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State of the spread of the exotic parasitoid wasp *Leptopilina japonica* tracking the route of its invasive host fly *Drosophila suzukii* in France

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Abstract

1. The spotted-wing drosophila, *Drosophila suzukii*, is one of the most damaging invasive fruit pests in the world. It infests a wide range of wild and crop host plants, impacting natural habitats and causing significant economic losses.
2. *Leptopilina japonica*, a predominant larval parasitoid of *D. suzukii* in the native areas of the fly, is now spontaneously expanding into non-native areas of its fly host. This study documents the presence and genetic structure of *L. japonica* collected from various wild and cultivated fruits across 11 sites in France in 2023.
3. *Leptopilina japonica* emerged from 15% of fruit samples and was strongly positively associated with *D. suzukii*, showing parasitism rates of up to 38.5%, notably in *Lonicera* fruits. Despite this, *D. suzukii* remained dominant, indicating a limited current biocontrol effect, while native parasitoids were nearly absent from samples.
4. Molecular analyses using COI markers revealed 10 distinct haplotypes of the *L. j. japonica* subspecies in France that clustered into three groups, suggesting multiple introductions and/or migration routes into France from Asia, North America and neighbouring European countries.
5. The lack of nuclear diversity measured from ITS2 markers suggests that the colonization is recent and that the populations experienced a bottleneck process. Nevertheless, a more extensive sampling combined with the use of additional genetic markers would be needed to better understand the origin and spread of *L. japonica* and its consequences on the equilibrium of *Drosophila* communities.

KEYWORDS

cherry, DNA barcoding, *Drosophila suzukii*, fruit fly, insect invasion, *Leptopilina japonica*, non-crop fruit, PCR, pest control

INTRODUCTION

Biological invasions are a major component of global change that alter ecosystem functioning and impact human activities (Daly et al., 2023). A major driver of biological invasions is the intensification of global trade, especially the transport of vegetables and fruits (Hulme, 2021), coupled with global climate change, which allows some non-native species to progress and persist in their new environment (Langille et al., 2017). This is the case of *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), a fruit pest fly also known as the spotted-wing drosophila, which has become invasive in regions outside its native range and causes significant economic losses worldwide (Asplen et al., 2015; de Ros, 2024). This fly pest attacks ripening small crop fruits, such as cherries and strawberries (Kanzawa, 1939; Mitsui et al., 2006; Rossi Stacconi, 2022), as well as the fruits of ornamental and wild plant species (Deconninck et al., 2025; Deconninck et al., 2024a; Deconninck et al., 2024b; Kenis et al., 2016; Mitsui et al., 2010; Poyet et al., 2015). A key feature that distinguishes *D. suzukii* from other *Drosophila* species is the serrated ovipositor, which allows it to pierce the fruit's skin for laying eggs in undamaged, ripening fruits, and even unripe green fruits (Ulmer et al., 2022). Larval feeding damages fruits, severely affecting production, with economic losses ranging from 30% to 100% (Green et al., 2019; Walsh et al., 2011). *Drosophila suzukii* also poses a threat to native ecosystems, as infested wild fruits rot prematurely and lose their attractiveness to seed dispersers (Bühlmann & Gossner, 2022; Poyet et al., 2014, 2015; Roche et al., 2021). This competition between *D. suzukii* and frugivorous bird species affects both plants—losing their dispersal capacity—and birds—losing a source of food—potentially affecting their fitness (Bühlmann & Gossner, 2022; Deconninck et al., 2024a; Roche et al., 2021, 2023).

Drosophila suzukii originates from South and East Asia, including China, Japan, Korea and neighbouring regions such as India (Rossi Stacconi, 2022). It was first observed and described in Japan in 1913 (Matsumura, 1931). In 1980, it was reported for the first time outside Asia, in Hawaii (Kaneshiro, 1983; Walsh et al., 2011). Since 2008, it has been found in Europe (Calabria et al., 2012), North America (Hauser, 2011), South America (Deprá et al., 2014) and Africa (Kwadha et al., 2021). The colonization in these non-native regions was associated with multiple introductions from different populations (Fraimout et al., 2017). In France, the expansion of *D. suzukii* was extremely fast, from the first report in 2009 in the South (Calabria et al., 2012; Mandrin et al., 2010) to its first detection in the north of France in 2011 (Poyet et al., 2014). Its invasion success can be attributed to several factors: the trade of fresh fruits vectoring its larvae on a global scale (Cini et al., 2014), the fly's high polyphagy enabling it to use a continuum of resources through time and space (Deconninck et al., 2025; Poyet et al., 2015), combined with its short life cycle allowing a high reproduction rate (Kanzawa, 1939) and rapid genetic adaptive shifts (Gibert et al., 2016).

The use of insecticides can be an effective control method against *D. suzukii* (Beers et al., 2011), but many of the compounds used have negative side effects on biodiversity and human health (INSERM Collective Expertise Centre, 2022) and resistances to insecticides commonly emerge (Civolani et al., 2021). Integrated management strategies such as cultural control, sterile insect techniques or biological control can be sustainable strategies that reduce the use of pesticides (Tait et al., 2021). One promising approach to control *D. suzukii* populations is the use of species-specific natural enemies, such as parasitoids from the native area (Baker et al., 2020).

European parasitoids are capable of parasitizing *D. suzukii* to varying degrees of success, but they have not proven effective in controlling pest populations in an agricultural context (Weydert et al., 2016). *Drosophila suzukii* is attacked by approximately 20 species of parasitoids worldwide from several taxonomic groups, targeting either the larvae or the pupae (Girod et al., 2018; Wang et al., 2020). European larval parasitoids, such as *Leptopilina boulardi* (Barbotin, Carton & Kelner-Pillault) or *Leptopilina heterotoma* (Thomson), exhibit low parasitism success due to strong encapsulation rates by *D. suzukii*, as high as 74% (Chabert et al., 2012; Iacovone et al., 2018). The pupal parasitoids *Pachycrepoideus vindemiae* (Rondani) and *Trichopria drosophilae* (Perkins) display high parasitism success rates and rapid adaptation capacity to *D. suzukii* as a host in laboratory conditions (Jarrett et al., 2022), but *in natura*, since they are mostly observed late in autumn once the season of crop fruit production is finished (Kremmer et al., 2017) and on rotten fruits (Fellin et al., 2023), their effectiveness in naturally controlling the pest in fresh fruits appears to be limited.

In the native area of *D. suzukii*, four larval parasitoid species are predominant: *Asobara japonica* Belokobylskij; *Leptopilina japonica* Novković & Kimura; *Ganaspis kimorum* Buffington; and *Ganaspis lupini* Buffington (formerly named *Ganaspis brasiliensis* (Ihering) G1 and G3 respectively, revised in Sosa-Calvo et al., 2024; Daane et al., 2016; Giorgini et al., 2019; Girod et al., 2018). Among these, only *G. kimorum*, a highly host-specific larval parasitoid, has been selected and regulatorily approved in some European countries and in North America for biological control (Gariepy et al., 2024; Kasuya et al., 2013; Le Navenant et al., 2025; Seehausen et al., 2020; Stahl et al., 2024; Wang et al., 2021).

However, *L. japonica* has recently also been found outside its native area, in North America, Argentina (Beckwith et al., 2025; Beers et al., 2022; Gallardo et al., 2022; Gonzalez-Cabrera et al., 2020), and in Europe, specifically in Germany (Martin et al., 2023), Italy (Puppato et al., 2020), France (Rousse et al., 2023) and Switzerland (Rossi Stacconi et al., 2025). From a taxonomic point of view, *L. japonica* is divided into two subspecies: *Leptopilina japonica japonica* Novković & Kimura and *Leptopilina japonica formosana* Novković & Kimura. These two subspecies are difficult to distinguish morphologically; phylogenetic analyses using molecular markers such as COI, ITS1 and ITS2 support their separation (Novković et al., 2011). They are undergoing allopatric speciation and are geographically isolated: *L. j. japonica* has been recorded in China, Japan and Korea, while *L. j. formosana* has been found in Taiwan and South Korea (Novković et al., 2011; Rossi Stacconi et al., 2025).

Some authors sustain that only one of the subspecies has been identified in Europe and America so far (Rossi Stacconi et al., 2025) and from a practical point of view, we will continue to use the name *L. japonica* for *L. j. japonica*. Compared to local parasitoids, *L. japonica* shows higher rates of parasitism of *D. suzukii*, and its establishment could therefore mitigate the success of this invasive pest fly. Nevertheless, given the novelty of the phenomenon in Europe (Puppato et al., 2020), and particularly in France, field data are lacking. Field studies are urgently needed to assess the efficacy of this non-native parasitoid to reduce *D. suzukii* populations, as well as to better understand its food web interactions (Rossi Stacconi et al., 2025), especially with other parasitoids and drosophila.

Here, our aim was to document the present distribution of *L. japonica* in France and the potential origin sources of its populations. Firstly, to achieve this goal, we compared the emergence of *L. japonica* and *D. suzukii* among a variety of wild fleshy-fruited plants and crop cherries from different regions of France to identify fruits preferentially used by the parasitoid. Secondly, we compared the genetic background of French populations of *L. japonica* to other European and Asian ones using two molecular markers, the mitochondrial gene COI and the nuclear marker ITS2, to better understand the introduction pathways of its populations. The knowledge of the relationships between this non-native parasitoid and the local flora as well as its colonization routes is a necessary preliminary step before the development of biological control strategies and the enhancement of monitoring efforts in France and more largely in Europe.

MATERIALS AND METHODS

Study sites and fruit sampling

The study was conducted at 11 sites representative of different climatic, agricultural or landscape conditions in France (Table 1). Most of the sites were sampled multiple times from May to November 2023 as well as in May and July 2024 (for one site) to cover the fruiting phenologies of the different fleshy-fruit-bearing plant species (Table S1). In this article, we have distinguished between wild cherry and cultivated sweet cherry trees. Since wild cherry and cultivated sweet cherry belong to the same species, we have chosen to use "*Prunus avium* L." for wild *Prunus avium* and "sweet cherry" for cultivated *Prunus avium*. For the same reason, we have used "sour cherry" for cultivated *Prunus cerasus* L. For each collection date, fruits were randomly collected from the canopy of each individual of the fruiting plant species located within and up to 150 m from the focal crop (Table 1), by walking around the plant to cover all sides of its canopy. The fruits were sampled by filling a 300 mL plastic container for each individual plant. After collection, each fruit sample was weighed and transferred into ventilated cylindrical plastic boxes (11 cm diameter and 8 cm height) with absorbent paper to control humidity. Samples were kept in the laboratory and insect emergence was checked every day for up to 8 weeks at 22°C, 16:8 (L/D) h and 60% relative humidity until all insects emerged. Emerging specimens were collected every day and placed in 70% ethanol for morphological and molecular identification.

TABLE 1 Sampled sites in France.

Site codes	Locality	Region	Year	Sampling periods	Focal crop	Geographic coordinates N, E	Surrounding landscape
DORD1	Douville	Southwest	2023	May–Jul	Strawberry, raspberry	45.020286 0.612289	Forest margins, hedgerows
GIR1	Toulenne	Southwest	2023	May–Nov	Sweet cherry	44.569753 0.285041	Hedgerows, small orchards, and grassland
VAUC3	Malaucène	Southeast	2023	May–Nov	Sweet cherry	44.167816 5.113995	Forest margins, hedgerows and orchards
VAUC1	Malemort-du-Comtat	Southeast	2023	August–Nov	Sweet cherry	44.006113 5.140366	Hedgerows, small orchards, and grassland
VAUC1T	Venasque	Southeast	2023	August–Nov	Sweet cherry	44.008663 5.156443	Hedgerows, small orchards, and grassland
MAR1	Vence	Southeast	2024	May–Jul	Sweet cherry	43.711723 7.128390	Garden, urban area
AM1	La Gaude	Southeast	2023	May–Nov	Strawberry, fig	43.729505 7.177360	Hedgerows, small orchards
AM1T	Gattières	Southeast	2023	May–July	Strawberry	43.755879 7.185247	Hedgerows, small orchards
MEUR1	Lagney	Northeast	2023	May–Nov	Sweet cherry	48.733193 5.832172	Forest margins, hedgerows and orchards
MEUR1T	Trondes	Northeast	2023	May–Nov	Sweet cherry	48.720955 5.775539	Forest margins, hedgerows and orchards
BASR1	Breitenbach	Northeast	2023	May–Nov	Blueberry	48.367620 7.289106	Hedgerows, small orchards, and grassland

Morphological and molecular identification of insects

Morphological identification

First, among the insects that emerged from the harvested fruits, specimens belonging to the genus *Drosophila* were separated. Subsequently, *D. suzukii* individuals were identified based on characteristic morphological traits, such as the crenate ovipositor in females and the black spot on the wings in males (Withers & Allemand, 2012). All other drosophilid species were not identified to species level but were counted and classified collectively as "other drosophilids".

Parasitoids were sorted by family. For the individuals belonging to the Figitidae family, identification was firstly performed using an online, user-friendly determination key "the World Subfamilies Lucid Matrix Key to World Subfamilies of Figitidae" (accessed on 15 October 2025, https://www.waspweb.org/Cynipoidea/Keys/Lucid_Matrix_keys/World_Figitidae_subfamilies/figitidae_world_subfamily_key.html) also published in Buffington et al. (2020), and then completed by keys and descriptions for species-level identification (Lue et al., 2016; Martin et al., 2023).

Biological material used in molecular analyses

Molecular analyses were performed on parasitoids morphologically identified as *L. japonica* from all localities and plant species of the study. We also included *L. japonica* specimens from their native areas in Asia (China and Japan) as well as from some areas in Europe (Germany, Italy and Switzerland) in the analyses (Table S2). In Asia, individuals were collected in 2015 from four locations (three in China and one in Japan) during an exploratory survey to identify native parasitoid species of *D. suzukii* (Girod et al., 2018; Girod et al., 2018). European individuals were collected (i) in Germany, from three locations between 2021 and 2023, (ii) in Switzerland, from two locations in September 2023 and (iii) in Italy, from one location in September 2023.

DNA extraction, PCR and sequencing

Two molecular markers were used: the mitochondrial protein-coding gene Cytochrome Oxidase subunit I (COI) and the ribosomal Internal Transcribed Spacer 2 (ITS2). Individual DNA extraction was performed on intact specimens using the NucleoMag™ DNA Extraction Solution kit with incubation at 65°C for 15 min followed by 2 min at 98°C. However, for some individuals, the amplification or sequencing failed, so another extraction kit, the QuickExtract™ extraction kit (Macherey-Nagel) including a purification step, was then used according to the manufacturer's instructions. For the PCR, 2 μL of DNA extract was added to mix 10.25 μL of Milli-Q water, 0.125 μL of 100 μM primer cocktail, and 12.5 μL of 2× Qiagen Multiplex PCR Master Mix (Qiagen, Hilden, Germany); total volume of 25 μL.

Since the standard COI region primers LCO1490 and HCO2198 (Folmer et al., 1994) only amplified a pseudogene in our conditions, we turned to the COIpF2 and COI2437d primers, developed by Simon et al. (1994) and modified by Kaartinen et al. (2010). This amplified region partially overlaps with the standard DNA barcode region, sharing approximately 400 base pairs with the fragment typically amplified using the primers LCO1490 and HCO2198.

The PCR conditions used were the following: initial denaturation at 94°C for 15 min, followed by 35 cycles of 95°C for 30 s, 46°C for 90 s, 72°C for 1 min, and a final extension at 50°C for 10 min. The ITS2 region was amplified using the primer pair described by Yara (2006), ITS2-F and ITS2-R2, with the same PCR conditions as COI except for the annealing step at 53°C.

Amplified PCR products were visualized using the capillary electrophoresis method QIAxcel Advanced System (Qiagen, Hilden, Germany) and sequenced in both directions using the Sanger method (Azenta-Genewiz, Radolfzell, Germany).

Molecular data analysis

Sequences were assembled and corrected using Geneious v.2024.0.2 (Kearse et al., 2012). All COI sequences were aligned in MEGA v6.06 (Tamura et al., 2013) using the ClustalW algorithm (Thompson et al., 1994) and translated to amino acid sequences to check for the presence of stop codons. MEGA v.6.06 was also used to calculate the pairwise distance (p-distance) within the *L. japonica* cluster. Additionally, we used the BLOSUM62 matrix to check the frequency of amino acid substitutions (Henikoff & Henikoff, 1992). For both COI and ITS2 sequences of *L. japonica*, the number of haplotypes was calculated using DnsSP v.6 (Rozas et al., 2017). Haplotype networks and geographical distributions were constructed using PopART v1.7 (Leigh & Bryant, 2015) and the TCS network method (Clement et al., 2002). The background map was created using QGIS v3.28 (QGIS Development Team, 2019) with the Natural Earth Quick Start Kit, which was developed by Made with Natural Earth (naturalearthdata.com). A data matrix of haplotype frequencies in the different studied countries was built. The haplotypes resulting from sequences with negative values of amino acid substitution, were not considered in this dataset. To examine the genetic proximity between the samples from the three main regions of France (northeast, southeast and southwest) and those from other countries, we performed a cluster analysis of the haplotype frequency matrix using Euclidean distance measures and Ward's linkage method (McCune & Grace, 2002) with PC-ORD v.7.03 (McCune & Mefford, 2016).

To confirm the identification of the parasitoids, phylogenetic analyses of the COI gene were performed on the CIPRES Science Gateway v3.3 (Miller et al., 2010) using RAxML v.8 (Stamatakis, 2014) with 1000 bootstrap iterations to support the maximum likelihood. For this, we included data from the DROP (Lue et al., 2021) reference database for molecular data of *Drosophila* parasitoids. The topology of the tree was examined using FigTree v1.4 and then edited in Adobe Illustrator.

DATA ANALYSIS

We examined variation in the abundance and frequency of *Drosophila* and parasitoids in fruit using two common infestation variables adapted from Deconninck et al. (2025) to balance insect numbers by fruit mass. These infestation variables were either centred at the fruit level using the Fruit Infestation Rate (FIR) for a given insect species in a given plant species or on the plant species level using the Plant Infestation Rate (PIR):

- FIR = 100 × (number of emerged insect individuals from fruits collected from a given plant individual)/(total mass of fruit collected from the same plant individual).
- PIR = 100 × (number of infested plant individuals of a given plant species in a given area)/(total number of sampled individuals of this plant species in this area).

The fresh fruit mass unit used in this formula is expressed in grams. These two variables can be interpreted as follows: FIR measures the density or abundance of insects per 100 g of fruit and reflects the load or burden of the infestation for a given plant species (Deconninck et al., 2025; Deconninck et al., 2024a). PIR varies between 0% and 100%, and measures the frequency or proportion (as it is in %) of contaminated plant individuals in a landscape area or region and reflects the occurrence rate of the insect among a pool of plant individuals. These infestation variables were calculated for each plant taxon.

For each fruit sample, we also calculated the percentage of emerging individuals of *L. japonica*, *D. suzukii*, other *Drosophila* and other parasitoids, namely, the relative eclosion percentage *sensu* Fellin et al. (2023). For *L. japonica*, this percentage corresponded to a measure of the *Drosophila* parasitism rate (PR) by the wasp (PR = 100 × number of *L. japonica* / [number of *D. suzukii* + other *Drosophila* + *L. japonica* + other parasitoids]), as it represented the proportion of *L. japonica* that emerged from a calculated initial pool of *Drosophila* individuals.

To examine potential relationships between the abundance of parasitoids and drosophila, Pearson correlation tests were conducted after log10 $(x + 1)$ transformation. A negative correlation would suggest a top-down control of the parasitoid on its host, while a positive correlation would suggest bottom-up control of parasitoid abundance by prey/resource availability. Pearson correlation tests were also used to determine whether there was any correlation between the FIR and PIR values for both *D. suzukii* and *L. japonica*.

Data processing and analysis were conducted in R (R Core Team, 2025) using RStudio version 4.3.3. The data visualization was carried out using the *ggplot2* package (Wickham, 2016). The plant species are ordered in descending order according to the average FIR value for *D. suzukii* which was maintained for all the figures. All supplementary data are available from the Dryad Digital Repository (Viciriuc et al., 2025).

RESULTS

Fruit and plant infestation rate by *Drosophila suzukii*

Twenty-eight (cultivated or wild) plant species were sampled in the study for a total of 249 fruit samples collected. The number of fruit samples per plant species varied from 1 to 33 according to their frequency of appearance in the field (Table S1).

A total of 24,722 *Drosophila* individuals emerged from 46.18% of the 249 fruit samples and 57.14% of the 28 plant species encountered. *Drosophila suzukii* adults represented 76.8% ($n = 18{,}996$) of the emerging *Drosophila* and emerged from 16 of the 28 plant species collected (Figure 1). The 12 plant species with no emergence of *D. suzukii* were mostly native shrubs or chamaephytes (e.g. *Crataegus monogyna* Jacq., *Ligustrum vulgare* L. etc.– Table S1). The FIR highly varied between the plant species, the highest values being observed for *Sambucus ebulus* L. followed by *Rubus fruticosus* L., *Prunus avium*, and *Sambucus nigra* (L.) (Figure 1). The PIR, information in brackets in Figure 1 also greatly varied between plant species, six of them exhibiting a PIR of 100%: *S. ebulus*, *S. nigra*, *Rhamnus frangula* L. (but only one individual found for this plant), *Amelanchier lamarckii* Martin, *Fragaria* sp. L., and *Rubus caesius* L. Besides plants with no *D. suzukii*, plant species with the lowest PIR were *Prunus spinosa* L. and *Cornus sanguinea* L. The Pearson correlation between FIR and PIR values showed a significant positive association ($r = 0.53$, $p = 0.034$).

Parasitoid distributions among fruits and sites

A total of 1,064 individuals of Hymenopteran parasitoids emerged from only 15.42% of the fruit samples (39 samples with parasitoids) and 35% of the 28 plant species. *Leptopilina japonica* accounted for almost the totality (99.24%, $n = 1{,}056$) of individuals, with very few occurrences of the other two species, *Asobara rufescens* (0.66%, $n = 7$) and *Pachycrepoideus vindemiae* (0.1%, $n = 1$). *Leptopilina japonica* was found in 39 fruit samples; 100% of them also contained *D. suzukii* and 54% other *Drosophila* species. Among the 16 plant species infested by *D. suzukii*, *L. japonica* occurred in 10 of them.

Distribution of *Leptopilina japonica* among fleshy-fruited plants

The FIR by *L. japonica* actually varied between plant species, with the highest values being observed in *Lonicera* sp., *Rubus fruticosus*, *Sambucus ebulus*, *Prunus avium* (wild cherry) and sweet cherry (Figure 2). The PIR also varied between plant species, with the highest values being observed for sour cherry, sweet cherry and *Lonicera* sp. The Pearson correlation between FIR and PIR values was not significant ($r = 0.11$, $p = 0.761$).

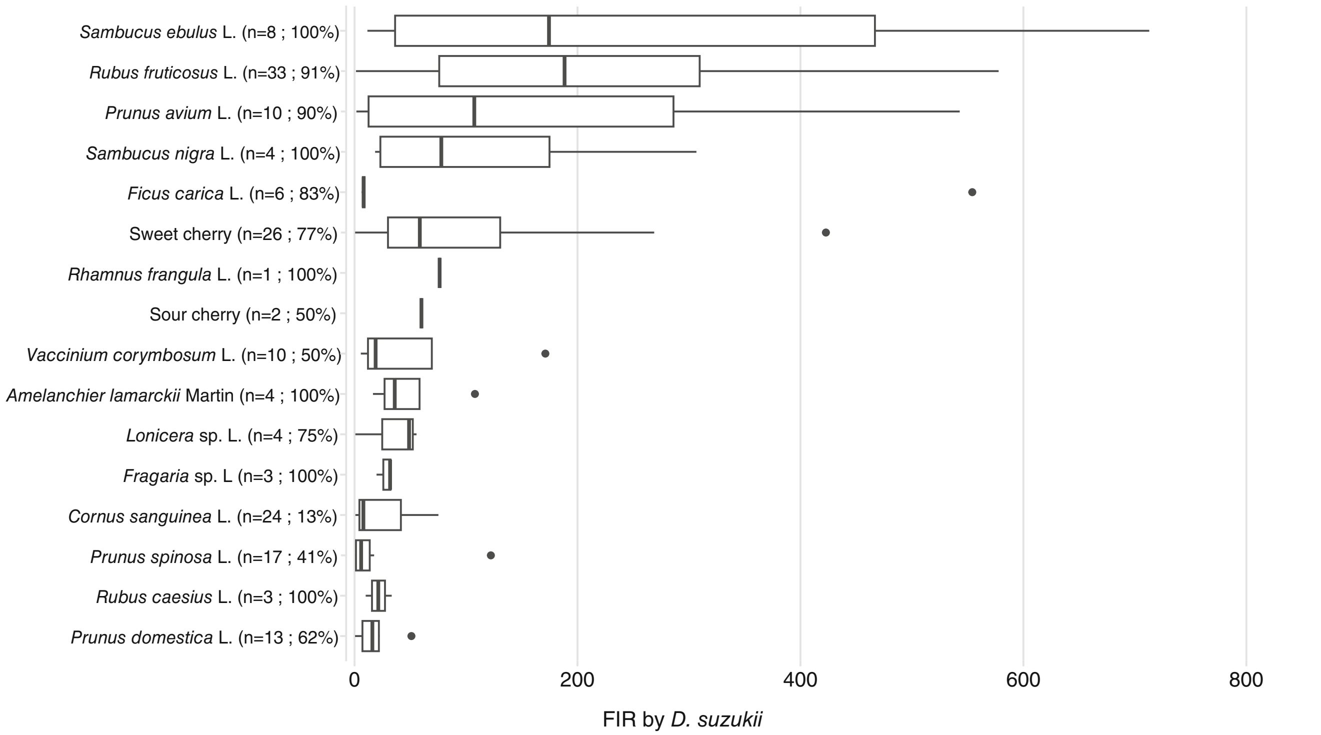

FIGURE 1 The Fruit infestation rates (FIR) by *Drosophila suzukii* among different plant species. For a given fruit sample, Fruit Infestation Rate: FIR = 100 × number of *D. suzukii* individuals from fruits collected from a given plant individual/total mass of fruit collected from the same plant individual; '*n*' represents the number of fruit samples collected per plant species followed by the values of Plant Infestation Rate (PIR) in percentage (Plant Infestation Rate: PIR = 100 × number of infested plant individuals of a given plant species in a given area/total number of plant individuals of this same sampled plant species in the same area). Only plant species with the presence of *D. suzukii* in fruits were considered here.

Distribution of *Leptopilina japonica* among sites

Among the 11 localities sampled, *L. japonica* was identified in six of them: (i) three in northeastern France, from the 2 administrative departments of Meurthe-et-Moselle (sites MEUR1 and MEUR1T) and Bas-Rhin (BASR1), (ii) two in southeastern France from Vaucluse (VAUC3) and Alpes-Maritimes (MAR1), and (iii) one in southwestern France, Gironde (GIR1). It should be noted that pairs of nearby sites, one with and one without *L. japonica*, were frequently observed (Figure 3, VAUC3 vs. VAUC1 for example) indicating a spatial heterogeneity of its occurrence at local scales.

Drosophila parasitism rate by *L. japonica*

The *Drosophila* Parasitism Rate (PR) by *L. japonica* greatly varied between plant species and locations. The highest PR values were observed in *Lonicera* fruits (38.53%) and near Bordeaux in southwestern France (site GIR1 on Figure 3; Table S3). Among the plant species where *L. japonica* was present, PR by the parasitoid species varied from 0.15% to 38.53% (Table S3). The highest PR, 38.53%, was recorded in *Lonicera* fruits, followed by smaller values of 23.55% for sweet cherry, 12.98% for *Rubus fruticosus*, 4.2% for *Sambucus ebulus*, 4.05% for *Prunus avium*. The lowest parasitism percentage, 0.15%, was recorded in *Ficus carica*.

Drosophila parasitism rates by *L. japonica* varied across these sites with the highest PR recorded in southwestern France (GIR1 site: 38.53% in *Lonicera* sp., 4.2% in *Sambucus ebulus* and 4.05% in *Prunus avium*). In MAR1, the highest PR was 10.82% on the only sampled plant species observed (sweet cherry). At the MEUR1T site, *L. japonica* was found only in the fruits of sweet cherry with a PR of 4.89%. At BASR1, the highest PR of 12.23% was recorded in *Rubus fruticosus* while in MEUR1, it was observed in sweet cherries with 4.12%. Lastly, in the VAUC3 site, the PR was only 0.15% and recorded in the only sampled species, *Ficus carica*.

Figure 4 showed the relative proportion of insects emerging from the different studied fruits. *Drosophila suzukii* was dominant in the fruits of the majority of plant species. *Fragaria* sp., bearing fragile fruits in direct contact with the soil, which promotes their decay, was the only plant species where *D. suzukii* was not dominant. In 13 out of 16 plant species, *D. suzukii* relative infestation was over 75% (Figure 4). The other drosophilid species were found in the fruits of most plant species (except sour cherry and *Prunus spinosa*), but their relative infestation ranged from 1.5% to 25.5%. The only exception was the fruit of *Fragaria* sp. where other drosophilids were dominant and accounted for 61.1% of the emerging individuals. Among

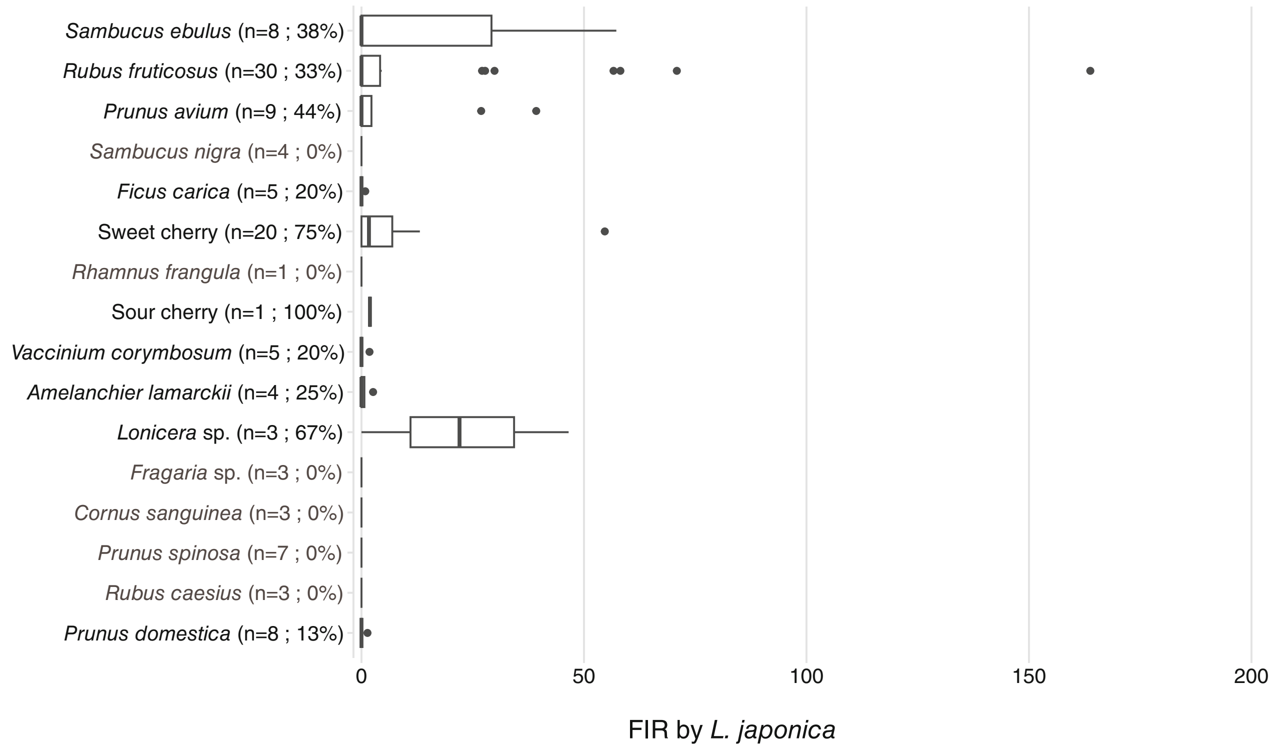

FIGURE 2 Number of *Leptopilina japonica* individuals per 100 g of fruits (i.e. FIR by *L. japonica*: FIR = 100 × number of *L. japonica* individuals from fruits collected from a given plant individual/total mass of fruit collected from the same plant individual) calculated for plant species infested by *Drosophila suzukii* (see Figure 1); '*n*' represents the number of fruit samples collected per plant species followed by the values of PIR in percentage (Plant Infestation Rate: PIR = 100 × number of infested plant individuals of a given plant species in a given area/total number of plant individuals of this same sampled plant species in the same area). The order of host plants is the same as those in Figure 1. Only plant species with the presence of *L. japonica* and/or *D. suzukii* were considered here.

parasitoids, *L. japonica* was dominant compared to other parasitoid species. It was found in 10 out of the 16 fruit species. The relative infestation of *L. japonica* typically ranged from 0.5% to 7.1%, peaking at 38.2% in *Lonicera* fruits. The other parasitoid species were found in only three plant species, with relative abundances not exceeding 1.5%.

When examining the relationships between fly and parasitoid FIR values, a significantly positive correlation was found between FIR of *L. japonica* and FIR of *D. suzukii* ($p = 0.017$, $r = 0.38$; Figure 5a). However, no significant relationship was found between FIR of *L. japonica* and FIR of other drosophilids ($p = 0.962$, $r = 0.008$; Figure 5b).

Molecular characterization of *L. japonica* using COI and ITS2 sequences

In this study a total of 76 COI sequences were obtained, including 24 sequences from *L. japonica* specimens from France, 23 from China, 10 from Germany, eight from Italy, seven from Switzerland and four from Japan.

For the phylogenetic analysis of the COI marker, we used sequences from the DROP database (accessed on 7 July 2025, DROP_sequences_fasta_COI_only_Cynipoidea.fas). We removed three sequences that did not correspond to our length (114 sp. 6-L. drop, 111 sp3-L. drop and 109 sp3 *Ganaspis* drop). All sequences were grouped with those belonging to the molecular cluster corresponding to the *L. j. japonica* subspecies, with an intraspecific p-distance ranging from 0.02% to 3.8%. A sister cluster containing three sequences from Taiwan (AB583600, AB583605 and AB583599) is linked to this molecular cluster which corresponds to the *L. j. formosana* subspecies with a divergence of 5.3% (Figure S1). For further molecular analysis, we decided to keep only the sequences corresponding to *L. j. japonica*, which we name *L. japonica* in the subsequent text.

For the haplotype network, we added 23 sequences from the DROP and NCBI databases to our obtained sequences. These represented sequences from Canada (six sequences), Japan (five), Germany (four), China (three) and South Korea (one) (Table S4). All sequences had a common length of 343 base pairs and corresponded to 25 haplotypes, with 31 variable (polymorphic) sites and a total of 38 mutations. The number of sequences per haplotype ranged from one to 18. Fifteen haplotypes were represented by a single sequence.

At the amino acid level, no stop codons were detected. Nine amino acid positions were variable: six showed negative BLOSUM62 scores (underrepresented substitution), one had a positive score (over-represented substitution), one position had both positive and negative scores, and one had a score of zero (neutral substitution).

The haplotypes H12, H14 and H17 had negative mutation frequency values and were marked with an asterisk in Figure 5. These

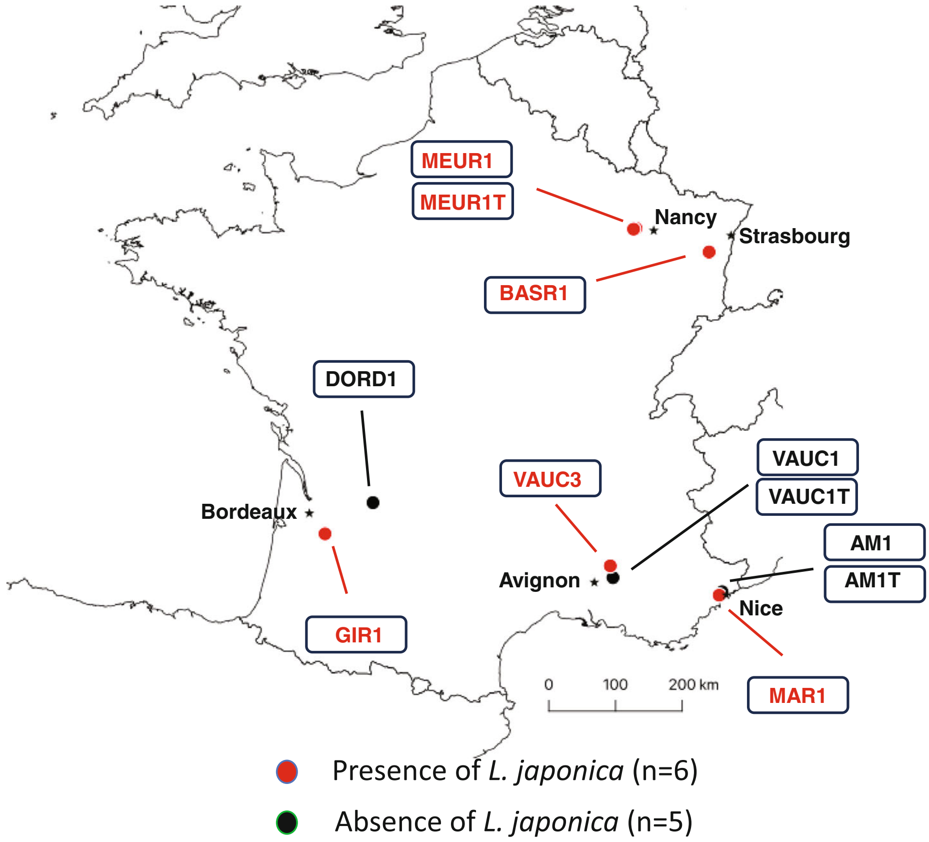

FIGURE 3 Location of sampling sites in France. Site codes and characteristics are detailed in Table 1.

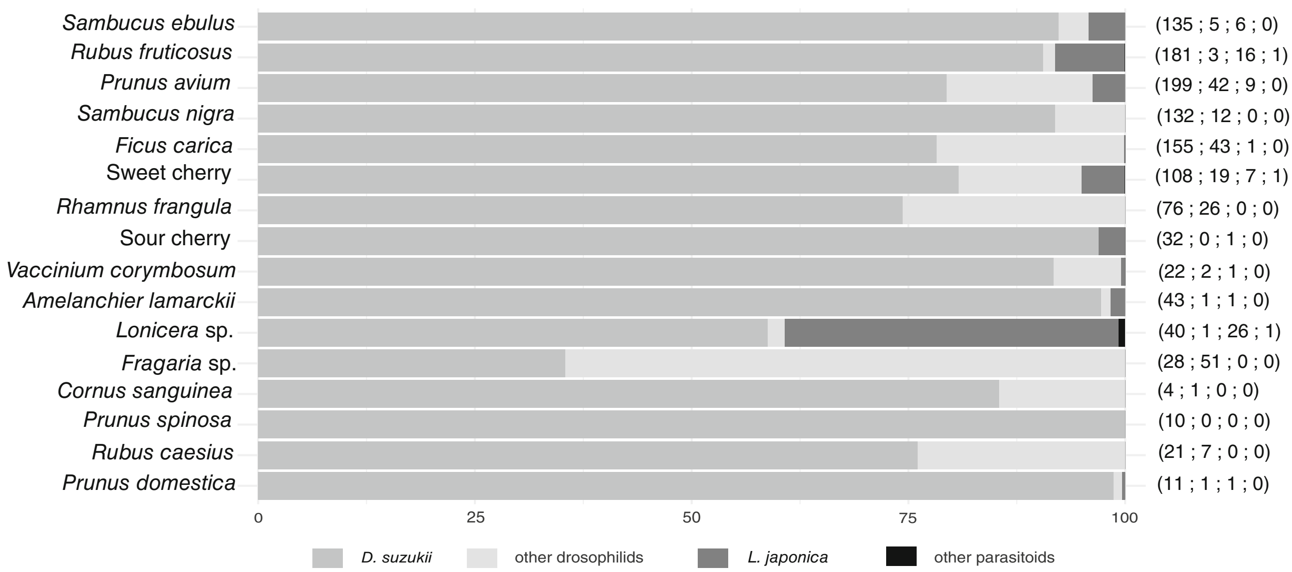

FIGURE 4 Relative fruit infestation rates (FIR) of flies and parasitoids in fruit of different host plant species. For each host plant species, the number of *D. suzukii*, other *Drosophila*, *L. japonica* and other parasitoid individuals is indicated in brackets, respectively, in this order and positively rounded. The category "other parasitoids" included *Asobara rufescens* and *Pachycrepoideus vindemiae*. The order of host plants is the same as those in Figure 1.

negative substitution rates were observed only for these haplotypes, and may indicate the presence of pseudogenes or sequencing artifacts.

Four haplotypes H5, H7, H1 and H4 were common (Figure 6) and included sequences from multiple geographic regions (Figure 7). Of these, H5 and H7 can be considered central haplotypes, each with

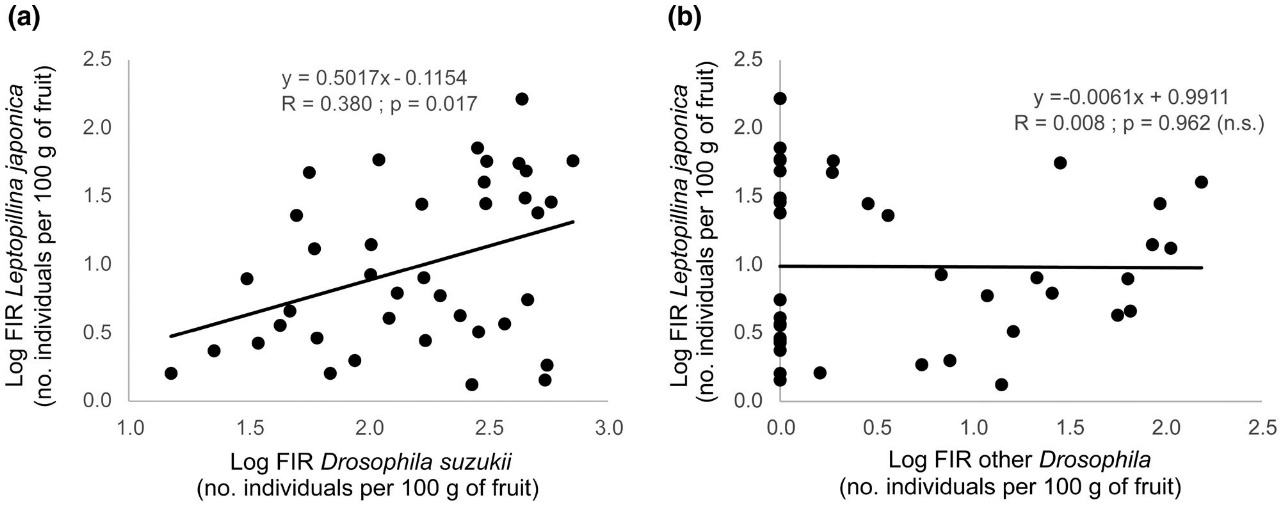

FIGURE 5 Relationships between the number of emerged *Leptopilina japonica* per 100 g of fruits (LOG FIR: Log10 ($x + 1$)-transformed Fruit Infestation Rate) and (a) the number of emerged *Drosophila suzukii* per 100 g of fruits, and (b) the number of other *Drosophila* (rotting fruit decomposer species) that emerged per 100 g of fruits. *R* and *p* corresponded to the correlation coefficients and *p*-values, respectively, from Pearson correlation tests after a log10 ($x + 1$)-transformation of variables. Only fruit samples with a presence of *L. japonica* were considered.

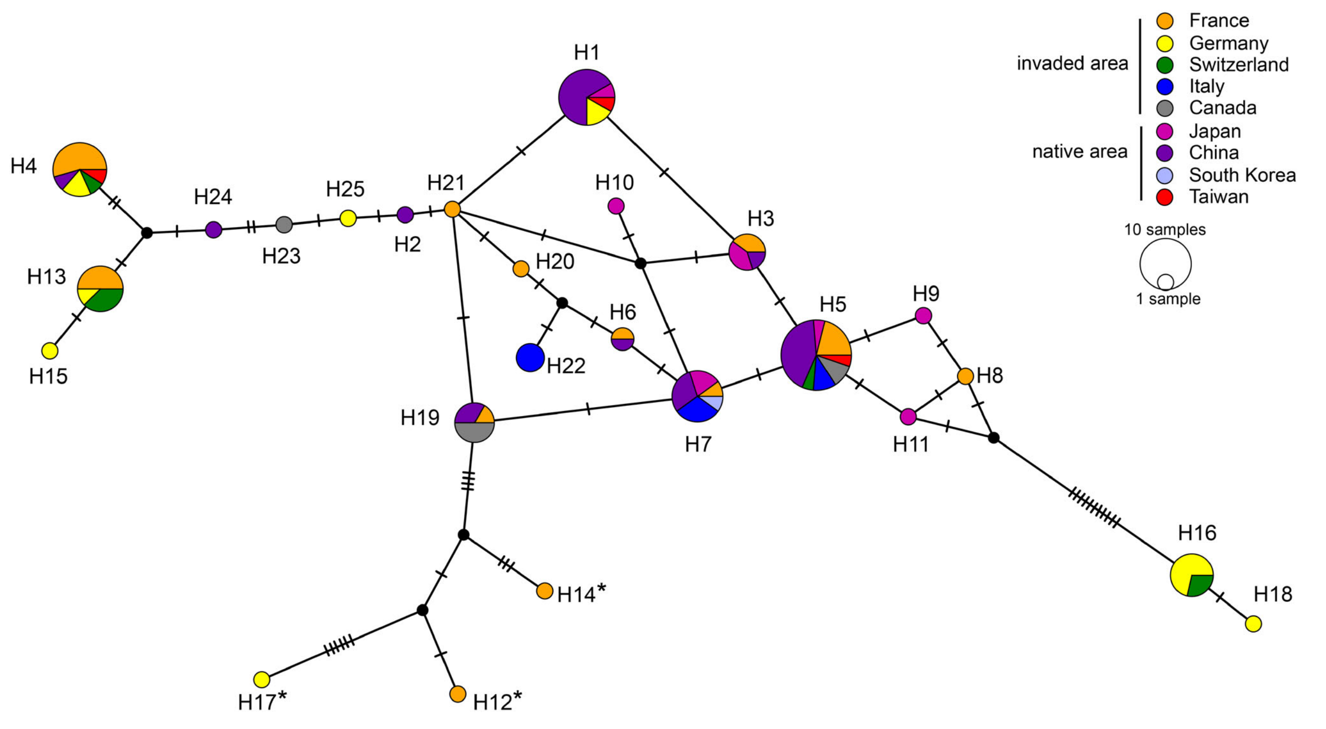

FIGURE 6 Haplotype network generated based on the genetic marker COI. The network contains haplotypes with sequences obtained in this study and those from available databases (Table S4). The colours indicate haplotypes from different countries. For each haplotype, the size of the circle is proportional to the observed frequencies. H, Haplotype. H*, Haplotype results from sequences with negative values of amino acids substitution.

four connections, and included sequences from all studied regions except Germany. Haplotypes H16 and H18 were located at the periphery of the network, showing at least 11 nucleotide substitutions, but no amino acid changes were observed for them.

The cluster analysis of the haplotype frequency matrix (Figure 8) identified four main groups of countries: (i) a group separating South Korean samples from the others and represented by a single haplotype H7, (ii) a group mixing Asian countries (China, Japan) with

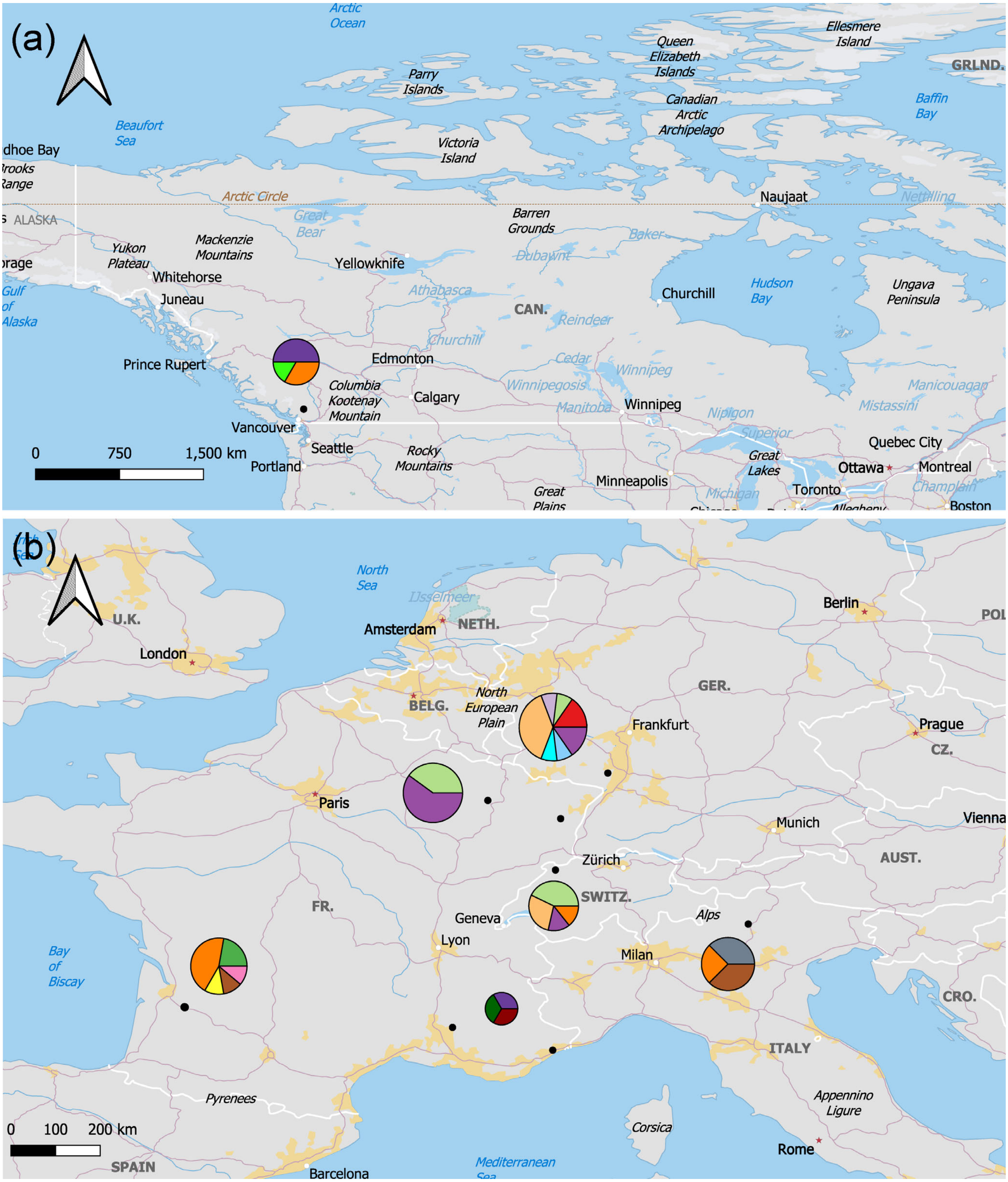

FIGURE 7 Geographical distributions and frequency of haplotypes of *L. japonica* in different countries (Table S5). Map (a) Canada; map (b) Europe; map (c) Asia. Since haplotypes H12, H14 and H17 are putative pseudogenes were not represented. Black dots indicate collection sites samples. The colour and the size of the pie charts represent the haplotype and frequencies at each location.

Mediterranean Europe (Italia and southwestern France), notably sharing H5 and H7 haplotypes, (iii) a group linking North America (Canada) to southeastern France, characterized by a common haplotype H19, and (iv) a group covering northeastern Europe (northeast of France with neighbouring countries, Germany and Switzerland) represented by H4, H13 and H16 haplotypes (Figure 7).

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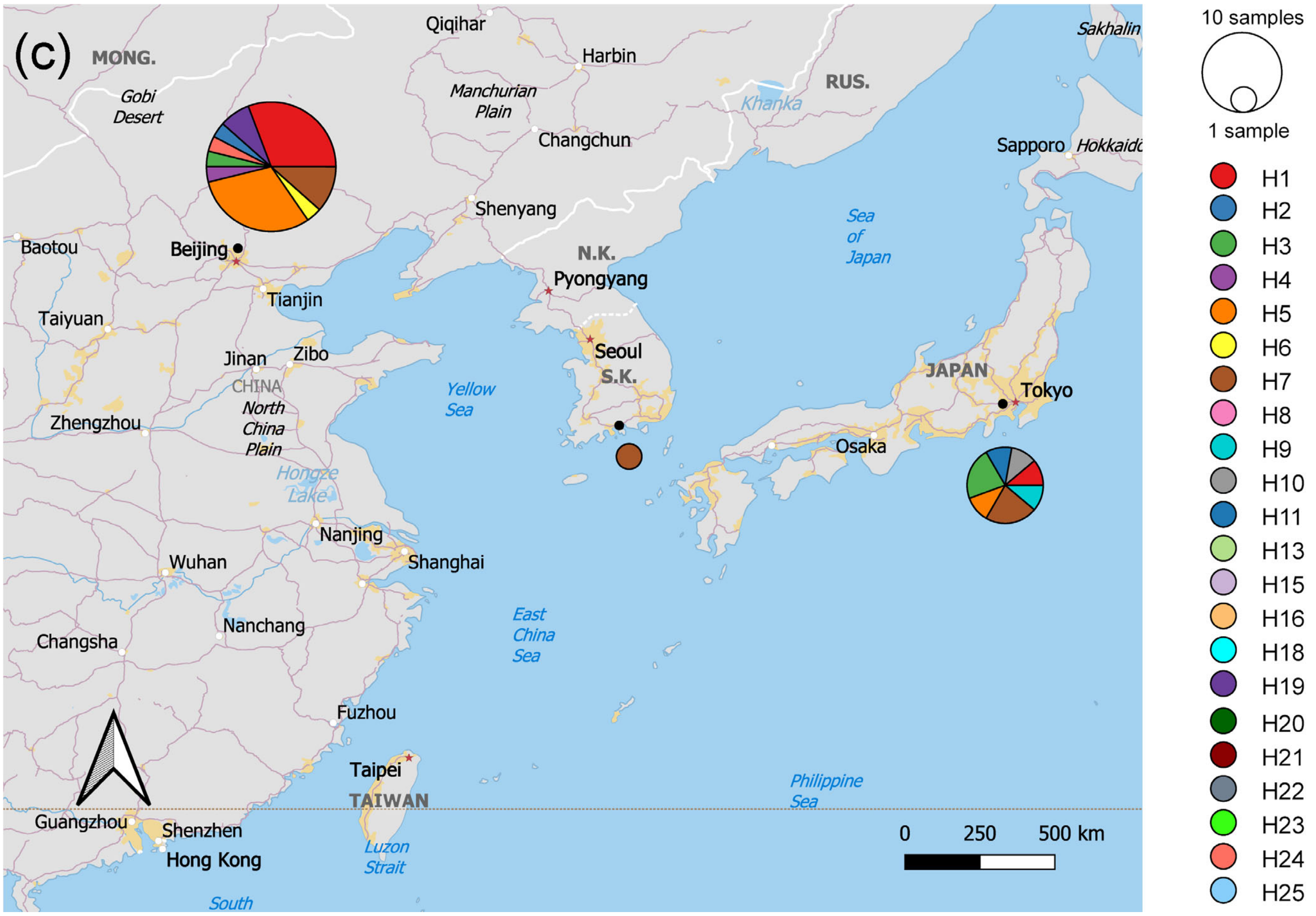

FIGURE 7 (Continued)

A total of 58 ITS2 sequences, each comprising 489 base pairs, were also analysed, originating from both Asia (China: 15; Japan: 4) and Europe (France: 22; Germany: 9; Switzerland: 8). All sequences were found to correspond with a single haplotype (Table S2). This haplotype exhibited 100% sequence identity with *L. japonica* sequences deposited in the NCBI database, specifically: MK937819, MK937820, MK937821 (China) (Buffington et al., 2020), and AB583702, AB583704, AB546888 (Japan) (Novković et al., 2011). The region of overlap between the sequences generated in this study and those available in public databases consisted of 465 base pairs with no observed nucleotide variation.

DISCUSSION

Relationships between *Leptopilina japonica* and local *Drosophila* and parasitoid communities

Our study highlights three important points that define the relationships between *L. japonica* and local *Drosophila* and parasitoid communities.

First, results showed a near-absence of native parasitoid communities in fresh fruits collected from the canopy of plants, both in areas with and without the presence of *L. japonica*. Only eight individuals from two species, comprising 0.67% of the parasitoids that emerged from fruits, were recorded despite the emergence of 5,726 individuals of local drosophilids. This absence of native parasitoids in fresh fruits is commonly observed in Europe and corroborates, for example, the findings of Fellin et al. (2023) showing a very low number of local larval and pupal parasitoids in fruits from the canopy compared to those lying on the ground. Particularly, common larval parasitoids are rarely or never recovered from *D. suzukii* during field surveys on all the continents invaded by *D. suzukii* (Daane et al., 2025), and laboratory tests confirmed their inability to parasitize the fly's offspring (Mazzetto et al., 2016). The absence of local parasitoids in canopy fruits can be explained, in part, by the trophic ecology of their European host *Drosophila* species. Most native *Drosophila* species in France are trophic specialists of decomposing organic matter, and are primarily found in fallen fruits (Deconninck et al., 2024b; Poyet et al., 2014). Therefore, native parasitoids typically target the fruits on the ground, containing their usual hosts, rather than those in the foliage. There is also a time lag between fruit infestation by *Drosophila* and *Drosophila* infestation

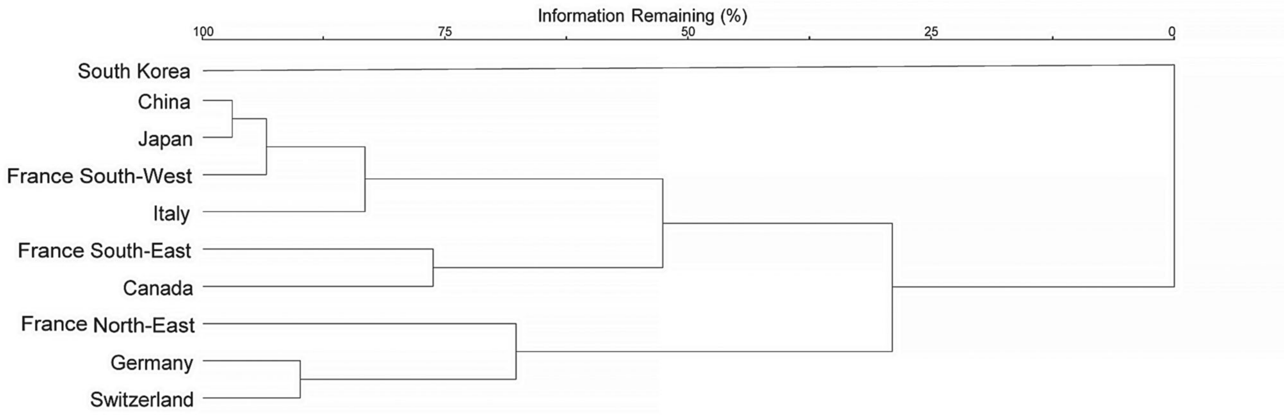

FIGURE 8 Dendrogram resulting from the cluster analysis performed on the matrix of haplotype frequencies in different countries, using Euclidean distance measures and Ward's linkage method.

by parasitoids, with the latter arriving later in fruits, especially pupal parasitoids, foraging on fruits already highly rotten and often dropped on the ground. The unripe and maturing fruits in the canopy therefore represent an underutilized trophic niche, occupied mainly by the invasive *D. suzukii*, a species functionally distinct from native *Drosophila* species (Atallah et al., 2014) and typically found alone in unripe or ripening fruits hanging on shrubs and trees (Deconninck et al., 2025; Deconninck et al., 2024a; Ulmer et al., 2022). A complementary explanation of the absence of European parasitoids in ripening fresh fruits is the high ability of *D. suzukii* to develop a strong immune response and to encapsulate their eggs (Kacsoh & Schlenke, 2012; Mazzetto et al., 2016; Poyet et al., 2013). This near-absence of indigenous parasitoid emergence in canopy fruits confirms their poor efficiency in controlling *D. suzukii* populations in the field, as already shown in other countries (Miller et al., 2015). In this way, the fly has escaped its major natural enemies in its invasion area. With the arrival of *L. japonica*, a new equilibrium in the tritrophic system plants–drosophila–parasitoids could be established. Given that *L. japonica* is a species that coevolved with *D. suzukii* in its Asian native area (Kimura & Novković, 2015; Matsuura et al., 2018) and is potentially better adapted to avoid the fly's defenses compared to native European parasitoids, *D. suzukii* populations may encounter a new obstacle to their proliferation. Moreover, *L. japonica* is known to forage on maturing fresh fruits in the canopy (Rossi Stacconi et al., 2025), corresponding to the typical trophic niche of the fly.

Second, the significant positive correlation between the density of *L. japonica* and *D. suzukii* per 100 g of fruit corroborates another very recent study in Italy (Rossi Stacconi et al., 2025) and could suggest that the fluctuations of the parasitoid population follow and depend on the dynamics of the host population, and not the opposite. Indeed, an effective control of the fly populations by the parasitoid would have produced a clear negative correlation, which is not the case here. This implies that, in our study and at this very early stage of *L. japonica* establishment in French sites, there could be a bottom-up limitation of the non-native parasitoid by the available resource quantity (i.e. host abundance) and not a top-down control of the invasive *D. suzukii* by the parasitoid (Chidawanyika et al., 2020; Han et al., 2022; Leroux & Loreau, 2015). This suggests that, in our study sites and at the present state of *L. japonica* colonization, the parasitoid does not exert a full regulation of the invasive pest fly populations, remaining high in the field both in natural and crop areas, as evidenced by the crisis in the French cherry production sector. Indeed, our results showed that the quantity of *D. suzukii* produced both by the fruits from the wild flora and the crop plants (sweet and sour cherries, strawberries) is still important. The low ratio between the quantity of *L. japonica* and *D. suzukii* found here (ratio = 0.072; i.e. 7 individuals of *L. japonica* for 100 individuals of *D. suzukii*) is close to those found in other studies (Fellin et al., 2023; Rossi Stacconi et al., 2025) and confirms this weak regulation. Further studies are, however, needed to examine the evolution of this early trend since it may change with the establishment and densification of *L. japonica* populations over a longer time scale.

Third, given that we used a field sampling methodology focused on *D. suzukii* trophic preferences (i.e. sampling restricted to canopy fruits), the lack of significant correlations observed between *L. japonica* and other *Drosophila* species doesn't allow us to draw conclusions on the overall impact of the non-native parasitoid on the resident Drosophilid community. *Drosophila* species other than *D. suzukii* only represented a quarter of the flies recorded. These proportions between indigenous drosophilids and *D. suzukii* are generally reversed when studying fruits on the ground (Deconninck et al., 2024b). In the canopy fruits, the lack of correlation between *L. japonica* and other drosophilids suggests that the latter are (i) less-preferred hosts (as shown in previous laboratory and field studies; Biondi et al., 2021; Kremmer et al., 2017; Rossi Stacconi et al., 2025) or (ii) that they escape most of the attack from *L. japonica* because of the ecological characteristics of *L. japonica* foraging mainly on fresh fruits (Rossi Stacconi et al., 2025). While no significant relation was found between *L. japonica* and other drosophilids, it may emerge over time as parasitoid populations become firmly established. Furthermore, the influence of *L. japonica* on other drosophilids should be searched in decaying, fallen fruits hosting native decomposer *Drosophila* species, rather than in the fresh fruits dominated by *D. suzukii* in the canopy. Thus, the next step would be to sample rotten fruits on the ground to disentangle the potential effects of *L. japonica* on indigenous *Drosophila* and parasitoid species. Finally, the relationships presented here are correlative, which limits their interpretation, and further investigations with more samples and more community metrics (species richness, evenness indices) would be needed before drawing conclusions.

These results highlight the use of specific plant species by *L. japonica*, suggesting that these plants provide favourable conditions to the parasitoids for host finding and ovipositing. As for *D. suzukii* (Santoiemma et al., 2019; Tonina et al., 2018; Ulmer et al., 2024), *L. japonica* can alternatively use cultivated plants (sweet and sour cherry trees, *Ficus carica*, *Prunus domestica*) and wild plants (*Lonicera* sp., *Sambucus ebulus*, *Rubus fruticosus* etc.), tracking the pendular migration of its host between crop systems and seminatural habitats to find resources and shelters (Delbac et al., 2020; Tonina et al., 2018). The varying role of these wild plants in the dynamics and equilibrium of the pest fly-parasitoid system could become a priority question soon (Van Timmeren et al., 2025), in each country concerned by the proliferation of *D. suzukii*. These wild plants and their associated seminatural habitats could be an essential link in the continuity of the parasitoid's life cycle between the ephemeral fruiting periods of cultivated plants. Wild plants could also serve as a backup of parasitoid populations at the landscape scale when crop fruits are heavily protected by pesticides. Some wild toxic plants can also help *D. suzukii* resist parasitoid attacks through transgenerational medication (Poyet et al., 2017). Overall, our study confirms that populations of *L. japonica* are already established in agricultural and natural systems in several regions of France, especially where *D. suzukii* is present. This finding supports observations made in 2022 in southwestern France (Rousse et al., 2023) and aligns with model predictions (Nair & Peterson, 2023). However, data are limited to one complete year, and long-term monitoring is needed to assess the persistence of these parasitoid populations. The detection of non-native parasitoid populations is increasingly common worldwide, and these populations are expanding rapidly.

Genetic variability in *Leptopilina japonica*

Molecular analyses based on COI information showed that individuals of the subspecies *L. japonica japonica* colonized the non-native area of the parasitoid. Analyses of COI haplotypes frequency distinguished three main genetic clusters among French populations of *L. japonica*: a group in the northeast, one in the southeast and one in the southwest of the country. The presence of *L. japonica* in northeastern France, showing genetic similarities with other northeastern European populations, is presumably explained by the fact that the species was previously recorded in neighbouring countries, such as Germany at least since 2021 and Switzerland. Indeed, the three countries are geographically close and found to be clustered into common haplotypes, including H4 and H13. The presence of a higher number of haplotypes (seven) in Germany compared to northeastern France (two) and the observation of an earlier presence can be explained by dispersal from this German side if it is confirmed that *L. japonica* has a very rapid dispersal capacity. This pattern was not observed in the southeastern French data, which exhibited a clustering pattern with the Canadian data. Conversely, haplotypes from southwestern France have been observed to cluster with those from China, Japan and Italy. However, it is imperative to exercise the utmost caution when interpreting these genetic variation patterns, and further data are required to elucidate potential introduction areas, dispersal routes and population structure. Within this mitochondrial cluster from France, sequences from the native region (Asia) are grouped with those from Europe. However, the high parasitism rate (38.53%) of parasitoids in the southwest sites of France suggests that local populations may have been established several years ago.

The genetic diversity observed in European populations of *L. japonica* (23 valid haplotypes) is relatively high compared to other studies of the *Leptopilina* genus (Novković & Kimura, 2015) or Hymenopteran parasitoids (Fujie et al., 2019) but is not unusual for an expanding population (Viciriuc et al., 2021). This result, together with the previous cluster analysis of haplotypes, reinforces the hypothesis of multiple gene flow between areas across the species' distribution (Doorenweerd et al., 2020). At the same time, the lack of nuclear diversity (one haplotype) can be explained by a recent bottleneck event. Globally, our results raise the possibility of various introduction sources or migration routes, but this hypothesis requires cautious evaluation with higher-resolution genetic markers. In their study of the route of invasion of *D. suzukii*, Fraimout et al. (2017) found similar geographic genetic patterns in fly populations across Europe. The *D. suzukii* populations in northern France belonged to the same genetic group as the fly populations in Germany, mirroring our findings for *L. japonica*. They also found that China is the most likely source of the southern European fly populations, with America contributing to the northern French population as a probable source. Nevertheless, a more extensive sampling combined with the use of additional genetic markers would be needed to better understand the origin and spread of *L. japonica* and its connection to the *D. suzukii* invasion.

Potential consequences of *Leptopilina japonica* on ecological equilibrium and biocontrol programmes

The presence of *L. japonica* in non-native territories where *D. suzukii* is invasive may contribute to reducing populations of this pest both in agricultural and seminatural habitats. However, *L. japonica* may also disrupt native *Drosophila* populations, as it is considered a polyphagous parasitoid. Indeed, this parasitoid is known to be able to successfully develop in several *Drosophila* species under laboratory conditions, with high parasitism rates on phylogenetically close species (i.e. *D. melanogaster* and *D. simulans*) and lower parasitism rates on some other species such as *D. immigrans* and *D. subobscura* (Girod et al., 2018; Girod et al., 2018). Over time, this parasitoid could impact native species, potentially leading to ecological imbalances. However, recent field data from Canada indicate that *L. japonica* stays closely associated with *D. suzukii* and the *melanogaster* group, and in low levels also with the *obscura* group in nature (Abram et al., 2024), explaining the increase in optimistic opinions about its potential use in biological control in some countries.

The overwhelming dominance of *L. japonica* in fruit samples raises the question of the future of its interaction with the biocontrol parasitoid *G. kimorum* commonly used in importation biological control programmes in Europe (Sosa-Calvo et al., 2024). The relationship between the two non-native parasitoids remains uncertain, given that they use the same host and could potentially compete (Abeijon et al., 2025). As a highly specific parasitoid of *D. suzukii*, *G. kimorum* has a more limited ecological niche. Morphologically, *L. japonica* possesses a longer ovipositor than *G. kimorum* (Earley et al., 2023), giving it an advantage in exploring and parasitizing larger fruits. In contrast, *G. kimorum*, with its shorter ovipositor, is better suited for attacking smaller fruits. The polyphagous nature of *L. japonica*, its ability to use various fruit types, and its already established populations in certain regions suggest it could become a significant competitor for *G. kimorum*. Nevertheless, these two parasitoids already coexist in their native area and the study of Abram et al. (2020) in Canada also showed a co-occurrence of adventive populations of the two species in the field in their non-native area. The study of Wang et al. (2019) supports this, showing that *G. brasiliensis* (now G. *kimorum*) strongly discriminates against hosts parasitized by *L. japonica* and that their combined impacts on host suppression are additive. While this co-occurrence in non-native areas is possible, it is important to study the conditions under which one species becomes more abundant than the other. Preliminary results from Italy show that four years after the introduction of *G. kimorum*, there is a slight negative correlation with *L. japonica* (Rossi Stacconi et al., 2025). This could lead to an exclusion phenomenon in areas where *L. japonica* is already established, which would have negative consequences for the establishment of *G. kimorum*. Experimental approaches in laboratories and long-term field monitoring would still be needed to answer the question of whether there is competition or synergy, and whether there are additive effects, in controlling *D. suzukii*.

PERSPECTIVES

Our study confirms the establishment of *L. japonica* in agricultural areas and seminatural habitats of several regions of France, using a variety of crop and wild fruits infested by its main host *D. suzukii*. The detection of locally high parasitism rates, particularly in specific wild fruits and in southwestern France, suggests that this non-native parasitoid may be adapting to local environmental conditions. However, the persistently high densities of *D. suzukii* across most sites indicate that population regulation by *L. japonica* remains limited today, likely reflecting an early stage of establishment and a strong dependence on host availability.

Genetic analyses revealed substantial haplotypic diversity among French populations, possibly resulting from different introduction events or migration routes. While some genetic affinities with Asian and other European populations were detected, the precise introduction or migration pathways remain uncertain and further investigations using higher-resolution molecular markers are needed to disentangle the history of its expansion.

Beyond its direct interaction with *D. suzukii*, the potential impacts of *L. japonica* on native European *Drosophila* species and its interactions with other non-native parasitoids, such as the biocontrol parasitoid *G. kimorum*, raise important ecological and applied considerations. Although niche differences between *L. japonica* and the other native parasitoid and *Drosophila* species make their coexistence possible, their competitive dynamics and trophic interactions should be closely monitored, particularly in the context of integrated biological control programmes.

Overall, our findings emphasize the need for long-term monitoring to evaluate the establishment, sustainability and ecological consequences of *L. japonica*. Future research should prioritize the exploration of natural habitats, including (but also extending beyond) fallen fruits, and the analysis of local trophic networks to better assess the ecological integration and potential risks associated with this introduced species.

AUTHOR CONTRIBUTIONS

IMV, NB and OC designed the study and wrote the original draft; NB acquired funding; IMV, LB, SW, OC and NR performed the formal analysis; IMV identified the insect specimens from France; IMV, LD, AF, AH, JM, MLS, MVRS and NB collected the insect samples; all authors provided critical feedback, discussed the results and contributed to the final manuscript. All authors approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All collection data and all trimmed molecular sequences generated in this study have been deposited in the Dryad Digital Repository and are publicly accessible at https://doi.org/10.5061/dryad.brv15dvp2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Phylogenetic tree inferred using RAxML. Bootstrap support values above 70 show at nodes. In red are marked the COI sequences of *Leptopilina japonica* obtained in this study.

Table S1: Collection information for insect specimens in France. FIR: Fruit infestation rates.

Table S2: Collection information for the *Leptopilina japonica* specimens for which DNA sequences were obtained in this study and were included in the haplotype network analyses. For each COI or ITS2 marker, GenBank accession numbers were included.

Table S3: The values of infestation and parasitism variables in different plant species and locations. FIR: Fruit infestation rates. PR: parasitism rate.

Table S4: Distribution of the COI haplotypes of *Leptopilina japonica*.

Table S5: Geographical distributions and frequency of haplotypes of *Leptopilina japonica* in different countries.

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