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ARTICLE

The establishment of the association between the Japanese beetle (Coleoptera: Scarabaeidae) and the parasitoid *Istocheta aldrichi* (Diptera: Tachinidae) in Québec, Canada

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Abstract
We explored ecological aspects of the early establishment of the association between the Japanese beetle, *Popillia japonica* (Newman) (Coleoptera: Scarabaeidae), and the adult tachinid parasitoid, *Istocheta aldrichi* (Mesnil) (Diptera: Tachinidae), in the province of Québec, Canada. The Japanese beetle started its invasion in the late 1930s, whereas *I. aldrichi* was detected only in 2009. It is assumed that *I. aldrichi* spread in the province from its introduced range in the northeastern United States of America. Throughout the summer, we used baited traps in eight localities of southern Québec (2018–2019) and in 13 raspberry (*Rubus idaeus*) fields (2022) localised along a latitudinal gradient to describe the distribution and seasonal occurrence of both species and the parasitism rates of *I. aldrichi*. We also mapped observational data from the online platform iNaturalist to further describe the current distribution of both the host and its parasitoid. Results indicate that *I. aldrichi* is well spread in southern Québec and along the St. Lawrence River in most areas where the Japanese beetle is present. Parasitism mostly occurs from late June to mid-July, before the peak of Japanese beetle populations, and levels of total seasonal parasitism range from 3.9 to 27.3% across sampled sites. Together, trap captures and data from iNaturalist provide evidence that *I. aldrichi* is now established in most areas of the province of Québec where the Japanese beetle is present.

Introduction

The Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), native to Japan, is a highly polyphagous invasive pest in North America, with both adults and larvae able to cause yield losses and aesthetic damage to ornamental plants and agricultural crops (Shanovich *et al.* 2019; Althoff and Rice 2022). The Japanese beetle is univoltine in most areas of its native and nonnative geographic ranges, although its lifecycle can take two years to complete in northern areas. Adults mostly emerge in late June or early July and live up to 40 days (Hadley and Hawley 1934). Females lay eggs individually in the top 7.5-cm layer of the soil during the summer, with each female laying up to 60 eggs over its lifetime (Dalthorp *et al.* 2000). The larvae feed on roots and moult until they reach the third instar. Larvae begin overwintering in October after moving down into the soil to a depth of 20–25 cm. In spring, larvae move back up, resume feeding, pupate, and emerge as adults.

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The Japanese beetle was first reported in North America in 1916 in New Jersey, United States of America (Clausen *et al.* 1927; Fleming 1976). It has since spread to and established in most of the states east of the Mississippi River, with localised infestations occurring in other states east and west of the Rocky Mountains (United States Department of Agriculture 2023). In Canada, a museum specimen from the Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada) was traced back the first detection of the Japanese beetle in 1929 in southern Ontario (Gagnon and Giroux 2019). In Québec, individuals were first trapped in 1939 in Lacolle (Garland 1990). Populations are now established throughout eastern Canada, from Ontario eastwards, with the exception of Newfoundland (Canadian Food Inspection Agency 2023).

More than a century ago, the solitary, adult parasitoid *Istocheta aldrichi* (Mesnil) (Diptera: Tachinidae), native to the eastern Palearctic region (Herting and Dely-Draskovits 1993), was selected for releases in the United States of America to control Japanese beetle populations (Clausen *et al.* 1927). Following repeated introductions from 1920 to 1950, *I. aldrichi* spread to and established in New York, Pennsylvania, New Jersey, Massachusetts, Connecticut, and the District of Columbia (O'Hara and Wood 2004) and more recently in Minnesota and North Carolina (Klein and McDonald 2007; Shanovich *et al.* 2021). It is assumed that Canadian *I. aldrichi* populations spread from its introduced range in the United States of America. Parasitised Japanese beetles were first observed in Granby, Québec in 2009 (Gagnon and Giroux 2019) and in the Ottawa region of Ontario in 2013 (O'Hara 2014). Surveys of entomological collections and community science databases (http://www.inaturalist.org) further provided evidence that *I. aldrichi* was present in several locations of southern Québec as of 2017 (Gagnon and Giroux 2019).

Most of the information on the biology and natural history of *I. aldrichi* come from Clausen *et al.*'s (1927) landmark study: the female parasitoid lays its eggs on the pronotum of its host. Upon eclosion, the fly larva drills downwards into the beetle and starts feeding on host tissues. Parasitised *P. japonica* next burrow into the soil and die. The fly larva pupates within the host cadaver and overwinters. *Istocheta aldrichi* is univoltine (Clausen *et al.* 1927), and the parasitoid appears to be specific to *P. japonica* (Arnaud 1978; O'Hara and Wood 2004), although rigorous host specificity testing has not been conducted.

The present study investigated the distribution, seasonal occurrence, and parasitism rates of *I. aldrichi* in Québec following its initial discovery. To accomplish this, we used baited traps in 2018 and 2019 to collect parasitised beetles in eight localities of southern Québec. In 2022, we recorded parasitism rates in 13 raspberry (*Rubus idaeus*) fields localised along a latitudinal gradient. Finally, we used data from the online platform iNaturalist to further complement the current distribution of *I. aldrichi*. This study is part of a larger research program designed to first monitor the spread, establishment, and dispersal of *I. aldrichi* in Canada and then to evaluate the population-level impact of *I. aldrichi* on *P. japonica* in invaded areas.

Materials and methods

Parasitism in southern Québec

In 2018 and 2019, parasitism of *P. japonica* by *I. aldrichi* was monitored from July to October at eight sampling sites where Japanese beetle populations were presumably established based on information from agronomists and iNaturalist observations (Fig. 1A; Table 1). Parasitism was estimated using Bioprotec® traps with a dual lure system comprised of a floral bait (phenethyl propionate + eugenol + geraniol (3:7:3); Ladd and Klein 1986) and the synthetic sex pheromone of the Japanese beetle, "Japonilure" ((R,Z)-5-(1-decencyl)-dihydro-2(3H)-furanone; Tumlinson *et al.* 1977). These traps provide reliable estimates of parasitism rates (Legault *et al.* 2023).

Traps were positioned in or nearby botanical gardens, plant nurseries, resident gardens, or experimental farms (Table 1). Each sampling site was characterised by a relatively diverse plant community. Within each sampling site, one trap was placed on a U-shaped bamboo pole 1 m

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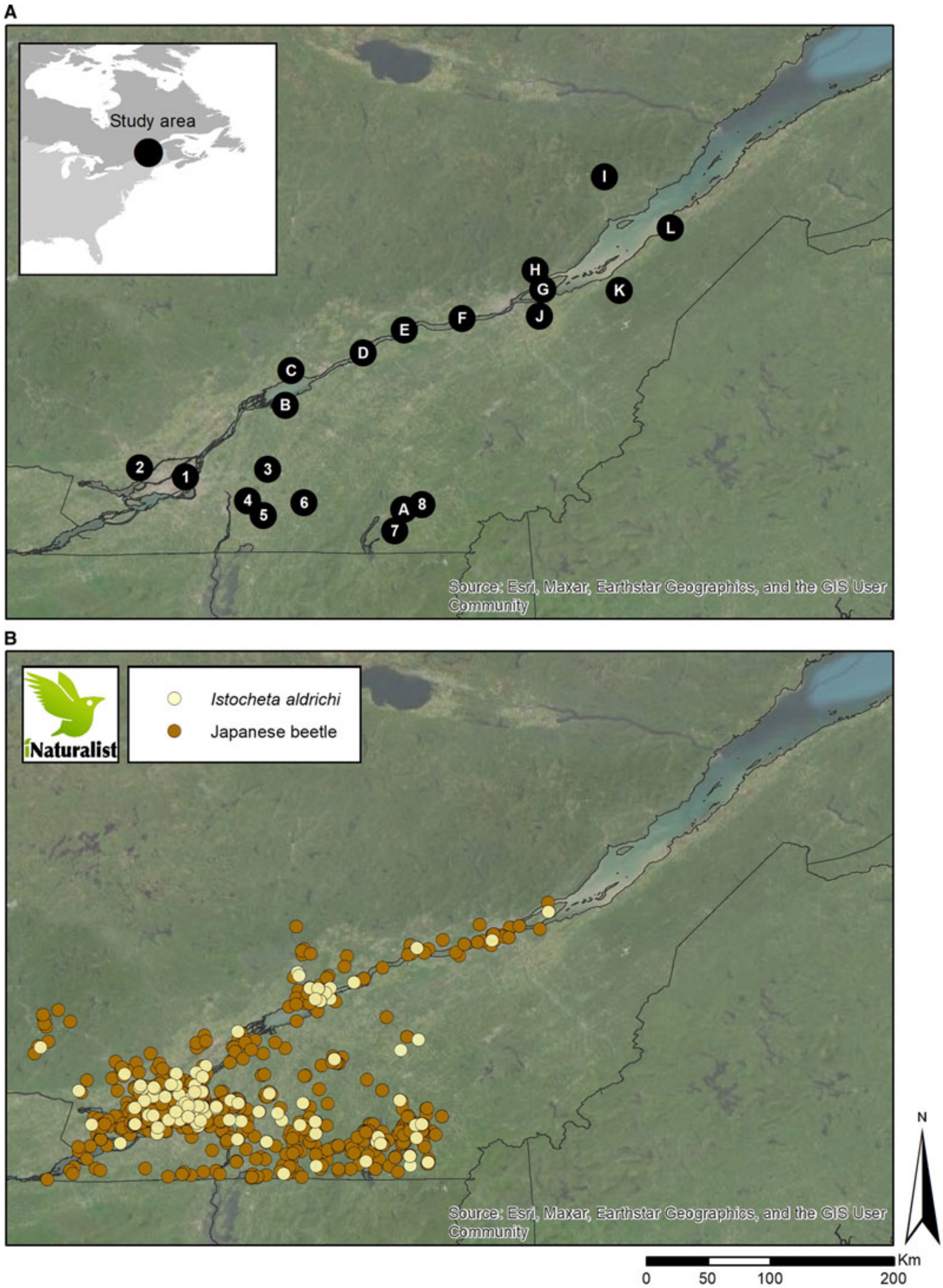

Figure 1. **A**, Sampling locations in southern Québec in 2018–2019 (1–8) and 2022 (1; A–L). **B**, Spatial distribution of the Japanese beetle (orange dots) and *Istocheta aldrichi* (yellow dots) in Québec as of 2022, based on iNaturalist.

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Table 1. Parasitism of Japanese beetles' adults by *Istocheta aldrichi* in eight sampling locations in southern Québec, Canada, in 2018–2019. Site numbers correspond to Figs. 1A and 2. For each sampling period, $\%_{Em}$ corresponds to the estimated cumulative emergence of Japanese beetles based on the degree-day model of Ebbenga *et al*. (2022; see Methods section for details). $Max_{I.a.}$ – maximum parasitism rate by *I. aldrichi*; $Date_{Max}$ – date for $Max_{I.a.}$ estimation, Adj. $Tot_{I.a.}$ – total parasitism rate by *I. aldrichi* over the season, adjusted for missing Japanese beetle collections based on the degree-day model of Ebbenga *et al*. (2022); N – number of Japanese beetles examined for parasitism estimation.

Site	Type	Longitude	Latitude	Year	Sampling period	(%Em)	**$Max_{I.a.}$ (N)**	**$Date_{Max}$**	**Adj. $Tot_{I.a.}$ (N)**
1. Montréal	Botanical garden	−73.57	45.56	2018	4 June–27 August	(0.0–95.7)	25.8 (423)	9 July‡	3.2 (9125)
				2019	11 July–10 October	(0.1–100.0)	19.4 (2435)	29 July	9.5 (11691)
2. Boisbriand	Plant nursery	−73.89	45.63	2018	25 June–24 September	(0.0–99.9)	20.0 (5)	2 July‡	7.6 (185)
				2019	27 May–15 October	(0.0–100.0)	16.7 (6)	15 July	3.9 (382)
3. St-Hyacinthe	Botanical garden	−72.97	45.62	2018	4 July–12 September	(0.4–98.7)	19.2 (1025)	25 July	11.5 (3372)
				2019	11 July–2 October	(0.5–100.0)	23.7 (354)	25 July	15.9 (1575)
4. Ste-Angèle	Resident's garden	−73.11	45.39	2018	26 June–10 September	(0.1–98.8)	33.8 (71)	26 June‡	7.6 (3035)
				2019	5 June–13 October	(0.0–100.0)	18.4 (76)	22 July	5.7 (2120)
5. Farnham	Resident's garden	−73.00	45.28	2018	28 June–5 September	(0.1–98.5)	37.1 (70)	28 June‡	9.1 (4830)
				2019	5 June–26 September	(0.0–99.9)	20.9 (1204)	25 July	8.7 (7358)
6. Granby	Resident's garden	−72.70	45.37	2018	29 June–6 September	(0.1–98.4)	26.3 (19)	11 July‡	7.4 (465)
				2019	5 June–26 September	(0.0–100.0)	33.3 (3)	12 July	6.0 (468)
7. Ayer's Cliff	Resident's garden	−72.04	45.17	2018	25 June–5 September	(0.0–96.5)	50.0 (20)	2 July ‡	27.3 (565)
				2019	5 June–16 September	(0.0–94.5)	16.8 (202)	25 July	10.5 (840)
8. Sherbrooke	Educational farm	−71.85	45.36	2018	20 June–19 September	(0.0–99.4)	25.5 (513)	25 July	15.7 (3230)
				2019	1 July–30 September	(0.0–99.8)	14.1 (313)	5 August	5.9 (2233)

‡$Date_{Max}$ corresponds to earliest captures of Japanese beetles.

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above the ground. In 2018 and 2019, traps were deployed no later than 4 July and 11 July, respectively (Table 1), when Japanese beetles became active in the field, based on information from collaborators. Sampling ended in late August–early September in 2018 and late September–early October in 2019, when Japanese beetle populations were declining (Table 1). The same lures were used because their attractiveness does not decrease throughout the season (Ladd *et al.* 1974). Traps were emptied once a week, and beetles were sent to the Institut de Recherche en Biologie Végétale (Montréal, Québec, Canada) and frozen at −20 °C in plastic bags until processing. For each sample, all beetles were counted and examined under a stereomicroscope for the presence of *I. aldrichi* eggs to estimate weekly and total seasonal parasitism rates (*i.e.,* number of beetles bearing at least one parasitoid egg/total number of beetles × 100%).

For each location, total parasitism rates over the course of the season were calculated based on the total number of Japanese beetles trapped. Because we suspected that we missed some beetles in early and late season, we used the degree-day model of Ebbenga *et al.* (2022) to estimate the proportion of unsampled Japanese beetles. For each location, we used the weather generator of BioSIM 11 (cfs.nrcan.gc.ca/projects/133) to estimate daily minimum and maximum air temperatures. Temperatures for each location were estimated through distance-weighted interpolation using up to eight weather stations nearest to each of the sampling locations (Régnière and St-Amant 2007). For each sampling location and year, simple degree-day accumulations were calculated using a biofix date of 1 January and lower and upper thresholds of 15.0 and 21.7 °C, respectively (Ebbenga *et al.* 2022). Accumulated degree days for each sampling date were then converted to the expected proportion of emerged Japanese beetles using Ebbenga *et al.*'s (2022) equation (1). These proportions of expected unsampled Japanese beetle captures were then used to adjust total parasitism rates by *I. aldrichi* throughout the season.

Parasitism along the St. Lawrence River

In 2022, parasitism of *P. japonica* by *I. aldrichi* was monitored during the seasonal peak activity of *I. aldrichi*, from early July to early August, at 13 sampling sites along the St. Lawrence River (latitudinal gradient; Fig. 1A; Table 2). Insects were sampled on raspberry farms, except for at Site 1 (Montréal Botanical Garden) and Site A, which consisted of an open area with wild raspberry bushes, raspberry plants being commonly exploited by Japanese beetles North America (Burkness *et al.* 2022). At each location, one Bioprotec® trap was positioned near raspberries on a wooden pole 1 m above the ground. Traps were emptied twice during the sampling period (Table 2). All the samples were processed as described for previous years.

iNaturalist observations

iNaturalist (http://www.inaturalist.org) is an open-access platform where anyone, including naturalists and scientists, can share their observations of biodiversity. We accessed the database on 3 April 2023 to document the occurrence and distribution of naturalised Japanese beetle and its parasitoid, *I. aldrichi*, in the province of Québec using the following search terms: "*Popillia japonica*" and "*Istocheta aldrichi*". We downloaded and mapped the geographic coordinates of all "Research Grade" observations from iNaturalist using the package *rinat* (Barve and Hart 2022) for R (R Core Team; https://www.R-project.org).

Results

Parasitism in southern Québec

A total of 24 807 and 26 667 adult Japanese beetles were captured in baited traps in 2018 and 2019, respectively. Total beetle abundances among site–years are shown in Table 1. Japanese beetles first appeared in traps in late June–early July, and population densities generally increased

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Table 2. Parasitism of Japanese beetle adults by *Istocheta aldrichi* in 13 sampling locations along the presumed expansion front of *I. aldrichi* in Québec, Canada, in 2022. Site numbers correspond to Fig. 1A. For each site and sampling period, $P_{I.a.}$ is the parasitism rate by *I. aldrichi* over the period, and N is number of Japanese beetles examined for parasitism estimations.

Sites	Long.	Lat.	Sampling period	$P_{I.a.}$	(N)
1. Montréal	−73.57	45.56	7 July–21 July	23.7	(1832)
			21 July–4 August	17.4	(2737)
A. Sherbrooke	−71.98	45.33	6 July–20 July	4.6	(1693)
			20 July–3 August	17.6	(1714)
B. Pierreville	−72.84	46.08	7 July–21 July	17.4	(476)
			21 July–4 August	13.0	(843)
C. Yamachiche	−72.80	46.34	7 July–21 July	5.8	(1997)
			21 July–4 August	5.7	(1709)
D. Batiscan	−72.27	46.46	7 July–21 July	16.8	(380)
			21 July–4 August	16.7	(1174)
E. Deschambault	−71.97	46.63	7 July–21 July	12.3	(406)
			21 July–4 August	10.7	(929)
F. Neuville	−71.55	46.71	7 July–21 July	5.3	(243)
			21 July–4 August	10.3	(292)
G. Île d'Orléans	−70.99	46.83	7 July–21 July	–	(0)
			21 July–4 August	–	(0)
H. Château–Richer	−71.02	46.97	7 July–21 July	–	(0)
			21 July–4 August	–	(0)
I. St-Urbain	−70.52	47.55	7 July–21 July	–	(0)
			21 July–4 August	–	(0)
J. Beaumont	−70.99	46.83	8 July–21 July	–	(0)
			21 July–4 August	0.0	(1)
K. Cap-St-Ignace	−70.41	47.02	8 July–21 July	–	(0)
			21 July–4 August	–	(0)
L. La Pocatière	−70.04	45.33	8 July–21 July	–	(0)
			21 July–4 August	–	(0)

rapidly for several weeks before declining more gradually (Fig. 2). Overall, seasonal abundances were more or less unimodal, with maxima occurring from mid-July to early August.

In 2018 and 2019, parasitised Japanese beetles were found at all sites. The appearance of *I. aldrichi* eggs on its host in late June coincided with the emergence of the first Japanese beetles. In all sites and for both years, with the exception of Sherbrooke, maximum parasitism (Table 1) occurred during the first two weeks following Japanese beetle emergence before declining gradually. Parasitoid eggs were rarely observed after mid-August (Fig. 2). Over all sites and sampling dates, maximum parasitism levels ranged from 14.1 to 50%, with the caveat of small sample size ($N < 30$) in most sites early in the season (Table 1; Fig. 2). Total parasitism rates over the course of the two years ranged from 3.9% in Boisbriand in 2019 to 27.3% in Ayer's Cliff in 2018 (Table 1).

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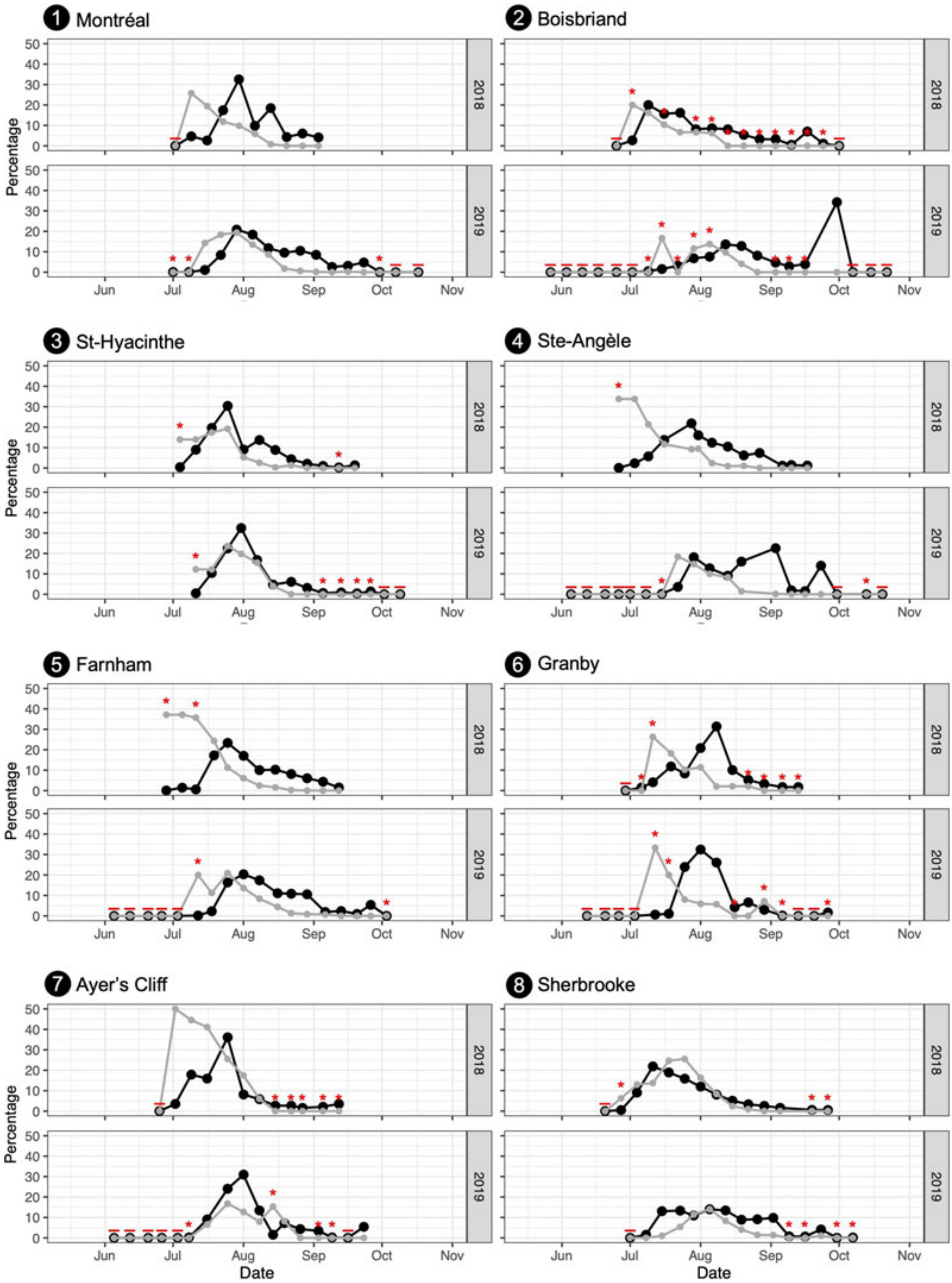

Figure 2. Seasonal distribution of the relative (%) abundance of *Popillia japonica* (-•-) and percent parasitism by *Istocheta aldrichi* (-•-) in eight locations in southern Québec, Canada, in 2018–2019. Site numbers are as in Table 1 and Fig. 1A. Records with low sample sizes (1 < N > 30) are indicated with a * symbol. Records with no Japanese beetles are indicated with a – symbol.

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Parasitism along the St. Lawrence River

In 2022, surveys indicated that both the Japanese beetle and its parasitoid were present in raspberry fields from Montréal (southwest) to Neuville (northeast; Table 2). However, a single unparasitised beetle was trapped in Beaumont (site K), 60 km east of the current front of expansion of the Japanese beetle along the St. Lawrence River (Table 2). Parasitism rates over the sampling period ranged from 4.6 to 23.7%.

iNaturalist observations

The iNaturalist website reported a total of 1792 and 167 occurrences of Japanese beetles and *I. aldrichi*, respectively, between 2003 and 2022 in the province of Québec. The first observations of the Japanese beetle and *I. aldrichi* were in 2003 and 2014, respectively. These observations, presented in Fig. 1B, indicate that, as of 2022, the Japanese beetle was present throughout southern Québec and along the St. Lawrence River, up to Ile d'Orléans (46.8306, –70.9934), north of Quebec City. The reported observations of *I. aldrichi* in iNaturalist are spatially similar to that of the Japanese beetle within the province.

Discussion

This study aimed to explore ecological aspects of the early establishment in Québec, Canada, of the association between two exotic and now naturalised insects: the Japanese beetle, *P. japonica*, and the tachinid parasitoid, *I. aldrichi*. Our results indicate that (1) *I. aldrichi* is well spread in most areas where the Japanese beetle is present in southern Québec, (2) parasitism mostly occurs from late June to mid-July, before the peak emergence of Japanese beetle populations, and (3) levels of total seasonal parasitism ranged from 3.9 to 27.3% across sampled sites in 2018, 2019, and 2022.

The surveys conducted in eight locations in 2018 and 2019 and 13 in 2022, combined with the information retrieved from iNaturalist, show that the Japanese beetle and its parasitoid are widespread in Québec. There is no comprehensive record of the spread and invasion routes of the Japanese beetle in Canada. Data from the Canadian Food Inspection Agency indicate that in 1996, populations of the Japanese beetle were restricted to five regulated areas in southern Québec within the boundaries of the regional county municipalities (MRC) of Brome-Missisquoi, Le Haut-Richelieu, Champlain, Roussillon, and Le Bas-Richelieu, with no observations on the north shore of the St. Lawrence River and northeast of the area of Lac St. Pierre (Canadian Food Inspection Agency 1996). In 2005, the beetle had expanded its distribution to 28 regulated areas, up to the Centre-du-Québec region (Bois-Francs; Canadian Food Inspection Agency 2005). In 2006, the Canadian Food Inspection Agency stopped monitoring the Japanese beetle in Québec (Canadian Food Inspection 2006). Our survey and the information retrieved from iNaturalist constitute the most updated observations on the current distribution of the Japanese beetle. In Québec, *I. aldrichi* was first detected (a single mention) in Granby (see location on Fig. 1) in 2009, and the present study indicates that it rapidly spread through other parts of the province where the Japanese beetle is present.

In Japan, the parasitoid–host's life cycle is well synchronised, and parasitism begins upon the spring emergence of the first beetles and extends through most of the period of host activity (King 1931). Our trap captures in 2018–2019, however, suggest a mismatch in the spring emergence of diapausing Japanese beetles and *I. aldrichi* in Québec. This results in early emerging beetles experiencing the highest levels of parasitism, followed by a long period of less vulnerability to parasitism when beetle populations are peaking. Such a pattern has been observed in several areas in North America following the repeated introductions of *I. aldrichi* in 1920–1950 (King 1931; Fleming 1968; Shanovich *et al.* 2019). Postrelease monitoring revealed that *I. aldrichi* emerges approximately 2–3 weeks before the peak of its host's emergence (King 1931). This host–parasitoid phenological asynchrony could greatly reduce the effectiveness of *I. aldrichi* as a biological control agent of the Japanese beetle.

Clausen *et al.* (1927) and King (1931) concluded that *P. japonica* is of minor economic importance in its native range in Japan. This was attributed to biological control exerted by multiple natural enemies, the most effective of which was thought to be *I. aldrichi* (Clausen *et al.* 1927). Those authors reported total seasonal parasitism of Japanese beetles by *I. aldrichi* fluctuating between 20 and 90% in Hokkaido and 50% on the island of Honshu. In North America, total seasonal parasitism has rarely been quantified. To our knowledge, the only published records come from the studies of Shanovich *et al.* (2019, 2021) in Minnesota, where approximately 10 and 9.3% parasitism was observed in urban areas and apple orchards, respectively. Our sampled sites in Québec were distributed widely across the province, covering an estimate of 35 000 km^2, and total seasonal parasitism varied from 3.9 to 27.3% across sites and years.

Our results provide an overview of the early establishment of the relationship between the Japanese beetle and *I. aldrichi* in Québec. Surprisingly, despite the pest status of the Japanese beetle and given the repeated efforts to release and redistribute *I. aldrichi* in North America, postrelease data are insufficient to understand several important aspects of their ecology, such as their phenology, response to climatic conditions, and seasonal population dynamics. This information is essential not only to prevent further Japanese beetle introductions but also to maximise the management of established pest populations through a better understanding of the impact of naturalised *I. aldrichi* populations within the continent. Ongoing research in Canada aims at providing quantitative analyses of the seasonal population dynamics of the Japanese beetle–*I. aldrichi* association, the continuous spread of both insects, the effectiveness of *I. aldrichi* as a biological control agent, and its redistribution in new invaded areas, as well as information on the biology of *I. aldrichi* to complement the pioneering work conducted a century ago by Drs. Clausen, King, and Teranishi.

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Competing interests. The authors declare they have no competing interests.

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