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REVIEW

Adventively established *Leptopilina japonica*: a new opportunity for augmentative biocontrol of *Drosophila suzukii*

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Abstract

The invasive spotted-wing drosophila, *Drosophila suzukii*, has emerged as a significant global pest over the past decade, threatening fruit production worldwide. The parasitoid *Leptopilina japonica*, presumed native to East Asia, has established adventive populations in Europe and North America and is increasingly recognized for its ability to parasitize substantial proportions of *D. suzukii* larvae across diverse habitats. Here, we provide a broad review of the biology, establishment, distribution, and potential impacts of *L. japonica*. Using field data from international monitoring programs, we document the seasonal dynamics of plant–host–parasitoid associations and assess evidence for *L. japonica*'s impact on *D. suzukii* and non-target organisms. Findings indicate that *L. japonica* has successfully established in several areas where *D. suzukii* is present in Europe and North America, showing promise as a biological control agent to support sustainable pest management. Current data suggest it provides some suppression of *D. suzukii* populations with minimal non-target effects. However, long-term studies are necessary to clarify its food web interactions and efficacy as a biological control agent. In areas where *L. japonica* has been established, we propose its use in augmentative biological control programs to enhance its impacts in specific agricultural settings. Case-specific evaluations of its ecological effects and role in integrated pest management, supported by continued monitoring, are essential. The case of *L. japonica* illustrates the need for clear, research-informed policies to guide the use of adventively established non-indigenous natural enemies in pest management.

Keywords Adventive establishment · Spotted-wing drosophila · Figitidae · Biological control · Invasive species

Introduction

The subfamily Eucoilinae (Hymenoptera: Figitidae) is best known for parasitoid species that attack the larvae of brachyceran flies (Fleury et al. 2009). Their diversity and abundance make Eucoilinae critical players in regulating dipteran populations in various ecosystems. Alongside the Opiinae (Hymenoptera: Braconidae), they rank among the most significant natural enemies of frugivorous flies, including members of the Tephritidae and Drosophilidae families (Quilici and Rousse 2012). Eucoilinae wasps are found worldwide, exhibiting a host range that varies from generalist to highly specific, depending on the species. Within this group, *Leptopilina japonica* Novković & Kimura is a larval parasitoid that has been identified as an important natural enemy of *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), the spotted-wing drosophila, one of the more damaging invasive pests in soft and stone fruit production worldwide (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019). Since its adventive establishment in Europe and North America, *L. japonica* has been documented actively parasitizing

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D. suzukii larvae across different ecosystems. This has generated significant interest in its potential for augmentative biological control, with stakeholder discussions in extension meetings indicating interest in its expanded use in IPM programs (authors' personal observations). *Drosophila suzukii* poses substantial challenges to fruit growers due to its ability to infest ripening fruit, causing widespread damage and significant economic losses. In regions where *D. suzukii* has become invasive, annual damage estimates have reached several millions of dollars (USD) (De Ros 2024). Conventional control strategies primarily rely on the frequent application of insecticides (Tait et al. 2021). Nonetheless, the high reproductive rate of *D. suzukii*, combined with its broad host range and rapid spread, has rendered conventional chemical controls often insufficient and unsustainable due to concerns about pesticide resistance, environmental contamination, non-target effects, and the added production costs (Shawer 2020; Disi and Sial 2021). Classical biological control programs in the USA, Italy, France, Israel, and Switzerland are currently evaluating the effectiveness of *Ganaspis kimorum* Buffington (Hymenoptera: Figitidae), formerly known as *Ganaspis brasiliensis* (Ihering) G1 (Sosa-Calvo et al. 2024), a highly host-specific larval parasitoid, to decrease *D. suzukii* populations (Lisi et al. 2022; Seehausen et al. 2022; Gariepy et al. 2024). However, *L. japonica* may represent an additional biological control tool, as field studies in the pest's native range have shown that *G. kimorum* and *L. japonica* are the two parasitoids most commonly attacking *D. suzukii* (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019). Moreover, their combined host suppression might be additive due to reciprocal interspecific discrimination (Wang et al. 2019). In areas where *L. japonica* has become adventitiously established, it has been documented to actively parasitize *D. suzukii* larvae, with parasitism rates fluctuating seasonally. These rates range from 0% to approximately 30%, depending on factors such as host plant species, geographic location, and environmental conditions (Abram et al. 2022a; Fellin et al. 2023). Under laboratory conditions, *L. japonica* has been shown not to be entirely specific to *D. suzukii* (see 2.3; Girod et al. 2018b; Daane et al. 2021), which makes it less likely to be approved by regulators for use in biological control programs. In both Europe and North America, the release of biological control agents (BCAs) is heavily regulated to minimize the risk of unintended ecological consequences. These regulations are designed to protect native species and ecosystems but can create barriers to the use of beneficial organisms (Barratt et al. 2021). However, with increasing pressure from growers and stakeholders to adopt more sustainable pest management strategies against *D. suzukii*, it is essential to evaluate whether *L. japonica*, which is becoming established in many areas without deliberate releases and may continue to spread, could be a valuable and safe addition to current IPM programs. If field studies can demonstrate the absence of or very limited detrimental effects on non-target species in Europe and North America (Abram et al. 2022a; Fellin et al. 2023; Martin et al. 2023; Gariepy et al. 2024), *L. japonica* could become a viable candidate for augmentative biological control strategies in specific contexts. In this paper, we first provide a comprehensive review of all relevant published information on *L. japonica* to date, along with new data on its distribution and ecology. Based on this information, we then offer future perspectives and recommendations for the use of *L. japonica* as a biological control agent against *D. suzukii*.

Current knowledge on *Leptopilina japonica*

Taxonomy

Leptopilina japonica has a body length of 1.3–1.9 mm in females and 1.3–1.5 mm in males, with dark brown to black mesosoma and slender, yellow legs (Fig. 1). The antennal length in females is about 0.6–0.8 times the body length, with the 5th and 6th segments slender and elongated. In males, the antennae are longer, exceeding 1.5 times the body length, with 15 segments. The scutellar plate is wide and shiny, with 4–6 hairs, and the posterior pit is large. The metasoma is dark, with a ventrally dense hairy ring that gradually thins and then disappears dorsally (Novković et al. 2011). Within *L. japonica*, two subspecies are recognized: *L. japonica japonica* Novković & Kimura, which has been recorded in many temperate regions in China, Japan, and South Korea (see 2.2) and *L. japonica formosana* Novković & Kimura occurring in Taiwan and occasionally recorded in South Korea (Murata et al. 2013; Kimura and Novković 2015; Daane et al. 2016; Giorgini et al. 2019; Buffington et al. 2020). The two subspecies are difficult to separate morphologically, as distinguishing traits are not extensively documented. It is noted that *L. j. japonica* has adapted to temperate climates, which may influence its physical characteristics, whereas *L. j. formosana* has adapted to a subtropical environment (Murata et al. 2013). Such differences in climatic adaptations could lead to variations in size, coloration, or other morphological traits, although specific morphological descriptions remain limited in the literature (Novković et al. 2011). Furthermore, genetic studies could provide additional insights into the distinctions between these subspecies, with analysis of the COI, ITS1 and ITS2 nucleotide

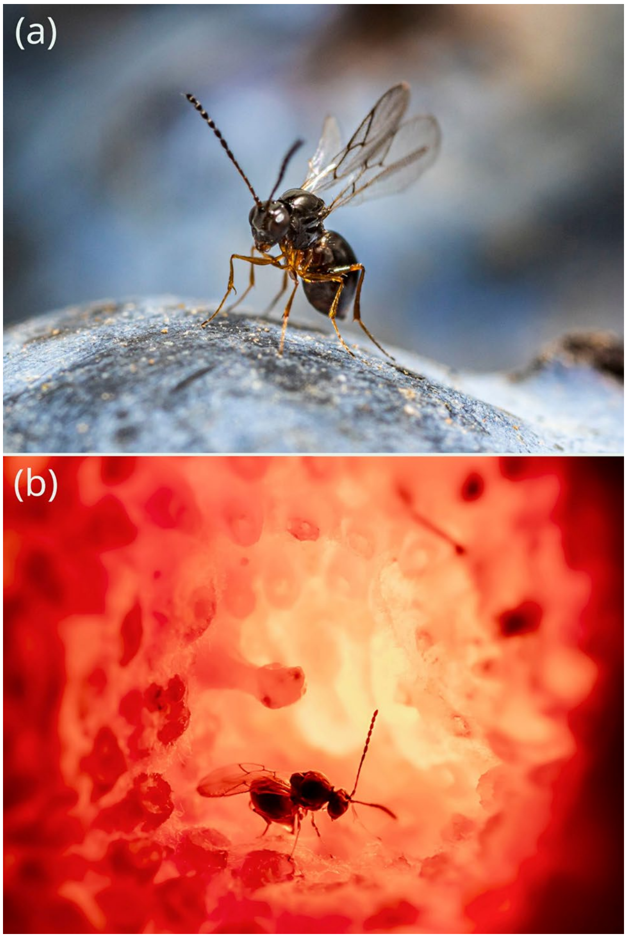

Fig. 1 **a** *Leptopilina japonica* adult female on a blueberry. **b** *Leptopilina japonica* parasitoid wasp extending her ovipositor inside a raspberry to parasitize a spotted-wing drosophila fly larvae, *Drosophila suzukii*. Photographs © Warren H. L. Wong (University of British Columbia, BC, Canada)

sequences showing separated phylogenetic groups for *L. j. japonica* and *L. j. formosana* (Novković et al. 2011). From this point onward, references to *Leptopilina japonica* in the text specifically pertain to *L. j. japonica*, unless otherwise stated, as the populations introduced to Europe and North America have been identified as belonging to this subspecies.

Outside its native range, *L. japonica* can be distinguished from most of the other *Leptopilina* species found in Europe (Nordlander 1980; Van Alphen et al. 1991) and North America (Lue et al. 2016) by a combination of key morphological characteristics. These include the antennal segments, the scutellar plate, the posterior pit, the metapleural ridges, and the presence of a hairy ring on the metasoma. These features were identified and reported by Novković et al. (2011). *Leptopilina japonica* is closely related to *L. victoriae* Nordlander, but features darker antennae, with the 5th and the 6th segments longer and slenderer than in *L. victoriae* (Buffington et al. 2020). Additionally, *L. japonica* has a wider scutellar plate and a larger posterior pit compared to *L. victoriae* (Novković et al. 2011). *Leptopilina japonica* could be misidentified as *L. heterotoma* (Thompson) (Abram et al. 2020), although a fine morphological analysis would reveal differences in the shape of the scutellar plate and the sculpture of the mesoscutellar surface (Novković et al. 2011). The different scutellum morphology, the dorsally incomplete metasoma hairy ring and the glabrous posteroventral corner of female metapleuron allow for separation of this species from two other *D. suzukii* parasitoids, *G. kimorum* and *G. lupini* Buffington (formerly known as *G. brasiliensis* G3) (Sosa-Calvo et al. 2024; Stahl et al. 2024). Consulting the database of DNA sequence data for parasitoids of Drosophilidae developed by Puppato et al. (2020), Lue et al. (2021) and Martin et al. (2023), and diagnostic PCR primers (Gariepy et al. 2024), are useful pathways to accurate identification.

Distribution

Recent studies have documented the expanding distribution of *L. japonica* in regions outside its native range, including Europe and North America, where it has emerged as a significant natural enemy of *D. suzukii* (Puppato et al. 2020; Martin et al. 2023; Nair and Peterson 2023; Gariepy et al. 2024). In Fig. 2, we present a synthesis of original data and previously published records on the presence and absence of *L. japonica*, compiled from available records in East Asia and field surveys conducted between 2020 and 2024 across Europe, and North America. These surveys employed a variety of methodologies, including direct fruit sampling, trapping, and sweep netting. The variability in these approaches, as well as differences in timing and sampling effort, may influence the completeness of the data and should be considered when interpreting the distribution map. Data show that *L. japonica* has not been detected in certain regions, including most of the coastal areas of Mediterranean countries such as Spain, France, and Italy, as well as California, inland Washington state, and the central interior of British Columbia (Fig. 2). Interestingly, according to the Humid Climate World Map (Lobo et al. 2023), all locations in *L. japonica*'s native range (eastern Asia) where the parasitoid was recovered fall within humid zones. Conversely, regions where *D. suzukii* has established but *L. japonica* was not recovered fall outside these humid zones, as classified by the Köppen-Geiger climate classification map (Beck et al. 2018). While this pattern suggests that climatic factors, particularly humidity, may influence *L. japonica* establishment, this conclusion is based on broad climate classifications rather than direct measurements of the parasitoid's physiological tolerance to

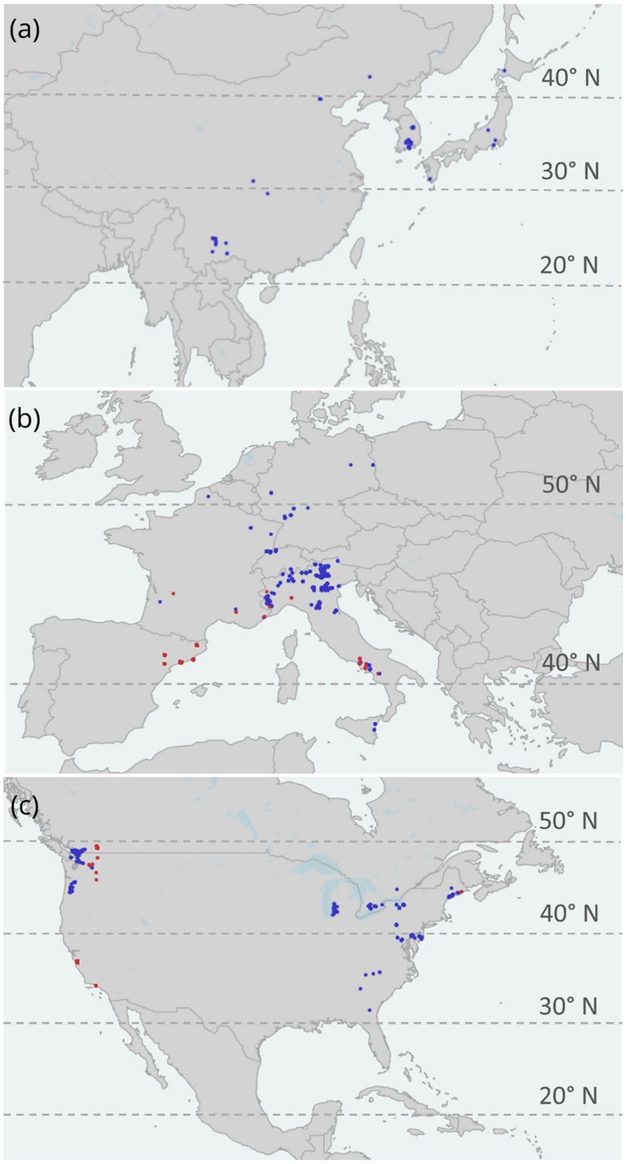

Fig. 2 Distribution map of *L. japonica* based on field surveys conducted in eastern Asia (a), Europe (b), and North America (c) between 2020 and 2024. Surveys utilized various methodologies, including fruit sampling, trapping, and net swiping, with timing and sampling efforts varying by region and year. Blue dots indicate the detection of *L. japonica*, while red dots indicate its absence following the monitoring activities

humidity. At present, data on the specific humidity requirements of *L. japonica* are lacking. Further research, including controlled studies on its survival and reproductive success under varying humidity levels, would be necessary to determine whether humidity acts as a limiting factor for its establishment. Additionally, the absence of *L. japonica* in these regions may reflect not only climatic constraints but also limited dispersal or insufficient survey coverage. Clarifying whether these areas are inherently unsuitable for *L. japonica* or if its absence is due to other ecological or methodological factors remains an important research priority.

Host range

Leptopilina japonica is recognized as an oligophagous parasitoid, primarily parasitizing members of the *D. melanogaster* species group, that includes *D. suzukii* (Kimura and Novković 2015; Kimura and Suwito 2015; Wang et al. 2020). Prior to *D. suzukii* Euro-American invasion, field surveys of *Drosophila* parasitoids in Asia were limited to Japan, where *Drosophila* parasitoids were surveyed mainly using sentinel traps baited with banana fruit (*e.g*. Mitsui et al. 2007). These traps, however, attract numerous drosophilids species and rarely caught *D. suzukii* or its primary parasitoids—*G. kimorum*, *G. lupini* or *L. japonica* (see Kimura and Mitsui 2020). Similarly, foreign explorations for native *D. suzukii* parasitoids in various native regions in China and South Korea mostly trapped other *Drosophila* species and other parasitoids in fruit traps, whereas *L. japonica* was collected largely from fresh fruit infested by *D. suzukii* along with two other closely related *Drosophila* species, *i.e.*, *D. pulchrella* Tan, Hsu & Sheng and *D. subpulchrella* Takamori & Watabe (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019). However, several *L. japonica* were also collected from other *Drosophila* species in Yunnan, China in traps baited with banana (14% of the overall trapped-parasitoid composition), and in South Korea with traps baited with melon and peach (Giorgini pers. comm.). In Japan, *L. japonica* was predominantly collected from wild cherry fruit infested by *D. suzukii*, indicating a strong association with this host in cherry habitats (Matsuura et al. 2018). Another study investigating parasitoid associations with mycophagous drosophilid across different locations in Japan, including Tokyo and Sapporo, recorded numerous *Drosophila* and parasitoid species, yet did not capture any *L. japonica* individuals, suggesting that mushrooms are not a preferred habitat for this parasitoid (Kasuya et al. 2013). Overall, field studies in East Asia provide insight on habitat preference in the native range and suggest *L. japonica*'s field host range is largely limited to *D. suzukii* and its closely related species as mentioned above which infest fresh fruits (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019).

In the laboratory, Kimura and Novković (2015) tested 17 different *Drosophila* species belonging mainly to the *melanogaster* and *immigrans* species groups in Japan. They tested two populations of *L. j. japonica* collected from Northern (Sapporo) and central (Tokyo) Japan, and a population of *L. j. formosana* collected from Taipei, finding that parasitoid virulence and host resistance may varied geographically because of local adaptation. Each population was highly virulent to some *Drosophila* species from its original locality, but parasitized hosts less successfully from other localities. The northern Japanese population was successful only in *D. biauraria* Bock & Wheeler, the central Japanese population in *D. rufa* Kikkawa & Peng, *D. biauraria* and *D. suzukii*, and the Taiwan population only in *D. albomicans* Duda. Quarantine laboratory studies conducted in the USA and Switzerland tested the capacity of *L. japonica* to attack and develop from 24 and 6 non-target fruit fly species, respectively (Girod et al. 2018b; Daane et al. 2021). Overall, these studies confirmed a relatively narrow physiological host range for *L. japonica* (Daane et al. 2021). Among the tested hosts in no-choice tests, *L. japonica* showed the highest parasitism success on three phylogenetically closely related species: *D. suzukii*, *D. melanogaster* and, to a lower extent, *D. simulans.* Conversely, parasitism success was much lower on seven non-target species (*D. immigrans* Sturtevant*, D. subobscura* Collin, *D. pseudoobscura* Frolova, *D. persimilis* Dobzhansky and Epling, *D. funebris* (Fabricius), *D. montana* Stone, Griffen and Patter, *D. robusta* Sturtevant and *Hirtodrosophila duncani* (Sturtevant)), where only a few offspring successfully emerged. Notably, encapsulation rates (a defensive response from the host to prevent parasitoid development) were low across all parasitized species, suggesting that *L. japonica* is generally able to overcome host immune responses. These experiments also showed that *L. japonica* does not attack other tested non-drosophilid hosts. For instance, the larvae of the Mediterranean fruit fly (*Ceratitis capitata* Wiedemann) were not parasitized, either when exposed in artificial diets or fresh fruit (Girod et al. 2018c). Field host range surveys in British Columbia, Canada done from 2022–2023 have largely validated predictions about the host range of *L. japonica* generated from laboratory studies (P. Abram, in prep.).

Reproductive biology and life cycle

Leptopilina japonica is a larval koinobiont endoparasitoid of drosophilids. Like many other hymenopteran parasitoids, *L. japonica* females produce haploid male offspring from unfertilized eggs and diploid female offspring from fertilized eggs (Heimpel and De Boer 2008). Females are moderately proovigenic, emerging with a high load of mature eggs, which corresponds to approximately 60% of their lifetime offspring production (Wang et al. 2018). On average, *L. japonica* males emerge 3 to 4 days before females (Wang et al. 2018) and dispersal of both males and females occurs directly after emergence from the natal patch. This allows males to disperse before sibling females emerge. Such post-emergence dispersal is beneficial as individuals that emerge and disperse in the absence of conspecifics may engage in off-patch matings which avoids inbreeding and reduces local mate competition (Quicray et al. 2023). While female *Leptopilina* dispersal is mostly mediated by odors from the host patch, male dispersal varies in relation to pheromonal compounds released by females (Böttinger and Stökl 2020). Specifically, *L. japonica* females emit highly volatile iridoid compounds as sex pheromones for long-range mate attraction (Böttinger and Stökl 2020). After locating a patch of drosophilid hosts, female *L. japonica* likely uses chemical and vibrational short-range cues to locate host larvae within the fruit (Fellin et al. 2024) and then pierce them with the ovipositor to lay a single egg within each host larva. First-instar larvae are preferred over later instars for oviposition (Wang et al. 2018). Females of other *Leptopilina* spp. inject venom at oviposition, which contains immune suppression factors to protect the egg against encapsulation by the host (Lemauf et al. 2021), although these have not yet been characterized in *L. japonica*. The parasitoid's first instar larva hatches within 54–72 h at 22 °C and starts feeding inside the host body. It develops into a second instar larva around 120 h post-oviposition and into a third instar larva around 144–168 h, at which point it kills the host after its pupariation (Wang et al. 2019). The third instar larva then becomes ectoparasitic and continues its development concealed within the host puparium, fully consuming the host's body before its own pupariation. Pre-imaginal development is completed after 28 and 32 days at 20 °C for males and females, respectively (Hougardy et al. 2019). Adult females begin parasitizing hosts within the first two days after eclosion, with the greatest number of host larvae parasitized when the adult wasps are 5–10 days old. At 22 °C, fed with honey-water and given *D. suzukii* as hosts, *L. japonica* females survive approximately 19 days with a lifetime production of 110 offspring, and with the proportion of female progeny decreasing as the maternal age increases (Wang et al. 2018). The estimated net reproductive rate is 47.3, intrinsic rate of increase is 0.138, mean generation time is 28.1 days, and doubling time is 5.0 days (Wang et al. 2018). In laboratory experiments, *L. japonica* shows a linear (type I) functional response to the tested host densities of *D. suzukii* in artificial diet (Wang et al. 2020).

Seasonal ecology and host plant associations

The ecology of *L. japonica* reveals a highly adaptable, fruit-specialist parasitoid with diverse habitat associations and complex interactions with its hosts. In the native range, *L. japonica* is commonly found on a wide range of fruit species, including fresh fruits on the plant and rotting fruits, highlighting its ecological flexibility (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019), although it has never been recovered from other substrates commonly exploited by drosophilids, such as mushrooms and decomposing leaf matter (Kasuya et al. 2013; Kimura and Mitsui

2020). In contrast to the *D. suzukii* specialist *G. kimorum*, laboratory studies have confirmed that *L. japonica* can successfully parasitize host larvae in artificial media (Girod et al. 2018b; Daane et al. 2021). A comprehensive list of host plants from which *L. japonica* has been recovered worldwide is summarized in Table 1. The parasitoid's seasonal pattern shows consistency among studies carried out in Asia on native populations and those carried out in Europe and North America, where adventive populations of *L. japonica* have established. In China, South Korea and Japan *L. japonica* emerged from field-collected fruit from May to September (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019; Kimura & Mitsui 2020). Similarly, multi-year seasonal monitoring carried out in Italy, Switzerland and Germany showed emergence of *L. japonica* in a variety of non-crop fruiting host plants from May to October, with early and late emergence generally recorded at sites with lower altitudes and in regions at more southern latitudes (Fellin et al. 2023; Martin et al. 2023). In Canada (British Columbia) and the USA, *L. japonica* was first recorded parasitizing *D. suzukii* in early-fruiting host plants, such as salmonberry (*Rubus spectabilis* Pursh), and then recorded throughout the growing season until October when it was collected from late-fruiting host plants, such as Himalayan blackberry (*Rubus armeniacus* Focke), pokeweed (*Phytolacca americana* L.) and honeysuckles (*Lonicera* spp.) (Beers et al. 2022; Abram et al. 2022a; Gariepy et al. 2024; Van Timmeren et al. in revision). This information, coupled with temperature-related life table parameters (Hougardy et al. 2019), suggests that *L. japonica* may complete two to four generations in a growing season. This will provide a reservoir of *L. japonica* on drosophilid hosts in wild areas outside the treated crop fields that may suppress *D. suzukii* populations in these areas and lower to level of immigration from non-managed habitat to managed areas of the landscape.

Overwintering

The two *L. japonica* subspecies, the temperate *L. j. japonica* and the subtropical *L. j. formosana*, exhibit different adaptations to their respective climates (Murata et al. 2013). Along with other *Leptopilina* spp., *L. j. japonica* undergoes diapause (developmental arrest) to endure unfavorable winter conditions (Murata et al. 2013; Nomano and Kimura 2025). Diapause enables the parasitoid to survive environmental stress, such as cold temperatures and food scarcity. Laboratory studies indicate that, at 15 °C and irrespective of photoperiod, *L. j. japonica* individuals of Japanese populations enter diapause as pre-pupae, while *L. j. formosana* individuals collected in Taipei only slow down their development and eventually die if unfavorable conditions persist (Murata et al. 2013). When testing prepupal resistance to acute cold stress (0 °C for 48 h) about 20% of *L. j. japonica* survived, while all *L. j. formosana* died. Adult emergence for *L. j. japonica* occurred 32–45 days and 65–85 days after oviposition at 18 °C and 15 °C, respectively (Murata et al. 2013). Laboratory trials, on Chinese and South Korean *L. j. japonica* populations showed similar results (Hougardy et al. 2019). For both populations, diapause was induced between 17.2 and 14.4 °C with parasitoids stopping their development at the 3rd larval instar. Adult emergence occurred 57 and 49 days after oviposition at 17.2 °C for South Korean and Chinese *L. j. japonica*, respectively (Hougardy et al. 2019). Field research in British Columbia confirmed that *L. j. japonica* overwinters within the host puparia and, based on the degree days needed to emerge from their overwintering stage, it was not active until quite late in the spring (Capko et al. 2024). In contrast, the closely related *L. heterotoma* overwinters as an adult (Kimura et al. 2019) and is found earlier in the season (Miller et al. 2015; Fellin et al. 2023).

Interactions with other parasitoids

Interspecific competition among *L. japonica*, *G. lupini* and *Asobara japonica* Belokobylskij (Hymenoptera: Braconidae) has been investigated in the evaluation of BCAs for managing *D. suzukii* (Wang et al. 2019). The outcomes indicated that *L. japonica* larvae outcompeted both other parasitoids when they co-occurred in the same host. Specifically, the faster developmental time of eggs conferred a critical competitive advantage to *L. japonica* in exploiting the host and suppressing the competitors before their larvae hatched. Notably, the study also revealed that both *A. japonica* and *G. lupini* discriminated against hosts previously parasitized by *L. japonica* and that *L. japonica* discriminated against hosts parasitized by *G. lupini*. These interactions translated into additive suppression of *D. suzukii* when *L. japonica* co-occurred with *G. lupini*, suggesting the presence of ecological adaptation to co-existence between these two species in their native range (Wang et al. 2019). Moreover, *L. japonica* has a longer ovipositor than *G. kimorum* or *G. lupini*, potentially enabling it to attack hosts in a wider range of fruit sizes (Earley et al. 2023; Fellin et al. 2023), while those with a shorter ovipositor such as *G. kimorum* may be limited to attack hosts in smaller fruits or young larvae feeding near the fruit surface. Differences in ovipositor length may further facilitate co-existence and 'biological control complementarity' among these larval parasitoids by allowing them to exploit hosts in different feeding niches. A key aspect of *L. japonica*'s ecology is that its association with host plants is primarily linked to the habitat of *D. suzukii*. Field studies in both native and colonized ranges show that *L. japonica* occurs more frequently in fresh fruits, often co-occurring with *G. lupini* and *G. kimorum*, but differing from species such as *Leptopilina boulardi* (Barbotin, Carton & Kelner-Pillault), *L. heterotoma* and *Asobara* spp., which are more frequently associated with drosophilids colonizing decaying fruits (Daane et al.

Table 1 Host plants from which *L. japonica* has been recovered worldwide. New records from monitoring activities are carried out by the authors highlighted in bold and unpublished. Previously reported records from existing literature are accompanied by their source references

Family	Host plants	Country	Reference
Adoxaceae	*Sambucus adnata* Wall	China	Giorgini et al. 2019
	***Sambucus ebulus* L**	**Italy**	
	Sambucus nigra (L.)	Italy, **Switzerland, Ontario**	Fellin et at. 2023
	Sambucus racemosa L	Canada	Abram et al. 2020, 2022a, b
Araliaceae	***Hedera helix* L**	**Italy, Switzerland**	
Asparagaceae	***Asparagus officinalis* L**	**Italy**	
Caprifoliaceae	*Lonicera maacki* Maxim	China	Girod et al. 2018a, b, c
	***Lonicera sempervirens* L**	**Italy**	
	***Lonicera* sp.**	**New York**	
Coriariaceae	*Coriaria nepalensis* Wall	China	Girod et al. 2018a, b, c
Cornaceae	***Cornus amomum* Mill**	**Ontario**	
	***Cornus mas* L**	**Italy**	
	***Cornus racemosa* Lam**	**Ontario**	
	Cornus sanguinea (L.)	Italy	Fellin et at. 2023
Dioscoreaceae	*Dioscorea communis* (L.) Caddick & Wilkin	**Italy**	Fellin et at. 2023
Elaeagnaceae	***Elaeagnus* × *submacrophylla* Servett**	**Italy**	
	***Elaeagnus umbellata* Thunb**	**Ontario**	
Ericaceae	*Gaultheria shallon* Pursh	Canada	Abram et al. 2020, 2022a, b
	***Gaylussacia baccata* (Wangenh.) K. Koch**	**New Jersey**	
	Vaccinium corymbosum (L.)	Canada, **Italy, France, New Jersey**	Abram et al. 2020, 2022a, b, Fellin et at. 2023
	***Vaccinium myrtillus* L**	**Italy**	
	Vaccinium spp.	Japan	Girod et al. 2018a, b, c
	Viburnum sp.	Italy	Fellin et at. 2023
Grossulariaceae	***Ribes rubrum* (L.)**	**Italy**	
	***Ribes uva-crispa* (L.)**	**Italy**	
Liliaceae	*Prosartes hookeri* Torr	Canada	Abram et al. 2020, 2022a, b
Moraceae	*Ficus carica* (L.)	Italy	Fellin et at. 2023
	***Morus alba* L**	**Italy**	
Myricaceae	*Myrica rubra* Siebold & Zucc	China	Girod et al. 2018a, b, c
Oleaceae	*Ligustrum vulgare* (L.)	Italy	Fellin et at. 2023
Phytolaccaceae	***Phytolacca americana* L**	**Italy**	
Rhamnaceae	***Rhamnus cathartica* L**	**Ontario**	
	***Rhamnus frangula* L**	**New York, Italy**	

Table 1 (continued)

Family	Host plants	Country	Reference
Rosaceae	*Cerasus jamasakura* (Siebold ex Koidzumi)	Japan	Matsuura et al. 2019
	Cerasus speciosa (Koidzumi)	Japan	Matsuura et al. 2019
	Crataegus monogyna Jacq	Italy	Fellin et at. 2023
	Fragaria x *ananassa* Duchesne	Canada, **Germany, Italy**	Abram et al. 2020, 2022a, b
	Fragaria moupinensis Cardot	China	Giorgini et al. 2019
	***Fragaria vesca* L**	**Italy**	
	Malus domestica (Suckow) Borkh	Italy	Fellin et at. 2023
	Oemleria cerasiformis J.W.Landon	Canada	Abram et al. 2020, 2022a, b
	***Prunus armeniaca* L**	**Italy**	
	Prunus avium L	Canada, **Germany, Italy, Switzerland**	Abram et al. 2020, 2022a, b
	***Prunus cerasifera* Ehrh**	**Italy**	
	Prunus cerasoides D. Don	China	Girod et al. 2018a, b, c
	***Prunus cerasus* L**	**Italy**	
	Prunus domestica (L.)	Italy	Fellin et at. 2023
	Prunus donarium Sieb	Japan	Kasuya et al. 2013
	Prunus emarginata (Dougl. ex Hook.) Eaton	Canada	Abram et al. 2020, 2022a, b
	***Prunus mahaleb* L**	**Italy**	
	***Prunus persica* (L.) Batsch**	**Italy**	
	Prunus serrulata Lindl	Japan	Girod et al. 2018a, b, c, Matsuura et al. 2018
	Prunus spinosa (L.)	Italy	Fellin et at. 2023
	***Pyracantha coccinea* M. Roem**	**Italy**	
	Rosa canina (L.)	Italy	Fellin et at. 2023
	***Rubus allegheniensis* (Porter) Porter**	**Ontario**	
	Rubus armeniacus (Focke)	Canada, Oregon	Abram et al. 2020, 2022a, b, Beers et al. 2022
	Rubus caesius (L.)	Italy	Fellin et at. 2023
	Rubus coreanus Miq	South Korea	Daane et al. 2016
	Rubus ellipticus Sm	China	Girod et al. 2018a, b, c
	Rubus foliosus Weihe	China	Giorgini et al. 2019
	Rubus fruticosus (L.)	British Columbia, Italy, **Germany, Switzerland, Maine, Washington**	Abram et al. 2020, 2022a, b, Fellin et al. 2023
	Rubus idaeus L	Ontario, China, Italy, Germany, **Oregon**	Girod et al. 2018a, b, c, Abram et al. 2020, 2022a, b, Beers et al. 2022, Wang et al. 2022, Fellin et al. 2023, Martin et al. 2023
	Rubus niveus Thunb	China	Giorgini et al. 2019
	***Rubus occidentalis* L**	**Italy, Ontario**	
	Rubus parviflorus Nutt	Canada	Abram et al. 2020, 2022a, b
	Rubus phoenicolasius Maxim	South Korea	Daane et al. 2016
	Rubus sp.	China	Girod et al. 2018a, b, c
	Rubus spectabilis Pursh	Canada	Abram et al. 2020, 2022a, b
	Rubus spp.	South Korea	Daane et al. 2016
	Rubus ulmifolius Schott	Italy, **Maine**	Fellin et at. 2023
Solanaceae	*Solanum nigrum* L	China, **Italy**	Girod et al. 2018a, b, c
Vitaceae	*Parthenocissus tricuspidata* Planch	Italy	Fellin et at. 2023
	Vitis vinifera (L.)	Italy	Fellin et at. 2023

2016; Giorgini et al. 2019; Fellin et al. 2023). This preference for fresh fruits might reflect co-evolutionary adaptation, in the parasitoid's native range, to *D. suzukii* and other drosophilids that oviposit in undamaged, ripening fruits using their serrated ovipositor, creating an ecological niche that *L. japonica* can exploit (Biondi et al. 2021). On the other hand, the ability of *L. japonica* to parasitize a few other drosophilid species in decaying fruits, allows this species to persist in the environment even in absence of the preferred host developing in fresh fruits. In terms of interactions between *L. japonica* and resident larval parasitoids in the regions invaded by *D. suzukii*, this may imply reduced interspecific competition, assuming only partial niche overlap. Moreover, the inability of the resident parasitoids to develop from *D. suzukii* hosts should further decrease their direct competition with *L. japonica* in decaying fruit substrates (Chabert et al. 2012). However, while host range and niche separation are key factors determining how parasitoid species coexist and interact in different habitats, specific tolerance to environmental factors, searching efficiency and life-history strategy are also major contributors to the outcome of extrinsic competition (Hawkins et al. 2000). For example, interspecific competition of *L. japonica* against idiobiont pupal parasitoids of drosophilids, such as *Trichopria* spp. (Hymenoptera: Diapriidae) and *Pachycrepoideus vindemiae* Rondani (Hymentoptera: Pteromalidae), will likely result in the latter two species being superior competitors to *L. japonica* as they are able to permanently paralyze the host and the primary parasitoid upon attack (Van Alphen and Thunnissen 1982; Wang and Messing 2004).

Potential impacts of biological control measures

Risks of *Leptopilina japonica* augmentation

Leptopilina japonica has adventive populations in several regions of Europe and North America and is now considered established in these areas. Although a comprehensive assessment of population control of *D. suzukii* by *L. japonica* has not yet been conducted, preliminary field data indicate variable but widespread parasitism activity across a range of host plants in managed and unmanaged habitats throughout the entire season (Abram et al. 2022a; Fellin et al. 2023; Gariepy et al. 2024; Van Timmeren et al. in revision). This widespread establishment raises the possibility of using the non-indigenous parasitoid for augmentative biological control of *D. suzukii*. However, two key points must be addressed to assess the viability of this approach: 1) the potential risks *L. japonica* poses to colonized ecosystems, and 2) the benefits it may offer for biological control of *D. suzukii*.

Potential risks from non-indigenous species, including BCAs, may involve unintended effects on non-target organisms, ecological interactions, or local biodiversity (Van Lenteren et al. 2006). In the case of *L. japonica*, environmental concerns seem to be the primary issue, as its presence is expected to be neutral to beneficial for human health and the economy, depending on its effectiveness in reducing insecticide applications and *D. suzukii* populations (Abram et al. 2024). Ecological factors that influence the environmental risks posed by a non-indigenous BCA are often related to its host range, potential for establishment, effects on other trophic levels (*e.g.* non-target herbivores, intraguild predation, vectoring, apparent competition, enrichment), and other indirect effects (*e.g.* competition, hybridization) (Van Lenteren et al. 2006; De Clercq et al. 2011). Regarding the parasitoid's host range, laboratory studies and short-term field reports (*i.e.*, based on monitoring datasets of less than 10 years) in the colonized regions, consistently identify *D. suzukii* as the primary host, with only a few other species occasionally parasitized (see Sect. 1.3). However, while notable risks could arise from a broader host range not yet detected by current observations, it is important to distinguish between opportunistic non-target parasitism and non-target impact: occasional attacks on non-target species should not be considered problematic if they do not lead to significant changes in the distribution or abundance of those non-target species (Van Lenteren et al. 2006). Moreover, the availability of alternative reproductive resources, aside from the target species, can be crucial for the survival of BCAs in environments where host availability fluctuates seasonally or due to other factors (Waage 2002). A further distinction to consider is between native and non-native non-target species. If a biological control agent affects non-indigenous species (other than those intentionally introduced), this impact should not necessarily be regarded as negative (Van Lenteren et al. 2006). The non-target species predominantly parasitized by *L. japonica* are cosmopolitan, including *D. melanogaster* and *D. simulans*, both of which are non-native to their current habitats in Europe and North America. In fact, species within the *melanogaster* subgroup originated from Africa and arrived in Europe post-glaciation, approximately 10,000 to 15,000 years ago, while they were introduced to North America much later (Ranz et al. 2007). Similarly, *D. subobscura* is native to Europe and only arrived in North America around 40 years ago (Ayala et al. 1989). The second factor, the establishment potential of *L. japonica*, has been extensively documented in recent years, with an increasing number of studies demonstrating a widespread distribution of adventive populations (Puppato et al. 2020; Beers et al. 2022; Abram et al. 2022a; Martin et al. 2023; Gariepy et al. 2024). Monitoring efforts following the parasitoid's initial detections in North America and Europe in 2016 and 2019, respectively, have revealed that it occupies a broad distribution in regions invaded by *D. suzukii*, suggesting that the initial arrival of *L. japonica* occurred sometime prior to these detections. However, these findings suggest that *L. japonica* has been present in some areas for a significant period and so far, no unacceptable non-target effects have become apparent, it is important to note that specific studies investigating the direct and indirect effects of *L. japonica* on non-target organisms are lacking. The parasitoid is still relatively new to these ecosystems and the long-term outcomes of its interaction with native species is not yet apparent. Moreover, in its new range, *L. japonica* is presumably both exerting and being subjected to strong selective pressures that could result in future adjustments in its interactions with other trophic levels (Fleury et al. 2009; Godfray 1994). This gap in research leaves some uncertainty about the long-term ecological impacts of the parasitoid's presence. Nevertheless, even if augmentative releases of *L. japonica* were considered as part of biological control strategies, these would likely have only local effects, primarily benefiting pest suppression in targeted areas, and would be unlikely to alter broader ecological dynamics on a large scale. This is because the impact of augmentative releases is typically constrained by several factors including the scale of intervention, the localized nature of the target pest populations, landscape composition, and ecological interactions, such as competition, predation, and environmental conditions (Bout et al. 2022). In this context, the potential risks of augmentative releases appear minimal when weighed against the benefits of controlling *D. suzukii*. Furthermore, any potential risks should be compared to the currently used control strategy, which is still very often the application of pesticides (Collatz et al. 2021). A reduced reliance on those because of successful *L. japonica* releases could help mitigate the broader non-target effects of chemical control strategies, which often impact beneficial insects and other organisms, and can have long-term environmental and economic impacts.

Challenges and opportunities for *Leptopilina japonica* augmentation

The considerations from the previous section lead to the second key point mentioned at the beginning of this chapter: would *L. japonica* provide additional benefits if released for augmentative biological control? In general, agents released for augmentative biological control in cropping systems are expected to provide important levels of pest population control and crop damage reduction within short timeframes, and this is especially the case for pests that directly attack the marketable commodity. In this context, some of *L. japonica*'s biological characteristics pose challenges for augmentative control efforts. As a koinobiont parasitoid, *L. japonica* allows its host to continue developing and causing fruit damage before ultimately killing it. This trait limits its effectiveness in providing short-term control of *D. suzukii*, which directly damages fruit crops. In contrast, most parasitoids that have been successfully used in augmentative biological control are either idiobionts, which kill the host quickly and prevent it from causing further damage, or are koinobionts that target indirect pests (*e.g.*, those pests not directly damaging or consuming the crop) for which there is a higher level of tolerance. Moreover, *L. japonica* has a longer generation time and a slower intrinsic rate of increase compared to *D. suzukii* (Wang et al. 2019), which means that without large and continuous releases, there would be temporal refuges where the pest population could escape parasitism (Abram et al. 2022a; Beers et al. 2022; Tsuruda et al. 2022). Even when released in substantial numbers, *L. japonica* has shown incomplete parasitism, often leaving viable *D. suzukii* in host patches such as berries, leading to suboptimal suppression levels (Wang et al. 2020). Despite these challenges, *L. japonica* has some practical advantages. Contrary to *G. kimorum*, *L. japonica* parasitizes *D. suzukii* on artificial media, making it feasible to develop relatively low-cost mass rearing and banker systems for this parasitoid (Girod et al. 2018c; Rossi Stacconi et al. 2022). However, while this trait facilitates rearing, the successful implementation of mass production and augmentative releases still faces significant challenges, including maintaining parasitoid quality, cost-effectiveness, and scalability for field applications. If these challenges can be addressed, *L. japonica* could be mass-reared and released over extended periods. However, such an inundative approach may still fall short of providing sufficient suppression in crops where *D. suzukii* tolerance thresholds are low. Nevertheless, integrating inoculative augmentative releases of *L. japonica* with other pest management strategies may increase its utility in fruit production systems, particularly where tolerance for *D. suzukii* damage is higher. Studies monitoring *D. suzukii* across growing seasons have found that population peaks vary by climate but generally occur after the beginning of June (Grassi et al. 2018; Guédot et al. 2018; Rossi Stacconi et al. 2016). Consequently, because *L. japonica* and other parasitoids rely on pre-established *D. suzukii* populations for their own increase, their numbers may not be sufficient to provide control during early season (May to mid-July) (Rossi Stacconi et al. 2019; Tsuruda et al. 2023). Field monitoring has shown that parasitism by natural populations of *L. japonica* and *Ganaspis* spp. may begin a few weeks after initial infestation on wild and cultivated hosts (Abram et al. 2022a). For this reason, early-season timed inoculation of *L. japonica* at local scale may have the greatest potential for impacting *D. suzukii* populations before their build up. Such a “parasitoid-in-first” approach is widely used to efficiently control greenhouse pests (Pijnakker et al. 2020) and has already been explored against *D. suzukii* in a field study conducted in Italy using *Trichopria drosophilae* (Perkins) as biological control agent (Rossi Stacconi et al. 2019). Despite *T. drosophilae* being a generalist pupal parasitoid, its release was associated with a significant reduction (34%) in pest infestation in unmanaged areas surrounding the crops and a sustained increase in the *T. drosophilae* population that persisted throughout the cherry fruiting period. The possibility of performing augmentative releases of *L. japonica* would allow farmers to spatially and temporally 'redistribute' the presence of this parasitoid to areas and the time of the season when it can be most effective, thereby enhancing its impact on *D. suzukii* populations. Clearly, these releases must be planned and executed according to a program that would consider the specific pest/parasitoid dynamics at local scale to tailor the interventions and maximize their positive impacts.

Regulatory frameworks for *Leptopilina japonica* release

Regulations relating to the introduction and release of BCAs, including *L. japonica*, vary notably across the regions where this species has recently established (Europe and North America). These differences reflect each region's environmental priorities, regulatory frameworks, and agricultural needs (Barratt et al. 2021). In Europe, BCAs are regulated primarily under biodiversity (Regulation (EU) 1143/2014) and plant health (Regulation (EU) 2016/2031) laws, rather than the plant protection product regulation (Regulation (EC) 1107/2009). Although BCAs are not directly targeted by these frameworks, they are indirectly addressed as "alien species" in the biodiversity regulation and as "herbivorous or omnivorous species" under the plant health regulation. Certain European countries, such as Austria, allow BCAs to be registered as plant protection products. However, the European regulatory landscape remains fragmented, with only 14 member states having specific provisions on the production, release, and transport of BCAs (Castella et al. 2022). In contrast, North American regions have specific regulations and more centralized systems, overseen by the United States Department of Agriculture (USDA) through the Animal and Plant Health Inspection Service (APHIS) in the USA and by the Canadian Food Inspection Agency (CFIA) and the Health Canada Pest Management Regulatory Agency (PMRA) in Canada (Mason et al. 2024). Unlike New Zealand, where regulatory evaluations explicitly balance risks with benefits, assessments in the USA, Canada, and most of Europe tend to focus almost entirely on risks (Barratt et al. 2021). Applicants must provide extensive dossiers that allow to identify and assess risks of releasing a non-indigenous BCA, showing they are either minimal or unlikely to occur. The information should be thorough, typically including data from host-range tests in quarantine and an assessment of the potential for establishment. Public consultations and post-release monitoring programs could also be part of the regulatory process, although the consistency and enforcement of monitoring efforts can vary between jurisdictions. International bodies such as the International Plant Protection Convention (IPPC) and the Plant Protection Organizations (*i.e.*, EPPO, NAPPO), provide guidelines and contribute to standards for the import, release, and risk assessment of non-indigenous BCAs, but individual countries retain authority over approvals, leading to varied processes across countries. Although these procedures are mostly well defined within the legislative frameworks, and several studies discuss the implications of introducing non-indigenous BCAs within new ranges (Hajek et al. 2016; Barratt et al. 2021; Paula et al. 2021), recommendations or regulations are not yet available for situations where the non-indigenous agent is already established in the area and is proposed for use in augmentative biological control. In this context, the main question shifts from "Is the non-indigenous BCA going to have negative impacts in the new range of release?" to "Will augmentative releases meaningfully intensify any potential non-target impacts of the extant non-indigenous BCA?". The case for *L. japonica* releases, which is already established in Europe and North America, falls within this category and should probably be evaluated from the latter standpoint. In this sense, it would be beneficial for policymakers and regulators to collaborate with researchers to implement evaluation criteria and specific procedures to evaluate the proposed use of established non-indigenous beneficial organisms for augmentative purposes, provided that proponents can demonstrate the safety and effectiveness of the candidate species.

Research agenda for *Leptopilina japonica*

With *L. japonica* already established in various regions, a crucial next step in its evaluation as a biological control agent is to assess the potential for redistribution or augmentation and their ecological implications. To ensure that these strategies do not introduce additional ecosystem-level harm beyond the effects already observed from its presence, specific evidence and carefully designed studies are needed. Here, we outline a possible research agenda to address these needs:

1—Extended field monitoring on parasitism of non-target organisms

While non-target host range testing has been conducted under laboratory conditions on a range of potential hosts, it has not been fully comprehensive in terms of species and environmental variables affecting the attack rates; it has mostly focused on Drosophilidae known to feed on decaying fruit and similar substrates. There is still a need to investigate *L. japonica*'s potential to parasitize drosophilids that feed in a wider variety of ecological niches, such as those that feed on mushrooms, decaying organic matter, or other specific substrates. Field research aimed at determining whether *L. japonica* is currently exploiting non-pest species in these environments, and thereby also impacting other native parasitoids, would allow for a more targeted assessment of the potential ecological impacts of augmentative releases.

2—Evaluation of dispersal ability and persistence, and the interacting influence of landscape features

To develop safe and effective augmentative release strategies, it is important to understand the spatial and temporal scale of the effects of augmentative releases—that is, how long and over what spatial scale will augmentative releases increase parasitism and lower densities of *D. suzukii* and non-target Drosophilidae by *L. japonica* above 'background levels' that occur in the absence of additional releases? This will need to include an evaluation of *L. japonica*'s natural dispersal capabilities and how landscape features (*e.g.*, crop systems and semi-natural habitats) influence the distribution and environmental persistence of released parasitoids and their progeny. Determining how different landscapes facilitate or hinder the dispersal and persistence of *L. japonica* could allow selection of release sites and optimization of release methods, maximizing the effectiveness of augmentative releases while minimizing the potential for undesirable ecological interactions. For example, current research is marking *L. japonica* with fluorescent liquid for field dispersal studies, this liquid mark persisted and had minimal impacts on other small parasitoids of *D. suzukii,* such as *G. kimorum* and *P. vindemiae* (Paul et al. 2024).

3—Long-term monitoring of establishment and biological control services of *Leptopilina japonica* populations

Long-term monitoring of *L. japonica* populations will provide essential data on its population stability, geographic range expansion, and effects on *D. suzukii* populations. Understanding these dynamics is critical for assessing *L. japonica*'s contribution to *D. suzukii* suppression in various environments. Monitoring efforts should capture not only population growth and spatial distribution but also the parasitoid's impact on *D. suzukii* densities over time. Collaborative regional and global monitoring networks that gather data with similar methodology, so that the data can be fed into analyses that can better interpret population-level impact of parasitism, can facilitate this effort (*e.g.* Abram et al. 2022b).

4—Identification of key factors influencing *Leptopilina japonica*'s performance

Several ecological factors may significantly affect the establishment and effectiveness of *L. japonica*. Investigating variables such as microclimatic preference, host fruit effects on parasitism rates, and interactions with other parasitoid species will improve our understanding of the conditions under which *L. japonica* thrives. Additionally, while laboratory studies have already examined its functional response (Wang et al. 2020), further research is needed to explore how *L. japonica* responds to temporal and spatial variation in host density under more realistic conditions. Field-based studies or mesocosm experiments incorporating different fruit types (*e.g.* varying in size and accessibility) could help refine our understanding of its density-dependent attack dynamics. By identifying the optimal conditions for its performance, it should be possible to model efficacy across diverse environments and adjust management strategies accordingly.

5—Developing a resilient biological control system through redistribution of adventive populations

Leptopilina japonica populations that have naturally established in various regions may exhibit local adaptations that affect their performance in different environmental conditions. Redistributing these adventive populations could promote a more resilient and adaptable biological control system. Studying the variability in effectiveness and adaptability across *L. japonica* populations will help refine redistribution practices to enhance control in areas where *D. suzukii* pressure is high. Distribution efforts in the USA are local, as releases of adventive *L. japonica* is permitted on a state-by-state basis, and only the adventive population originating from within a state can be reared and redistributed.

6—Integrate *Leptopilina japonica* into existing pest management programs

In case this parasitoid continues to expand its range and increase its influence on *D. suzukii* populations, it will be important to understand how to maximize its contribution to pest management. The methods for augmentative release will require extensive research to determine the best wasp density, locations within farms, and timing for achieving pest suppression. Integration with other management approaches will also need to be explored, including compatibility of pesticides used in different crop systems and regions, and synergy with current IPM strategies and tools, *e.g.*, the use of (bio)insecticides, mass trapping, protected cultivations, cultural control, release of generalist (pupal parasitoids) and specific (*G. kimorum*) parasitoids, and the burgeoning sterile insect approach. Therefore, specific studies on *L. japonica* activity and the implementation of other tools will need to be specifically assessed.

Of all the points listed in the agenda, the first, ensuring the absence of direct and indirect effects on non-target organisms, would likely provide the most important information needed before the augmentative release of *L. japonica* can be considered as safe. The second point could also provide valuable information, as it addresses the spatial and temporal scale of the effects resulting from augmentative releases. Even if there are significant non-target effects on a few species of drosophilids, demonstrating that augmentative releases only increase these effects above background levels for one or two seasons and within a limited range of a few hundred meters would demonstrate that the environmental impact and persistence of this technique are very low, particularly when compared to alternative methods like broad-spectrum insecticides. These insecticides kill far more than just a few vinegar fly species and may have comparable or greater spatial and temporal persistence than augmentative releases of *L. japonica*. The last four points will provide additional insights to assess whether the benefits of employing *L. japonica* in augmentative control are worth the effort and to optimize strategies. Therefore, in our opinion, any potential new *D. suzukii* biocontrol program based on augmentative *L. japonica* releases could be granted if point 1 has been addressed, with point 2 also contributing valuable context should non-target effects be detected, regardless of points 3–6.

Future perspectives and recommendations

In recent decades, the paradigm surrounding non-target effects, particularly among invasion ecologists, has shifted considerably toward the perspective that "any non-target effect is negative" (Heimpel & Cock 2018). However, it is important to recognize that exploitation of certain non-target species, especially if they are pests or non-native, can be beneficial, at least from an anthropocentric point of view. This issue has recently arisen for brown marmorated stink bug, *Halyomorpha halys* Stål (Hemiptera: Pentatomidae), where the egg parasitoid *Trissolcus japonicus* Ashmead (Hymenoptera: Scelionidae) was also attacking other non-target stink bugs that are themselves pests (Linder et al. 2023; Haye et al. 2024). What is particularly notable is that this concept is implicitly acknowledged in recent frameworks that balance biodiversity benefits against risks in biological control. These frameworks suggest that the "value" of non-target species varies in relation to human interests, with some species being considered of greater or lesser concern (Heimpel et al. 2024). In the case of *L. japonica*, some level of attack on common species like *D. melanogaster* and *D. simulans* might be viewed positively, both because these are occasional pests and because their parasitization could contribute to apparent competition with *D. suzukii*. Specifically, if *L. japonica* maintains stable populations by exploiting alternative drosophilid hosts, its presence in the environment could be sustained even when *D. suzukii* populations decline, thereby exerting continued parasitism pressure on the primary pest (Holt and Lawton 1993). This dynamic could help suppress *D. suzukii* populations over time, reinforcing the biological control effect. Moreover, populations of *Drosophila* species within groups that have not co-evolved with *L. japonica* (*e.g.* the *D. subobscura* species group native to the Mediterranean basin area), are, if at all, only impacted by low to moderate parasitism levels, as they are attacked at much lower levels than species closely related to *D. suzukii* (Fellin et al. 2023). From a benefit perspective, although the control exerted by *L. japonica* may not meet the extremely low tolerance for damaged fruit required for some marketable crops or exported fruit, boosting parasitism in untreated non-crop areas may help reduce the number of mated *D. suzukii* females dispersing from areas with high-density populations into commercial crops. The primary benefit of augmentative biological control in this context could be to establish a 'low-fly zone' at the crop borders, creating a buffer that reduces pest pressure on commercial crops. Incorporating *L. japonica* into IPM programs could complement other environmentally friendly approaches, such as cultural practices, habitat manipulation, and the use of exclusion netting. Augmentative releases of *L. japonica* early in the fruiting season could synergize with these methods by targeting pest populations before they peak, reducing the reliance on other pest control tools, such as chemical insecticides. This strategy aligns with the principles of sustainable agriculture by leveraging natural enemies to mitigate pest pressures while preserving beneficial insects and minimizing ecological disruption. The benefits of effective biological control of *D. suzukii* may also extend to other potential insect pests in commercial orchards, as reduced insecticide usage leads to increased activity of the natural enemies of secondary pests. Future research should prioritize evaluating the ecological impact and compatibility of *L. japonica* with existing IPM strategies to maximize its benefits within regulatory and practical constraints.

Author contributions

MVRS, AB and XW conceived and designed the research. All authors contributed to material preparation, field collection and laboratory identification of L. japonica, according to their specific expertise. MVRS, XW and AC analyzed the data. MVRS, AB, XW and PA drafted the manuscript. All authors read, revised, and approved the final version for submission.

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Declarations

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