. were removed, counted, and identified as *D. suzukii* or other native *Drosophila* species. After the first incubation period, samples were checked once a week and parasitoids were removed, stored in alcohol, and subsequently identified using morphological keys (Abram et al., 2022b). For each sample, the total infestation was calculated by summing the number of *D. suzukii*, other native *Drosophila* and parasitoid individuals emerging from the fruit, and then standardized by sample weight. In each sample, the proportion of *D. suzukii* emerging was calculated (i.e., number of *D. suzukii*/total *Drosophila* spp.). The parasitism rate by *L. japonica* was calculated as the number of *L. japonica* individuals that emerged from the sample divided by the total number of emerged insects (total infestation), thus not accounting for mortality factors affecting both parasitoids and hosts.

2.5. *Statistical analyses*

For each host plant, a separate linear mixed-effects model was built to analyse the relationship between parasitism rate by *L. japonica* and several biotic and abiotic factors. We did not fit a single model since the plants, in most cases, were present in different sites and at different times. We tested as fixed effects sampling year (2022 and 2023), *Drosophila* spp. infestation, local fruit abundance (3-level factor: low, medium and high), sampling date (Julian days), percentage of forest cover and forest patch density, while the sampling site was included as a random effect. For sampling date, we also included the quadratic term to allow for non-linear relationships. In preliminary analyses, we also tested all the two-way interactions. As they were never supported, we reported only the main effects in the main text. We present the results at the 750 m landscape scale, as parasitism rates by *L. japonica* showed the strongest response at this scale. Results of models evaluating effects at the 500 m and 1000 m scales are included in Supplementary Materials (Table S3 and S4). The parasitism rate by *L. japonica* and the *Drosophila* spp. infestation were log-transformed. We pooled all the *D. suzukii* and other native *Drosophila* since the large majority of individuals were *D. suzukii* (see 3.1. Fruit infestation and parasitism patterns) and *L. japonica* can attack multiple host species. Models using only the infestation from *D. suzukii* provided very similar results and are reported in Supplementary Materials (Table S5). To test for collinearity between explanatory variables, Variance Inflation Factors (VIFs) were estimated by fitting each model without interactions. VIF values were all around 1 indicating very little collinearity. Linear mixed-effect models were fitted with the *lme* function from the *nlme* package (Pinheiro et al., 2024). All model residuals were visually checked using diagnostic plots using the *DHARMa* package (Hartig, 2022) and graphs were plotted using *ggplot2* package (Wickham, 2024). All Analysis were performed using R (version 4.3.1) (R Core Team, 2021).

3. Results

3.1. *Fruit infestation and parasitism patterns*

Out of 241 samples, 201 were infested by drosophilids. In 2022, 42 % of elderberry, 25 % of wild blackberry, and 24 % of pokeweed samples had no *Drosophila* spp. infestation. Among the infested samples, *Drosophila* spp. infestation ranged between 0.052 and 6.72 individuals g^{-1} in elderberry (89.7 ± 26.0 % of *D. suzukii*), 0.091–13.3 in wild

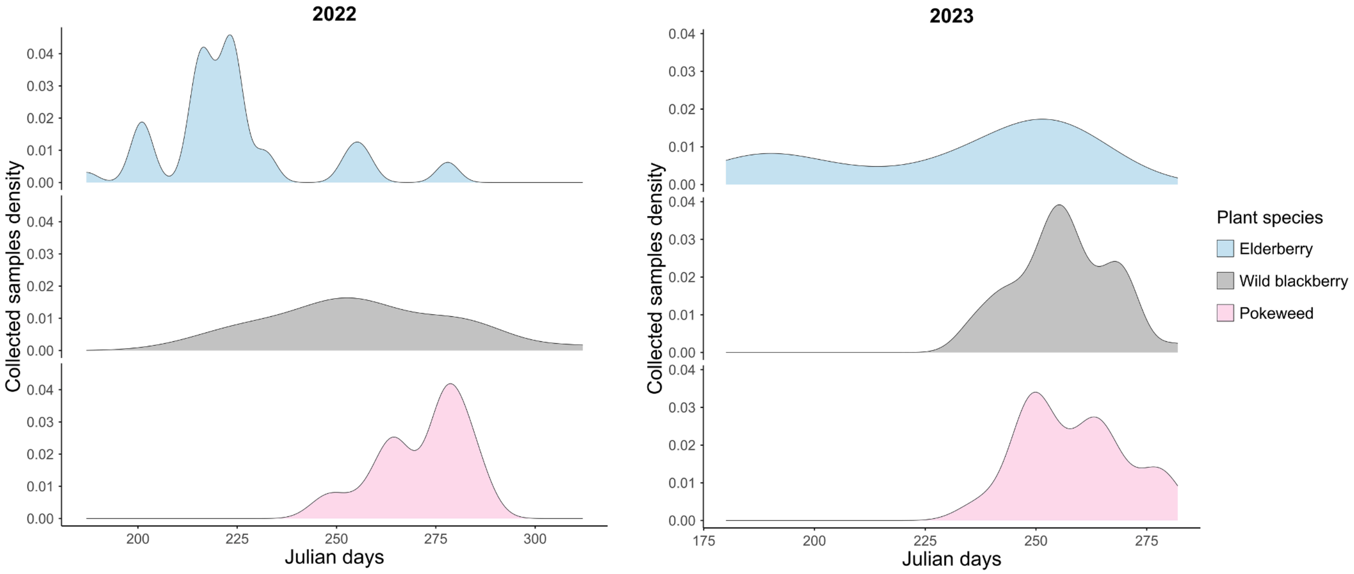

Fig. 2. Density plot showing the distribution of sample collection over time for elderberry, wild blackberry, and pokeweed during 2022 and 2023.

blackberry (95.8 ± 13.0 % of *D. suzukii*) and 0.027–10.0 in pokeweed (79.7 ± 32.5 % of *D. suzukii*). In 2023, 2 % of elderberry and wild blackberry, and 4 % of pokeweed samples showed no infestation. Infested samples exhibited *Drosophila* spp. infestation levels ranging from 0.020 to 5 individual g^{-1} in elderberry (95.2 ± 10.0 % of *D. suzukii*), 0.071–10.21 in wild blackberry (98.6 ± 2.90 % of *D. suzukii*), and 0.014–3.34 in pokeweed (91.0 ± 13.9 % of *D. suzukii*) (Fig. 3a). *Leptopilina japonica* was the most frequently detected parasitoid species, representing over 95 % of all specimens collected. Mean *L. japonica* individuals per gram of fruit and parasitism rate for the three host species are reported in Figs. 3b and 3c. Details on the number of samples yielding parasitoids and other parasitoid species detected are reported in Supplementary Materials (Table S6).

3.2. *Factors influencing the parasitism rate of Leptopilina japonica in different host plant species*

3.2.1. *Elderberry*

In elderberry, the parasitism rate of *L. japonica* varied significantly between the two years (Fig. 4a), with higher rates observed in 2023. Additionally, parasitism increased with higher *Drosophila* spp. infestation levels (Fig. 4b) and greater fruit availability (Fig. 4c). The parasitism rate did not increase as the season progressed, remaining relatively constant. The percentage of forest cover did not affect parasitism; however, forest patch density showed a positive effect on parasitism (Fig. 4d) (Table 1). No interactions were detected between years and environmental factors.

3.2.2. *Wild blackberry*

In wild blackberry samples, the parasitism rate of *L. japonica* varied significantly between years, with higher levels achieved in 2023 (Fig. 5a). Parasitism tended to increase with higher *Drosophila* spp. infestation levels (Fig. 5b) but was not significantly influenced by host fruit abundance. Furthermore, parasitism showed a tendency to increase progressively over the season (Fig. 5c) and was positively correlated with the percentage of forest cover (Fig. 5d) but not with forest patch density (Table 1). No interactions were detected between years and environmental factors.

3.2.3. *Pokeweed*

In pokeweed samples, the parasitism rate was not significantly influenced by year, fruit abundance, forest cover and forest patch density. However, it was significantly affected by *Drosophila* spp. infestation (Fig. 6a) and showed a tendency for higher parasitism rates as the season progressed (Fig. 6b) (Table 1). No interactions were detected between years and environmental factors.

4. Discussion

We found that wild blackberry was the most infested plant by *D. suzukii* and represented the most significant source of *L. japonica,* accounting for more than 95 % of the parasitoids observed. As hypothesized, the analysis of the drivers influencing *L. japonica* parasitism rate revealed that its activity was host-density dependent. This relationship was observed both temporally, with higher parasitism occurring later in the season when *D. suzukii* populations are known to peak (Poyet et al., 2015), and spatially, with higher parasitism rates in landscapes with high forest cover, where larger *D. suzukii* populations occurred (Santoiemma et al., 2018). *Leptopilina japonica* has a relatively narrow host range (Daane et al., 2021), with *D. suzukii* being its primary host in invaded areas (Abram et al., 2022a; Fellin et al., 2023). Such parasitoids, being closely associated with their hosts, are expected to play a major role in population regulation (Hassell, 2000).

The level of *D. suzukii* infestation was a key driver of *L. japonica* parasitism rate, indicating that the host-seeking activity is primarily influenced by host abundance, although the host plant identity can modulate infestation levels. This is further supported by the emergence patterns of *L. japonica*, which were predominantly reared from wild blackberry, followed by elderberry, and least from pokeweed, plants that exhibited decreasing levels of *D. suzukii* infestation. Laboratory studies showed that offspring production of *L. japonica* increased with the number of available host larvae (Wang et al., 2019). This aligns with the general ecological behavior of specialist parasitoids, which tend to perform best under high host population densities. Their close association with hosts allows them to rapidly increase in number, responding proportionally to changes in host abundance (Murdoch, 1994; Snyder and Ives, 2001; Walde and Murdoch, 1988). This finding indicates that this Asiatic parasitoid is probably not negatively affected by the host plants of *D. suzukii* that are not native to Asia.

The parasitism rate by *L. japonica* also tended to increase with higher local fruit availability, further supporting the host-density-dependent activity of the parasitoid, since higher fruit availability is correlated with a higher *D. suzukii* local population (Cini et al., 2012; Ulmer et al., 2022). The impact of fruit abundance at the local scale on the parasitism rate of *L. japonica* was particularly evident in elderberry, likely because it represents one of the few species to produce fruits shortly after cherries, and consequently is subjected to high host pressure, making it more attractive to the parasitoid. However, this relationship may be less pronounced in wild blackberry and pokeweed, as their fruiting periods overlap with those of other cultivated and wild plant species. Although these findings do not indicate that a specific host plant species directly influences the parasitism rate of *L. japonica*, as it is primarily driven by infestation levels, the abundance of fruit resources provided by a particular plant species may play a crucial role in shaping parasitoid

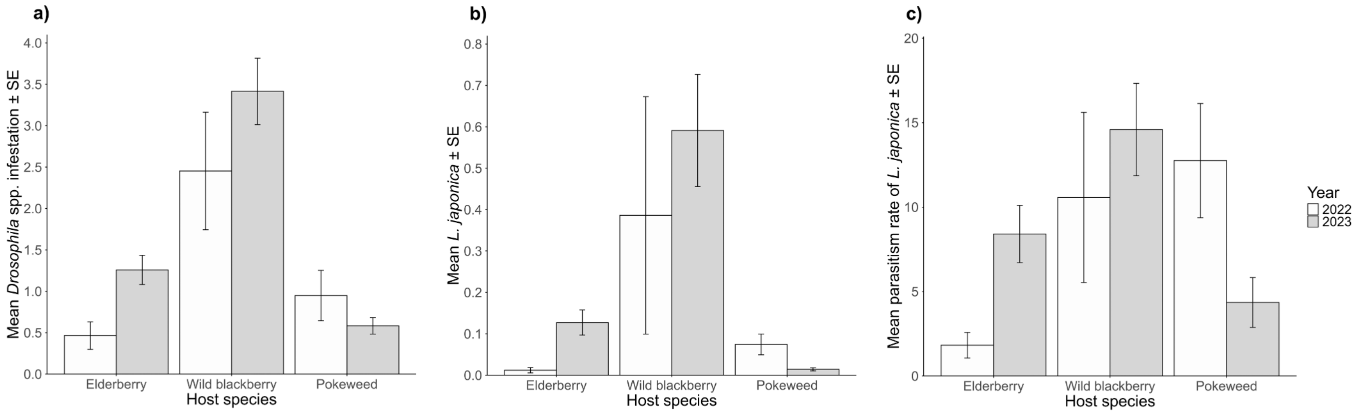

Fig. 3. a) Mean *Drosophila* spp. infestation expressed as individuals per gram of fruit ± SE, b) mean individuals of *L. japonica* per gram of fruit ± standard error c) Mean *L. japonica* parasitism rate ± standard error in samples of elderberry, wild blackberry, and pokeweed collected in 2022 and 2023.

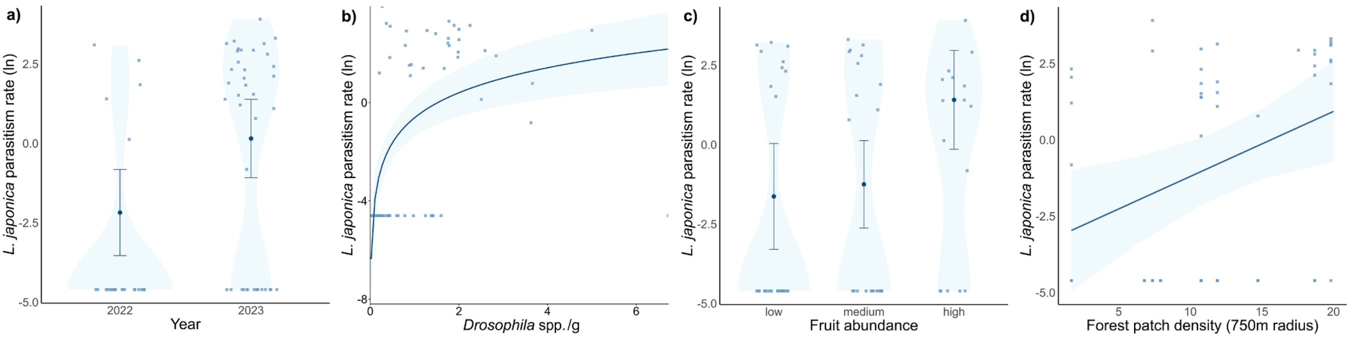

Fig. 4. Effect of a) year, b) *Drosophila* spp. infestation, c) fruit abundance, d) forest patch density on the parasitism rate of *L. japonica* in elderberry, as estimated by the linear mixed-effects model. Light-colored dots represent raw data. In violin plots (a, c), darker dots and error bars indicate the mean and 95 % confidence intervals, while the violin plots illustrate the distribution of raw data. In plots (b, d), lines represent model estimates, and shaded areas denote 95 % confidence intervals.

Table 1
Results from the three linear-mixeds effect models testing the effect of year, *Drosophila* spp. infestation, fruit abundance (low, medium, high), sampling date, sampling date (quadratic term) forest cover and forest patch density at (buffer 750 m) on the parasitism rate of L. japonica on a) elderberry, b) wild blackberry and c) pokeweed. No interactions were detected ($P > 0.05$) and only main effects are reported.

Plant species	Explanatory variables	Estimate	SE	Df	t-value	p-value
a) Elderberry	Intercept	-20.405	27.678	46	-0.737	0.465
	Year (2023 vs 2022)	2.303	0.735	46	3.133	0.003
	Ln(Infestation)	0.936	0.27	46	3.463	0.001
	Fruit abundance (medium vs low)	0.429	0.917	46	0.468	0.642
	Fruit abundance (high vs low)	3.06	1.015	46	3.015	0.004
	Sampling date	0.106	0.25	46	0.423	0.674
	Sampling date^2 (quadratic term)	-0.0002	0.001	46	-0.323	0.748
	Forest cover (750 m)	-0.003	0.028	11	-0.096	0.925
	Forest patch density (750 m)	0.212	0.081	11	2.637	0.023
b) Wild blackberry	Intercept	-119.539	60.281	44	-1.983	0.054
	Year (2023 vs 2022)	2.888	0.857	44	3.371	0.002
	Ln(Infestation)	0.567	0.331	44	1.711	0.094
	Fruit abundance (medium vs low)	1.716	0.895	44	1.917	0.062
	Fruit abundance (high vs low)	0.822	0.903	44	0.911	0.367
	Sampling date	0.842	0.462	44	1.824	0.075
	Sampling date^2 (quadratic term)	-0.002	0.001	44	-1.758	0.086
	Forest cover (750 m)	0.072	0.031	7	2.345	0.052
	Forest patch density (750 m)	-0.003	0.096	7	-0.03	0.977
c) Pokeweed	Intercept	251.151	171.994	59	1.46	0.150
	Year (2023 vs 2022)	0.525	0.971	59	0.541	0.591
	Ln(Infestation)	0.741	0.285	59	2.604	0.012
	Fruit abundance (medium vs low)	-1.245	1.043	59	-1.194	0.237
	Fruit abundance (high vs low)	-1.412	1.314	59	-1.075	0.287
	Sampling date	-2.047	1.31	59	-1.562	0.124
	Sampling date^2 (quadratic term)	0.004	0.002	59	1.657	0.103
	Forest cover (750 m)	0.016	0.017	7	0.926	0.385
	Forest patch density (750 m)	0.047	0.058	7	0.814	0.442

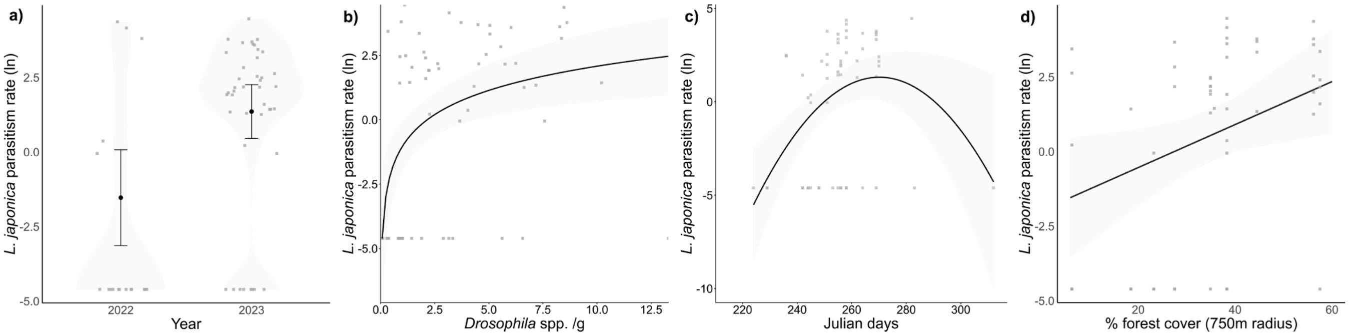

Fig. 5. Effect of a) year, b) *Drosophila* spp. infestation, c) season progression, d) percentage of forest cover on the parasitism rate of *L. japonica* in wild blackberry, as estimated by the linear mixed-effects model. Light-colored dots represent raw data. In violin plot (a), darker dots and error bars indicate the mean and 95 % confidence intervals, while the violin plots illustrate the distribution of raw data. In plots (b, c, d), lines represent model estimates, and shaded areas denote 95 % confidence intervals.

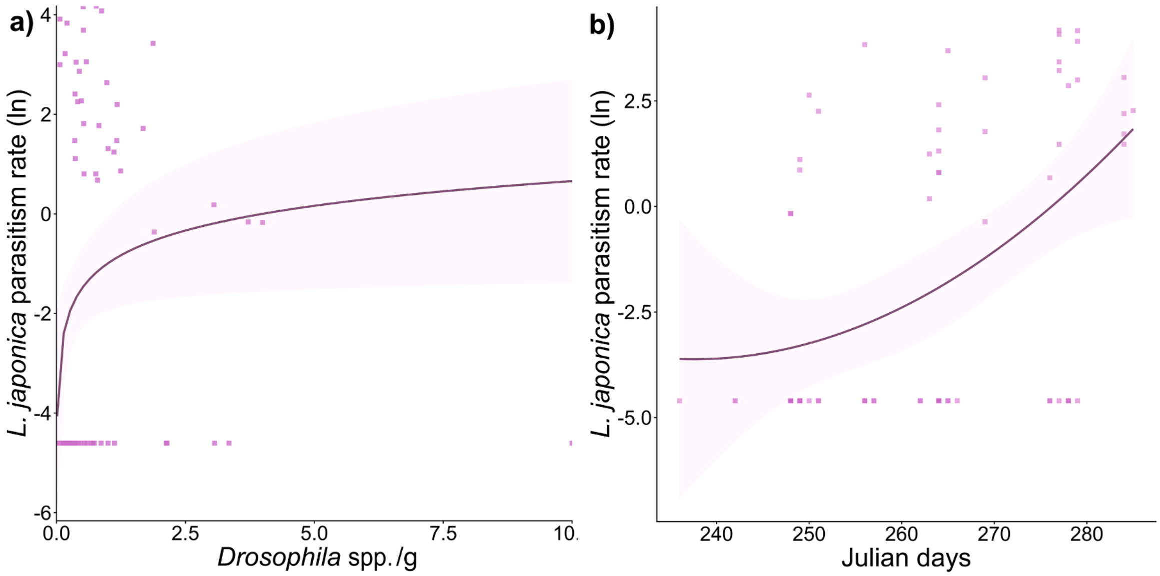

Fig. 6. Effect of a) *Drosophila* spp. infestation and b) season progression on the parasitism rate of *L. japonica* in pokeweed, as estimated by the linear mixed-effects model. Light-colored dots represent raw data while lines represent model estimates, and shaded areas denote 95 % confidence intervals.

population dynamics and its spatial distribution. Specifically, in the case of *D. suzukii* biocontrol, the host plant species that provides the most abundant fruit resources to the host is likely to play a key role in sustaining the parasitoid population (Kishinevsky et al., 2017).

The temporal trends in the parasitism rate of *L. japonica* across the three host species reveal a progressive increase throughout the growing season. Mitsui and Kimura (2010) suggested that the low presence of parasitoids associated with *Drosophila* species early in the season is likely an adaptation to avoid host searching when host populations are very low, highlighting that parasitoid phenology is often delayed compared to that of their hosts (Godfray et al., 1994). Therefore, as the season progresses, the gap between *D. suzukii* and parasitoid populations probably narrows, with the *L. japonica* peak coinciding with that of its host. This trend aligns with the findings of Abram et al. (2022a), who observed that parasitism by *L. japonica* is higher in late summer. These seasonal dynamics may have important implications for the suppression of *D. suzukii* populations, as the increased parasitism rate late in the season contributes to the reduction of the overwintering population of the fruit fly with benefits for the following growing season. Additionally, this heightened parasitism coincides with a period when insecticide applications have ceased, creating an optimal window for parasitoid activity even in more specialized agricultural landscapes.

Landscape composition and configuration are key drivers influencing the population dynamics of natural enemies (Bianchi et al., 2006; Grab et al., 2018; Tscharntke et al., 2007; Veres et al., 2013), particularly when their host shows a strong response to these variables (Holzschuh et al., 2010). *D. suzukii* thrives in complex landscapes rich in forest areas, while it is weakly associated with simplified landscapes with low availability of semi-natural areas (Santoiemma et al., 2018, 2019a; Tonina et al., 2018). We found that *L. japonica* parasitism rate responded to the same landscape metrics, with some variability depending on the host plant species considered. For elderberry, parasitism was not influenced by the percentage of forest cover but was positively correlated with forest patch density. This is consistent with the fact that elderberry typically grows along forest edges (Atkinson and Atkinson, 2002; Ulmer et al., 2022) and is therefore more dependent on landscape configuration than composition. In contrast, in wild blackberry, the parasitism rate of *L. japonica* responded to forest cover, as this species is also commonly found within forest interiors (Morin and Evans, 2012). For pokeweed, parasitism was not statistically affected by any forest-associated metrics. As an invasive species, pokeweed occurs in disturbed habitats, such as roadsides or riverbanks, and its growth is mainly independent of woodland habitats (Panero et al., 2024). Nevertheless, non-crop plants, whether closely associated with woodlands or not, play a crucial role in sustaining parasitoid populations of *D. suzukii*. Indeed, it is well-documented that the presence of spontaneous vegetation near crop areas can enhance the abundance and diversity of natural enemies (Krewenka et al., 2011; Thomson and Hoffmann, 2010).

In agricultural landscapes, biodiversity and the ecosystem services it provides are predominantly concentrated in semi-natural areas (Bianchi et al., 2006; Martin et al., 2019). These habitats are essential because they support a wide range of beneficial insects, including predators, parasitoids, and pollinators (Bartual et al., 2019; Holland et al., 2017; Martin et al., 2019). In the context of *D. suzukii* biological control, these areas serve as refuges from insecticide treatments (Roubos et al., 2014), provide optimal microclimatic conditions, and offer shelter from extreme temperatures (Santoiemma et al., 2018). Additionally, they supply continuous fruit and nectar resources that support parasitoid reproduction and feeding (Bianchi and Wäckers, 2008; Poyet et al., 2015). These characteristics make such habitats ideal focal areas for classical and conservation biological control programs targeting *D. suzukii* (Grab et al., 2018; Landis et al., 2000; Tscharntke et al., 2007). Conservation biological control aims to enhance native natural enemy populations. As *L. japonica* is known to have minimal non-target impacts on native drosophilids (Girod et al., 2018a,b), and, to date, no undesired effects have been observed, the benefits of its spread are expected to outweigh any potential side effects on native drosophilid populations (Rossi Stacconi et al., 2025). Since the large share of the *D. suzukii* population is expected to occur in non-crop areas, the parasitism from *L. japonica* is expected to play an important role in controlling the pest in these areas, with potential cascading effect on colonization pressure on crops. On the other hand, from the farmers' perspective, semi-natural habitats near crop areas still represent the main source of infestation of *D. suzukii*. Therefore, a conservation biological control approach must be accompanied by the implementation of integrated pest management guidelines to manage *D. suzukii* within cultivated areas effectively.

In the investigated area, climatic conditions greatly varied between the two surveyed years, affecting the population dynamics of *D. suzukii* and, consequentially its parasitism rate. The 2022 growing season was marked by low spring rainfall, and an extremely dry and hot summer with low availability of host plants for *D. suzukii* (Harris et al., 2014).

Late-summer rainfall stimulated the emergence of late-season fruiting plants such as pokeweed, which supported the *D. suzukii* population and its associated parasitoid community. In contrast, 2023 was more suitable for the fruit fly, as it was characterized by frequent rainfall events, which increased host fruit availability and mitigated the negative effects of extreme summer temperatures, therefore boosting *D. suzukii* populations. Despite these different climatic conditions, the observed local and landscape effects on parasitism from *L. japonica* were consistent across very contrasting years.

5. Study limitations

The relationship between *L. japonica* parasitism rate and *D. suzukii* density in our analysis was strong. However, there are several factors that limit the interpretation of this finding. First, host density was measured only on the sampled focal plants, without accounting for the overall availability of host resources from the three target species or from other species across the landscapes. Although technically challenging, even when relying on remote sensing technologies (i.e., mapping host plants during their flowering period), a more comprehensive quantification of host availability would have allowed us to investigate not only *L. japonica* density-dependence but also its host plant selection at the landscape scale. Second, the lack of measures of resource availability at the landscape scale raises the possibility that the observed host-density response of *L. japonica* may be biased by resource concentration or dilution effects. Third, sampling did not account for other co-occurring host plant species, which may have contributed to increasing *D. suzukii* density. Nevertheless, there is no clear evidence that the observed effects were substantially influenced by the simultaneous occurrence of the three sampled species at the same sites and sampling times. Indeed, the three species could be sampled at the same site and in the same period only in a few cases. In these few occasions, co-occurring hosts typically exhibited different levels of infestation due to phenological differences (i.e., peak ripening versus late ripening stages). When two species were simultaneously infested, the observed parasitism levels were consistent with the main results, with higher parasitism occurring on the most heavily infested samples.

6. Conclusion

This study highlights the pivotal role of *L. japonica* in the biological control of *D. suzukii* and underscores the importance of forests in supporting its populations. Our findings show that parasitism is primarily driven by host fruit infestation levels. We observed that *L. japonica* followed the temporal and spatial distribution of its host, *D. suzukii*, resulting in higher parasitism rate in late summer and in landscapes richer in forest habitats. These findings provide valuable insights for promoting landscape management practices to enhance the effectiveness of conservation and classical biocontrol of *D. suzukii* and emphasize the importance of raising farmers' awareness of the ecological value of forest areas and the essential ecosystem services they provide. Population dynamics theory suggests that recently introduced parasitoids require time to reach an equilibrium with their host populations and that parasitism rates may increase over time. Whether natural biocontrol will be sufficient to keep *D. suzukii* below economic thresholds in crop fields likely depends on the proportion of forest habitats in the surrounding landscape and on the arrival or deliberate release of additional natural enemies.

Funding sources

This study was funded by the Veneto Region as part of the program "Release of the non-native species *Ganaspis brasiliensis* in the Veneto Region as a biological control agent against *Drosophila suzukii*". Giovanni Dal Zotto PhD scholarship is funded by REACT-EU FSE in the frame of PON "Ricerca e Innovazione" 2014–2020 (DM 1061/2021). Scholarship code: BIO12, DOT1340225, Borsa 1 CUP B39J21026610001.

CRediT authorship contribution statement

Lorenzo Tonina: Writing – review & editing, Investigation, Data curation. **Giovanni Dal Zotto:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Lorenzo Marini:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Nicola Mori:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Silvia Ceroni:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

We thank the farmers and field technicians for their valuable support in site identification and for granting access to their fields. We also acknowledge the contributions of colleagues and students who assisted during fieldwork and laboratory activities.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.110184.

Data availability

Data will be made available on request.

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