

Ecology and biology of the parasitoid *Trechnites insidiosus* and its potential for biological control of pear psyllids

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Abstract

Pear cultivation accounts for a large proportion of worldwide orchards, but its sustainability is controversial because it relies on intensive use of pesticides. It is therefore crucial and timely to find alternative methods to chemical control in pear orchards. The psyllids *Cacopsylla pyri* and *Cacopsylla pyricola* are the most important pests of pear trees in Europe and North America, respectively, because they infest all commercial varieties, causing damage directly through sap consumption or indirectly through the spread of diseases. A set of natural enemies exists, ranging from generalist predators to specialist parasitoids. *Trechnites insidiosus* (Crawford) is undoubtedly the most abundant specialist parasitoid of psyllids. In our literature review, we highlight the potential of this encyrtid species as a biological control agent of psyllid pests by first reviewing its biology and ecology, and then considering its potential at regulating psyllids. We show that the parasitoid can express fairly high parasitism rates in orchards, and almost perfectly matches the phenology of its host and is present early in the host infestation season, which is an advantage for controlling immature stages of psyllids. We propose new research directions and innovative approaches that would improve the use of *T. insidiosus* in integrated pest management strategies in the future, regarding both augmentative and conservation biocontrol. We conclude that *T. insidiosus* has many advantages and should be included as part of integrated biological control strategies of pear psyllids, along with predators, in-field habitat conservation, and the rational use of compatible chemicals.

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Supporting information may be found in the online version of this article.

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1 GENERAL INTRODUCTION

Pear (*Pyrus communis* L.) is the second largest fruit economy in temperate regions, after apple, with an annual production of about 24 million tons.¹ In the European Union, more than 100 000 ha are dedicated to pear production in orchards (including the UK).² In pear orchards of Europe and North America, the main reported pests are psyllids (Hemiptera: Psyllidae), of which the 'pear psylla' *Cacopsylla pyri* (L.) and the 'pear sucker' *Cacopsylla pyricola* (Förster) are by far the most common and most damaging species.³ These sap-feeding insects infect all pear tree varieties—although some hybrids are highly resistant⁴—and cause heavy economical losses due to direct and indirect damage, such as reduced photosynthesis, sap consumption and transmission of phytopathogens.³ Since the 1960s, control of pear psyllids has relied extensively on the use of chemicals, which has led to the development of resistance and the progressive increase of psyllid populations.⁵ Due to the widespread emergence of pest-resistant phenotypes, the negative impacts of pesticides on biodiversity and the public demand for organic food production, the pear sector is striving to develop new methods for the control of psyllids.

Current control of *C. pyri* is increasingly reliant on integrated pest management (IPM) strategies, using both chemicals and natural methods, such as pulverization of natural products or biological control.^{3,6–8} In a recent overview, DuPont & Strohm⁹ concluded that IPM programs help maintain and increase populations of both predator and parasitoid natural enemies of psyllids in orchards, thus providing biological control in late summer, when conventional methods tend to be ineffective because of biotic resistance and because sprays fail to penetrate the tree canopy. Natural enemies of pear psyllids are mainly generalist predators (Anthocoridae, Araneae, Coccinellidae, Dermaptera, Formicidae and Miridae) and specialist Encyrtidae parasitoids.^{10–15} The natural presence of predators in orchards can fail to

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regulate psyllid populations below sustainable levels,^{3,16} especially in cases when they arrive too late in the season for long-lasting and effective biological control.¹⁷ Parasitoids better match the phenology of psyllids, but usually do not produce very high levels of parasitism before psyllids have built up their populations.^{11,18–20}

To address these issues, mass releases of predators have been tested over the last two decades in pear orchards, and have proven to be relatively effective in improving the control of *C. pyri*.²¹ For example, releases of the generalist predators *Anthrenus nemoralis* and *A. nemorum* (Hemiptera: Anthrenidae) in Denmark halved the pear psylla population in just two days.^{22,23} However, the large-scale development of such techniques faces many challenges, mainly because mass rearing is expensive, but also because *A. nemoralis* and *A. nemorum* are sensitive to pesticides, and because these generalist predators can attack nontarget insects.^{3,16,24} Therefore, alternative or complementary biological control solutions to the use of generalist predators need to be developed to protect pear orchards.⁸ In this regard, focusing on specialist parasitoids of psyllids, such as *Trechnites* species (Hymenoptera: Encyrtidae), is needed and could open up interesting avenues to integrate this auxiliary as part of both augmentative and conservation biological control programs.

The aim of this review is threefold: (i) to provide an overview of the genus *Trechnites* and in particular *Trechnites insidiosus* (Crawford) [Syn. *Trechnites psyllae* (Ruschka)] with respect to its biology and ecology, as it is the most common parasitoid species attacking *C. pyri* and *C. pyricola* in pear orchards; (ii) to consider the potential of the parasitoid *T. insidiosus* in controlling populations of psyllids, from a literature survey; (iii) to draw attention to unknown aspects of the biology of the parasitoid, and to propose innovative approaches for improving its use and/or efficiency in future biological control strategies in pear orchards.

2 OVERVIEW ECOLOGY OF TRECHNITES INSIDIOSUS IN PEAR ORCHARDS

Although *T. insidiosus* is the main parasitoid of pear psyllids, the species has been little studied, and few peer-reviewed references concerning this insect can be found in the scientific literature. Therefore, we acknowledge that a handful of the references we used in our review are nonpeer-reviewed academic sources, such as project reports, extension articles or conference abstracts, dealing with the biology and ecology of this parasitoid species.

2.1 The genus *Trechnites*

Trechnites (Thomson) is a cosmopolitan genus of chalcid wasps that includes 30 species worldwide,²⁵ with records throughout the Palearctic region (mainly Europe, India and China), Costa Rica, Southern Africa, Australia and North America (Table 1). These small-bodied wasps (body length of roughly 1 mm with females being slightly larger than males) are obligate koinobiont endoparasitoids of psyllid larvae.^{12,32}

2.2 Distribution of *Trechnites insidiosus*

The species *T. insidiosus* is endemic to Eurasia, and is distributed from Spain to Mongolia and Iran (for a detailed description of its geographical distribution, see Guerrieri and Noyes¹²). Furthermore, it extended its distribution range to North America during the 19th and 20th centuries, probably through successive events of (i) incidental establishment (i.e. through parasitized psyllids unintentionally introduced from Europe) and then (ii) intentional introduction (i.e. as a classical biological control agent to limit populations of introduced psyllid pests).^{12,35,36}

These deliberate introductions, as part of pest control programs, have involved *T. insidiosus* individuals coming from Europe and the Persian Plateau. For instance, *T. insidiosus* was introduced in 1965 from Switzerland into California for the control of *C. pyricola*, the most damaging psyllid pest for the pear economy in North America.³⁷ A few introductions from the Indo-Persian region were also recorded, but in a rather limited number.³⁶ It has been reported that following its initial introduction into California in the 1960s, *T. insidiosus* spread to the west^{6,33,38–40} and east coasts of the USA,⁴¹ reaching Canada in the process,^{32,42,43} either through multiple introductions or spread of naturalized populations. *T. insidiosus* has become the dominant parasitoid of pear psyllids throughout Western North America since the late 1960s, although little information is available on its establishment success and effectiveness in controlling psyllids.

2.3 Biological cycle and interactions with its host

T. insidiosus has been found to parasitize several species of pear psyllids: the main hosts are *C. pyri* (in Europe),⁴⁴ *C. pyricola* (in Europe and North America),⁴⁵ while parasitism is more occasional on the European species *Cacopsylla pyrisuga*⁴⁶ and *Cacopsylla vasilievi*.^{26,47} *Trechnites insidiosus* seems to attack only pear psyllids, although a degree of uncertainty exists; in a project report, Rendon et al.⁴⁸ mention that they searched for alternative hosts for this parasitoid such as the willow psyllids (*C*

Male *T. insidiosus* exhibit a courtship behaviour towards females.⁴⁹ First, the male initiates antennal contacts with the female, then it begins a dance by alternately raising the second left and right legs. The female then either chooses to reject the male before running away, or accepts to mate. If mating takes place, it is sometimes followed by a new antennal contact between the two partners (Video S1). The choice criteria used by females are still unknown but may be related to the age, size and overall perceived quality of the partner. Once mating has taken place, the female can lay its fertilized egg in a host. Escape behaviors have been observed in psyllids; when *T. insidiosus* females approach psylla colonies, psylla larvae tend to escape towards safer locations.⁴⁸ The set of behaviors that female parasitoids exhibit towards their hosts and mates may have consequences both for optimal breeding of this species for inundative biological control programs, and for developing orchard management strategies (detailed in the next sections).

Psyllids exhibit five larval instars in addition to the egg and adult stages (Fig. 1). They all feed on phloem sap and produce a lot of honeydew that eventually covers their entire body. Honeydew coating is used as a protective layer against predators⁵⁰ and parasitoids. This strategy is adopted by the first, second and third larval instars of psyllids, while the fourth and fifth larval instars are generally not associated with honeydew covering. It is hypothesized that honeydew acts both as an attractant for parasitoids to detect psyllids colonies,³² and as a lure and a mechanical defense that alters the foraging time budget of *T. insidiosus*. Indeed, even in the absence of a host, *T. insidiosus* females tend to oviposit in honeydew drops disseminated on the leaves (Video S2), which may reduce the time they allocate for searching other host patches.^{32,51} Under laboratory conditions, females of *T. insidiosus* are able to oviposit in all five larval instars of their host, and they can attack psyllids through the honeydew coating.^{32,52} However, the third and fourth psyllid larval instars appear to be the most

attractive and suitable. Le Goff *et al.*⁵¹ showed that the presence of third and fourth larval instars of *C. pyri* induced higher foraging responses by female parasitoids, and that 80% of the overall parasitism caused by *T. insidiosus* (i.e. total number of mummies formed) was on these two instars.

Trechnites insidiosus is a solitary parasitoid, and currently no data is available on possible superparasitism behavior in this species. Both arrhenotokous (unfertilized eggs develop into males) and thelytokous (females are produced from unfertilized eggs) parthenogenesis have been reported for this species,³⁶ possibly related to *Wolbachia* infection.⁵³ The parasitoid egg ($\approx 100\ \mu\text{m}$ long) usually requires 3–4 days to hatch within the host body.^{54,55} The newly hatched parasitoid larva ($150\text{--}200\ \mu\text{m}$) remains at the first developmental stage until the host reaches the fourth or fifth larval instar.^{32,40} The larva grows by consuming the contents of the host body, ultimately killing the psyllid during the second stage of its development ($\approx 1.4\text{--}2.0\ \text{mm}$ long larva).⁵⁵ The meconium (7–11 reddish pellets) is excreted during the prepupal stage, but no molting occurs between the second stage larva and the prepupal stage.⁵⁵ The parasitoid pupates within the desiccated remains of its host during the formation of the mummy. The pupal stage lasts 10–12 days, so that the adult wasp emerges from the mummy approximately 2 weeks after a nonparasitized psyllid would normally have completed its own developmental cycle (psyllids require 3–4 weeks to complete development at moderate temperatures). This allows *T. insidiosus* to synchronize its temporal window of activity with the occurrence of available hosts at a suitable developmental stage of the next generation³² (Fig. 1). The entire developmental time, from oviposition to adult emergence, lasts approximately 3 weeks at 22–24 °C. It is considerably shortened at higher temperature (around 14 days at 28 °C^{55,56}). Besides temperature, parasitoid development rates are also determined by the host stage. More specifically, parasitoids develop more slowly in first-instar larval hosts (around 30 days) than in

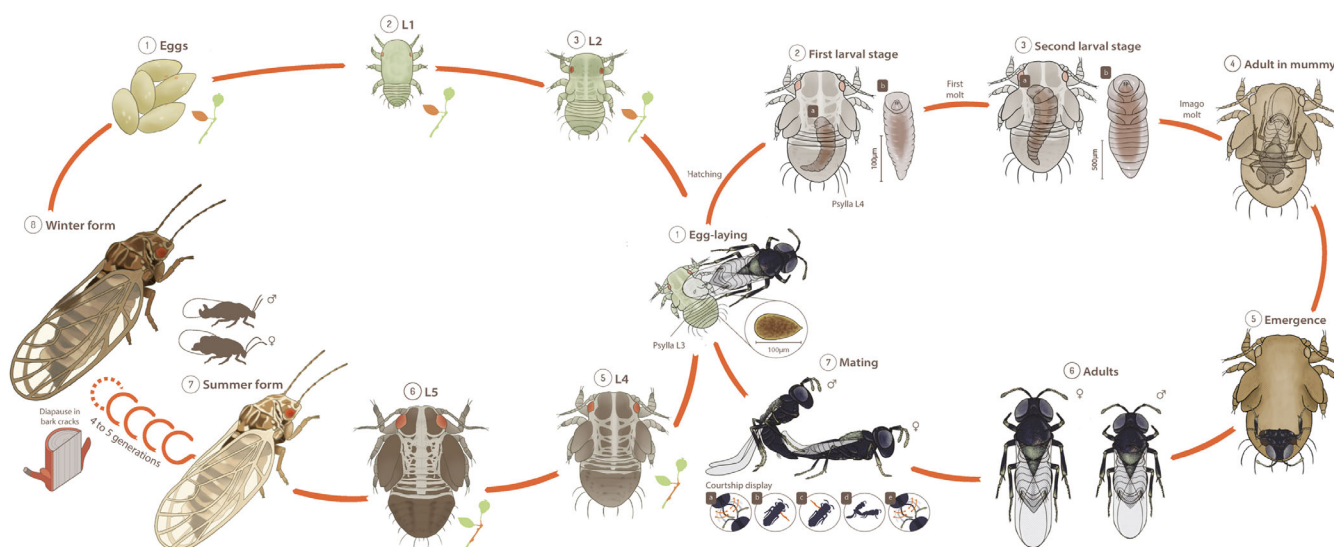


Table 2. Developmental time from oviposition to emergence of *Trechnites insidiosus* according to the temperature, the host developmental instar and the sex of the emerged parasitoid

Reference	Temperature	Parasitized instar	Sex of the parasitoid	Parasitoid developmental time $\pm$ SD (days)
51	22–24 °C	First larval instar	Male	31.33 $\pm$ 1.52
			Female	30.33 $\pm$ 2.65
	22–24 °C	Second larval instar	Male	26.25 $\pm$ 7.23
			Female	22.33 $\pm$ 3.74
	22–24 °C	Third larval instar	Male	22.84 $\pm$ 2.79
			Female	22.60 $\pm$ 2.83
	22–24 °C	Fourth larval instar	Male	20.50 $\pm$ 1.93
			Female	21.89 $\pm$ 2.07
56	24 °C	NA	Male	19.6 $\pm$ NA
		NA	Female	21.96 $\pm$ NA
	28 °C	NA	Male	13.35 $\pm$ NA
		NA	Female	14.81 $\pm$ NA

Data retrieved from Le Goff *et al.* and Bufaur *et al.*^{51,56} Detailed protocols can be found in their respective method sections.

the most advanced stages (around 21 days) at a given temperature.⁵¹ Finally, males and females develop at the same rate, regardless of temperature or host developmental stage (Table 2).

In addition to host parasitism, host-feeding behavior (whereby parasitoid adults predate host larvae) has been observed in female *T. insidiosus*⁵¹ (Video S3). Host-feeding consists of the consumption by the adult female parasitoid of host fluids exuding from oviposition wounds and is a common behavior in many parasitoid species^{57,58} and in Encyrtidae.^{59,60} Le Goff *et al.* analyzed host feeding behavior in *T. insidiosus* females exposed to each of the fifth developmental instars of *C. pyri*. They observed that this behavior is expressed at a low frequency by *T. insidiosus* with only one out of 200 second-, third- or fourth-instar larvae killed and then eaten by a female parasitoid, while no host feeding event was observed for the two other instars.⁵¹ The authors suggested that their experimental design where sugar sources were provided *ad libitum* to females with full egg load could have limited the expression of host-feeding behavior. Nevertheless, they proposed that host-feeding could provide the nutrients necessary for egg production of this parasitoid. *T. insidiosus* is, indeed, probably a synovogenic parasitoid (i.e. not all eggs are present at emergence) as suggested by its low egg load during early adult life (around 11 eggs for a 3-day-old virgin female) and its ability to feed on its host, but its requirements for oogenesis under different biotic and abiotic constraints remain to be elucidated in detail.^{49,51}

2.4 Parasitoid phenology and activity in pear orchards

T. insidiosus is a multivoltine species able to complete several generations, as suggested by successive population peaks during the pear growing season, perhaps primarily as a function of temperature, but also of other biotic and abiotic factors.^{40,61} Indeed, two to three peaks of adult emergence are usually detected in pear orchards, as evidenced by field surveys in Southern France,^{18,46} Spain^{19,62} and the USA.⁹ A higher number of generations can also be observed as a deviation from this general pattern. For example, a field study carried out in Syria reported that *T. insidiosus* could complete up to six generations per year,²⁰ probably due to the very permissive temperatures in this region (although this remains a hypothesis since the thermal biology of this species is unknown). On the contrary, Rendon *et al.*⁴⁸ showed that adult

wasps appeared in pear orchards in a single “explosive” peak in Oregon in the USA,⁴⁸ suggesting that local

Table 3. Selected references from field studies mentioning the phenology and presence of the psyllid parasitoid *Trechmites insidiosus* in different countries

References	Localization (country/region)	Trechmites insidiosus phenology				Psyllid phenology			Maximum parasitism rate	Presence of other natural enemies (*parasitoid, †predator)	Reported presence of hyperparasitoids	Sampling method	Notes
		Starting month	Peak	Ending month	Starting month	Peak	Ending month						
19	Spain	Apr	Late Jul	Mid Oct	Apr	Jun	Nov	100%	/	/	<i>Aphidencyrus mamitus</i>	(a)	
18	France	Apr	Late Jul	Late Nov	Apr	Jul	Dec	82%	<i>Prionomitus mitratus</i> *		<i>Aphidencyrus mamitus</i> , <i>Dilyta subclavata</i>	(a)	(1)
46	France	Apr	Late Jun	Early Jul	Early Apr	Jun	Late Jun	44%	<i>Prionomitus mitratus</i> *		<i>Dendrocerus psyllarum</i> , <i>Dilyta subclavata</i> , <i>Dilyta talitzkii</i> , <i>Pachyneuron aphidis</i> , <i>Pachyneuron muscarum</i>	(a)	
16	USA (Oregon)	May	Jul	Sep	Apr	Jun and Aug	Oct	80%	<i>Prionomitus mitratus</i> *, <i>Deraeocoris</i> spp.†, <i>Anthocoris antevolens</i> † and other Hemiptera†, Coleoptera†, Neuroptera†, Araneae†, Dermaptera†	<i>Aphidencyrus</i> sp., <i>Pachyneuron</i> sp.		(a)	
63	Bulgaria	Jul	Sep	Oct	/	/	/	13%	<i>Prionomitus mitratus</i> *, <i>Coccophagus</i> sp.†, <i>Anthocoris nemoralis</i> †, <i>Orius</i> sp.†, <i>Chrysopa</i> carneat†, <i>Coccinellidae</i> †			(2)	(a)
56	Bulgaria	Apr	Jun and Oct	Nov	Mar	Apr and Jun	Late Oct	41%	<i>Prionomitus mitratus</i> *		<i>Pachyneuron muscarum</i>	(a)(b)	
9	USA (Washington)	Apr	May and Jun	Late Oct	/	/	/	/	<i>Campylomma verbasci</i> †, <i>Chrysoperla plorabundant</i> †, <i>Chrysopa nigricornis</i> †, <i>Deraeocoris brevis</i> †			(c)	
11	Turkey	Treated orchards: May Untreated orchards: May	Sep	Oct.	/	/	/	46.3%	<i>Coccinellidae</i> †, <i>Dermaptera</i> †, <i>Heteroptera</i> †, <i>Neuroptera</i> †		<i>Aphidencyrus mamitus</i> , <i>Pachyneuron aphidis</i>	(b)(c)	
64	France	Early Apr	Apr, May and Jul	Late Oct	Early Apr	Apr, Jun and Oct	Late Oct	/	<i>Prionomitus mitratus</i> *, <i>Allothrombium fuliginosum</i> †, <i>Anthocoris nemoralis</i> †, <i>A. nemorum</i> †, <i>Campyloneura virgulat</i> †, <i>Chrysoperla carneat</i> †, <i>Coccinella septempunctat</i> †, <i>Coniopteryx borealis</i> †, <i>Heterotoma merioptera</i> †, <i>Orius horvati</i> †, <i>Orius vicinust</i> †, <i>Orthotylus nassatus</i> †, <i>Scymnus rubromaculatus</i> †, <i>Scymnus subvillosus</i> †, <i>Sterthorus punctillum</i> †	<i>Aphidencyrus mamitus</i> , <i>Pachyneuron aphidis</i> , <i>Pachyneuron aphidis</i>	(a)(b)		
52	USA (California)	/											

Table 3. Continued

References	Localization (country/region)	Trechnites insidiosus phenology			Psyllid phenology			Maximum parasitism rate	Presence of other natural enemies (*parasitoid, †predator)	Reported presence of hyperparasitoids	Sampling method	Notes
		Starting month	Peak	Ending month	Starting month	Peak	Ending month					
38	USA (Oregon)	Late May	Early Sep	Mid Sep	May	Jun	Sep	80%	Chrysopidae†, Hemerobiidae†, Coccinellidae†, Hemiptera†	/	(a)(b)	(7)
40	USA (Oregon)	May	/	Oct	Presence across the year			/	Deroecoris brevis†, Thysanopterat†, Araneae†, Neuropterat, Coccinellidae†	/	(c)	(c)

(1) No hyperparasitism in the first generation. (2) Parasitism rates include both *Trechmites psyllae* and *Prionomitus mitratus*. (3) Parasitoids reported but not counted. The authors simply mention that parasitoids were present at the same time as the psyllid peak. (4) No data before May and after October. (5) Observed parasitism rates could be caused by both *T. insidiosus* and *Psyllaephagus* sp. (6) First record of *T. insidiosus* West of Ontario, which may explain the low parasitism rates. (7) No data available beyond September, so the results could be biased (especially for the ending dates of host and parasitoid phenologies). Sampling methods: (a) psyllid larval sampling in the field followed by rearing and parasitism estimation in laboratory conditions, (b) beat sampling, (c) sticky traps, (d) direct mummy count in the fields.

The host phenology (pear psyllids) and the maximum reported parasitism rate over the monitoring season are displayed. The presence of other natural enemies of psyllids and hyperparasitoids are mentioned. This table is only intended to provide an overview of the available data and the variability in reported values reflects differences in sampling protocols, years and locations in the referenced studies. Refer to the notes for important details regarding comparisons among studies and interpretation of the data. Main sampling methods are also provided.

T. insidiosus could play the same role in orchards, as it is in most cases present as soon as the first generation of psyllids emerge from winter diapause. In some monitoring reports, however, *T. insidiosus* is not detected during the pre-bloom and bloom periods, and is only present around May.⁹ Interestingly, it has been proposed that one could control adult psyllids even before they break their overwintering reproductive diapause and lay eggs on dormant pear wood.⁴⁰ It is, however, difficult to achieve in a biological control context because of the low activity of most psyllids' natural enemies at low temperatures, and because winter morphs of psylla tend to overwinter in vegetation outside of pears. If winter temperatures are mild enough to allow activity, winter-active parasitoids could contribute, together with winter-active spiders and earwigs, to pest control during the cold season, focusing on nymphs present in the trees, although any intraguild predation could hinder parasitoid efforts. In any case, spraying chemicals at the end of winter before pear tree blooming, as classically applied in orchards, may be counterproductive for pest control.⁷²

Both *T. insidiosus* synchrony with the host and the overall parasitism rates expressed in the fields represent important assets for its effectiveness in psyllid control. First of all, we observed that the phenology of the parasitoid varied greatly according to the geographical context, most often due to latitudinal clines in thermal conditions between different locations (Table 3). In most cases, early-spring emergence of the parasitoid almost perfectly matched the psyllids outbreak (i.e. before the pear trees' blooming season). At the peak abundance dates, a short time lag was observed between the phenology of the two species. Further research is needed to understand the spring ecology of the parasitoid and better predict its emergence dates and phenology, as many factors, including temperature, food and host abundance and diversity (i.e. presence of alternative hosts) or pesticide use, could explain the observed variability in emergence date and overall phenology of *T. insidiosus*. In addition, overall parasitism rates of *T. insidiosus* were quite high, with more than half of the studies reporting rates &

The parasitoid complex of pear psyllids consists mainly of the parasitoid wasps *T. insidiosus* and, to a lesser extent, *P. mitratus*, that are mostly present during the first generation of the pest. It also includes a set of hyperparasitoid species that can have detrimental effects on the expansion of beneficial parasitoid populations and the resulting efficiency of biological control programs. Hyperparasitism on *T. insidiosus* has been given relatively little attention in the literature. Of all the hyperparasitoids identified, species of the genus *Pachyneuron* (Hymenoptera: Pteromalidae) have been frequently reported and are probably the most universally present in the field (Table 3). In British Columbia (Canada), the first, second and third generations of *T. insidiosus* incurred hyperparasitism rates of 50%, 33% and 85%, respectively, from *Pachyneuron* species.³² Furthermore, individuals of *Pachyneuron* sp. were found to emerge from 40% of the total of mummified psyllids sampled in Ontario (Canada).^{73,75} *Pachyneuron concolor* (Förster) is the most frequently observed hyperparasitoid species in orchards in Europe and in North America.^{13,32,64,67,76} It is a polyphagous obligate hyperparasitoid that attacks various primary parasites in soft scale insects, mealybugs, aphids and coccinellid larvae.⁷⁷ Nguyen *et al.*⁷⁸ described it as an ectoparasitoid of fifth-instar larvae, prepupae and pupae of *P. mitratus* and *T. insidiosus* inside *C. pyri* mummies. However, it is reported that *P. concolor* can also develop as facultative intra- or interspecific tertiary hyperparasitoids by parasitizing larvae and pupae of its own species.^{77,79} Other species of the genus, including the polyphagous hyperparasitoids *P. muscarum* (L.) and *P. aphidis* (Bouche), have been recorded more sporadically.^{11,32,46,68} Beside *P. concolor*, *Aphidencirtus mamitus* (Walker) [syn. *Syrphophagus mamitus* (Walker)] (Hymenoptera: Encyrtidae) is a very frequent hyperparasitoid of *C. pyri*.^{7,11,18,19,64} Although it has been recorded on various psyllid species (including *C. peragrina*, *C. melanoneura* and *C. crataegi*), its ecology remains largely unknown.⁸⁰ In Southern Spain, hyperparasitism by *A. mamitus* fluctuated between 0% and 19% of the mummies gathered over a 3-year period.⁷ Finally, other hyperparasitoid species less regularly encountered have been reported in some studies, including *Dendrocerus psyllarum* (Dessart), *Dilyta subclavata* (Förster), *Dilyta talitzkii* (Belizin) and *Dilyta rathmanae* (Menke & Evenhuis)^{18,46,48,68} (Table 3).

Concerning *T. insidiosus*, the body of available knowledge suggests that the hyperparasitism pressure could, in some cases, be high enough to limit its abundance and hamper its potential as biological control agents against pear psyllids.^{32,73} Few studies have examined the dynamics of hyperparasitoid populations in pear orchards. The few data on the subject come from studies carried out in the south of France (in the Avignon region),^{18,46} where the first generation of *C. pyri* does not appear to be parasitized by secondary parasitoids. *Dilyta subclavata* and *P. muscarum* tend to hyperparasitize larvae from the second generation during May–June. Thereafter, host larvae are not parasitized until the beginning of the fifth generation of *C. pyri*, which can host *A. mamitus* which is abundant in October and November.^{11,18} Hyperparasitoids usually appear late in the season because the completion of their cycle depends on the multiplication of primary parasitoids. However, an early-season hyperparasitism can be observed when *C. pyrisuga* coexists with *C. pyri* in orchards, as it favors the establishment of primary parasitoids.¹⁸

Given the large variability of hyperparasitism pressure in space and time, we stress that more research needs to be conducted on the biology and ecology of hyperparasitoids of psyllids to identify the *in situ* drivers of variations in recorded hyperparasitism

rates. This is especially true in the context of global warming, as it may advance the phenology of a lot of hyperparasitoid species and undermine the efficiency of biological pest control in many agricultural systems.⁸¹ This issue is very relevant in the pear orchard system, where the first generation of parasitoids is little prone to hyperparasitism, but is perhaps the most important for the regulation of pest populations.

Because *T. insidiosus* feeds on honeydew, competition could occur with ants attending psyllids or nonhost species for honeydew consumption.⁸⁰ Ants can also greatly reduce psyllid populations in pear orchards^{15,82} and consequently affect parasitoid population dynamics through reduction in host number.⁸⁰ In addition to intraguild competition (IGC) between different parasitoids and predators of pear psyllids, strong events of intraguild predation (IGP) would be detrimental for pest management in pear orchards. Although not commonly reported, it is very likely that generalist predators such as *A. nemoralis* consume already parasitized psyllids, therefore preventing the emergence of future parasitoid generations.^{17,63</}

psyllid consumers as a whole. Therefore, in the following sections, we try to examine the potential of these strategies if applied to *T. insidiosus*, and to highlight research priorities in this regard.

3.1 Augmentative biological control

The first step in the development of augmentative programs of *T. insidiosus* to control psyllids would be to create a mass rearing protocol that is effective for both the host and the parasitoid, which is far from being done in the current state of science, and which has not been considered by the BC industry, to our knowledge. Concerning the parasitoids, thelytokous populations would be easier to multiply in mass rearing cultures, because it avoids issues regarding the choice of mate, although arrhenotokous parthenogenesis has the advantage of allowing genetic mixing. Pear psyllids can be reared on pear trees and can then be used as hosts for the parasitoid. This strategy can work at a small-scale production for laboratory experiments,^{49,51} but is not yet adapted for industrial mass rearing. Indeed, pear trees have slow growth and maintaining year-round production in greenhouses would represent unsustainable costs in terms of energy, space and manpower. Moreover, pear psyllids themselves are an issue because they produce large amounts of honeydew, which leads to the development of fungi on pear trees and the need for frequent fungicide applications and frequent renewal of the pear trees. Another possibility to facilitate the mass rearing of *T. insidiosus* would be to look for alternative hosts that feed on host plants easier to cultivate than pear trees. As mentioned before, *T. insidiosus* seems to attack only pear psyllids, but a search for alternative hosts is worth further investigation (e.g. willow or potato psyllid). Moreover, it is important to keep in mind that rearing a parasitoid on a nonpreferred host could impact its development and decrease its fitness, and also its host foraging capacities once released, because natal host influences host preference.⁸⁹

One other way to address this issue and reduce the costs of mass production would be to develop an artificial diet for the rearing of pear psyllids. In addition, this would considerably reduce the area required for mass rearing compared to the use of the host plant relying on greenhouse cultivation. Such a rearing strategy would save space, water and manpower, and would allow the rearing of millions of individuals in climatic chambers. This solution, however, does not address the issue of fungal infection. The nutritional needs of pear psylla are now well understood⁹⁰ and could be used as a basis for developing a recipe for this artificial diet, but there is still some work to do because developing an artificial diet for these psyllids is much more complex than understanding the diet alone. Indeed, there are still things to develop regarding proper conditions for egg laying, for developing appropriate feeding membranes or for the use of phagostimulant to increase feeding before developing an artificial diet, as has already been done for some aphid species.⁹¹

We acknowledge that the mass rearing of the parasitoid is much more complicated than for Anthocoridae species. Yet, if commercial mass rearing protocols are to be developed in the future, some of the parasitoid characteristics highlighted above could be relevant for the development of a mass release strategy in pear orchards. First, we have shown that *T. insidiosus* has a phenology that generally matches that of its host at the beginning of the psyllid outbreak season. This phenological pattern suggests that the parasitoid is able to fly and forage on host patches even at relatively low spring temperatures, corresponding to the psyllid emerging period. However, we have also evidenced that local environmental conditions may generate variability in patterns of

parasitoid and host phenologies, which could modify the temporal overlap between the peaks of maximal abundance of the two trophic levels and have complex consequences in terms of pest control. Augmentative BC might be a useful approach to minimize such a temporal mismatch if the timing of parasitoid release in the field is chosen on the basis of empirically designed predictive models. The development of such decision support tools to match parasitoid release dates as closely as possible to the psyllid cycle is encouraged, and can be based on already established phenological models in psyllids.⁹²

Secondly, our literature review has witnessed important variations in parasitism rates between field studies (from less to 5% to more than 40%), and we have proposed that such variability in the biological control naturally provided by *T. insidiosus* could be caused by several environmental parameters, including hyperparasitism⁵⁴ and agrochemicals.^{12,32,73} We can also conjecture that temperatures prevailing during the early growing season and the peak of *T. insidiosus* activity should primarily determine the parasitism rates of psyllid populations. Formal ecophysiological studies on the parasitism efficiency of *T. insidiosus* at low temperatures, as well as the determination of its thermal optima for both parasitism and locomotor activity, have thus to be carried out. In this respect, research should also focus on the selection of parasitoid strains that are resistant and active at low temperatures, especially since parasitoids may have a different thermal optimum range than their hosts.⁹³ Such data combined with *in situ* meteorological records could serve as support for decision-making on the timing of release and the selection of *T. insidiosus* populations in augmentative BC strategies. Interestingly, *T. insidiosus* is able to attack almost all larval instars, meaning that an early mass release of parasitoids could affect psyllids just after they have broken diapause and begun to produce fresh larvae, which could have a significant impact on psyllid population dynamics in the long term. The action of the parasitoid at the beginning of the psyllid developmental cycle has the advantage of removing individuals from the pest population before they can reproduce and do damage to the trees. Future research should focus on the behavioral ecology of *T. insidiosus* to observe, for example, the expression of superparasitism and host-foraging behavior at low host density, as this would help determine the optimal release frequency and density of *T. insidiosus*

for oogenesis,⁵⁹ although the contribution of this behavior to reproduction and energy gains may be marginal and remains to be further investigated in *T. insidiosus*. Generally speaking, it is crucial to examine the combined impact of both parasitism and host-feeding behaviors on the overall biological control value provided by the natural enemy to better understand the complexity of host-parasitoid dynamics in the fields.⁹⁴

As a first lever for conservation BC, growers can adapt their methods by reducing pesticide use and changing agricultural practices such as mowing frequency.³⁹ There is a growing body of literature supporting the ability of IPM programmes to maintain natural enemy populations in pear orchards, although this is only effective if pesticide use is rational.^{9,95} Various responses to pesticide application exist among pear pest and natural enemy taxa,^{6,86,95} and these responses can also vary depending on the landscape and regional context.⁹⁶ This is putting at risk conservation BC strategies because of sometimes severe nontarget effects. In a meta-analysis on such nontarget effects, Beers *et al.*⁹⁵ showed that *Trechnites* sp., along with *Forficula auricularia* and parasitic Hymenoptera, are negatively affected by spinetoram chemical application compared to chlorantraniliprole treatment (a weakly harmful pesticide in the laboratory used as the control group). As also pointed out by the authors, there is no laboratory data on *Trechnites* sp. resistance to various kinds of pesticides in use in pear orchards, and few data are available on *Trechnites* sp. compared to other psyllid natural enemy species.⁹⁵ Next steps regarding the optimal inclusion and compatibility of *T. insidiosus* in conservation BC strategies should thus be to determine, in both the laboratory and the field, which pesticides are the most appropriate to both control pear psyllids and maintain parasitoid populations.^{9,95,96} In a report by Rendon *et al.*,⁴⁸ adult wasps incurred mortalities of 82%, 53% and 26% when sprayed with Abamectin, Esteem and Ultor insecticides, respectively, compared to 15% mortality with a control water spray. When spraying mummies with the same treatments, the authors report that mortality is high but does not differ from the water control, which suggests that wasp larvae developing inside psylla mummies could be protected from the detrimental effects of insecticide applications.⁴⁸

It is also well known that using high levels of fertilizers on plants has an indirect positive impact on phytophagous insect fitness traits,^{97,98} as well on upper trophic level species.⁹⁹ Therefore, reducing excessive plant growth and avoiding intensive fertilizers could help manage *C. pyri* on pear trees.³ Then, orchard management could focus on improving the survival and population growth of the set of natural enemies of pear psylla. It has already been shown that managing the plant environment can optimize orchard IPM through the manipulation of beneficial arthropods, including *T. insidiosus*.^{9,10} The establishment of perennial habitats around the orchard such as hedgerows or annual sown flower strips between tree rows are the most common practices. If the vegetation species composition is well chosen, it can provide food, alternative hosts and preys, shelters and overwintering habitats for natural enemies of orchard pests.^{100,101} The control strategy of deterring herbivores from trees in orchards, and favoring parasitoids and predators early in spring, would benefit from sowing a mixture of early bloom annual and perennial plants, such as *Alliaria petiolata*, *Anthemis arvensis*, *Anthriscus sylvestris*, *Bellis perennis*, *Capsella bursa-pastoris*, *Cardamine pratensis*, *Chrysanthemum segetum*, *Euphorbia helioscopia*, *Primula* spp., *Senecio vulgaris*, *Sinapis arvensis*, *Veronica persica*, etc.^{102–105} For example, Winkler *et al.*¹⁰⁶ showed that densities of *A. nemoralis* increased near flower strips in pear orchards, but it should be noted that

the potential benefits of habitat management in the field may vary between species, may increase IGC and may also benefit the pests more than their natural enemies.

Another conservation BC strategy is to use trap plants in or around fields. It has been shown that *C. pyri* is more attracted by some pear cultivars than by others.^{107–109} The use of sensitive pear trees or noncrop trees in pear orchards might be a good approach to lure away and trap the pear psyllid, and to simultaneously enhance the establishment and activity of the parasitoid *T. insidiosus* by making more hosts available and providing alternative hosts. To our knowledge, no specific trap-cropping systems have been developed for *T. insidiosus*, but it exists in other orchard systems. For instance, in apple orchards, the parasitism rate of the parasitoid *Ephedrus persicae* (Hymenoptera: Braconidae) increases on the rosy apple aphid *Dysaphis plantaginea* (Hemiptera: Aphididae) when cherry trees are intercropped with apple trees. Indeed, *E. persicae* can establish its population by attacking an alternative host, the aphid *Myzus cerasi*,

the case in the current state of knowledge about *T. insidiosus*. The release of a cocktail of both *T. insidiosus* and psyllid predators such as Anthocoridae could be an ideal solution in the early spring, when psyllid populations are low but so are natural populations of their enemies. On this point, however, released populations should show sufficient levels of activity at relatively low temperatures to control pear pests. Further investigations are needed to evaluate the impact of low temperatures on fitness traits of the parasitoid to predict its early activity in the field. Second, it would be necessary to improve both the persistence of the released natural enemies and the development of naturally occurring parasitoid and predator populations to gain control of psyllids later in the season through environmental management. For example, in French orchards, the action of *T. insidiosus* can be supported by the intervention in June and July of secondary species such as the predator bug species *A. nemoralis*, *Orthotylus nassatus*, *Heterotoma meriopterum* and *Campyloneura virgula*.⁶⁴ Taking measures to maintain field populations with the use of banker plants would additionally help in making the parasitoid an effective agent for the control of pear psyllids. Future research should assess whether initial control of psyllid populations by mass releases of natural enemies, combined with conservation BC strategies later in the season, would bring and maintain pear psyllid populations below a sustainable level. In the current state of knowledge, we suggest that focusing on conservation BC is more promising than augmentative BC, for the reasons exposed in the sections above.

4 CONCLUSION

Although *T. insidiosus* is the main parasitoid of pear psyllids, it has not historically been considered a promising beneficial insect for their control. The main reasons for this paradox are the reported parasitoid sensitivity to chemical treatments^{6,95} and high levels of hyperparasitism in orchards.^{7,18} Yet, this parasitoid presents a large window of activity, its first generation is usually free from hyperparasitism,^{18,46} it matches almost perfectly psylla phenology and it is active at relatively cold temperatures, which are great assets for rapidly controlling pest population dynamics during the pear growing season. Moreover, this parasitoid shows a preference for oviposition in the third and fourth larval instar of pear psyllids⁵¹ and expresses host-feeding behavior.⁵¹ Such behaviors confer an advantage to control psyllids, as they have an impact on the resulting reproducing population of the host and thus on its subsequent generations.

We provided evidence through our review that *T. insidiosus* has several qualities that could make it an interesting asset for biological control of pear psyllids as part of IPM strategies. However, we acknowledge that only scarce information and empirical evidence of the efficiency of this parasitoid is available in the literature so far. Therefore, we hope that this review serves as a platform and incentivizes future laboratory and field studies of *T. insidiosus* and its role as a biological control agent of pear psyllids. To fill the main gaps of knowledge on this species and its consideration for biological control strategies, we suggest future studies to primarily focus on basic ecology (behavior on psyllid colonies, thermal biology, nutrition and interspecific interactions), then on developing efficient mass rearing and mass release strategies, and finally on better determining the role of field and landscape management, which has great potential to improve the natural occurrence, persistence and population growth rate of parasitoids in pear orchards.

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SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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