

First exploration of parasitoids of *Drosophila suzukii* in South Korea as potential classical biological agents

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Abstract The invasive spotted wing drosophila, *Drosophila suzukii* Matsumura (Dipt.: Drosophilidae), a native of East Asia, has widely established in North America and Europe, where it is a serious pest of small and stone fruit crops. The lack of effective indigenous parasitoids of *D. suzukii* in the recently colonized regions prompted the first foreign exploration for co-evolved parasitoids in South Korea during 2013 and 2014. We collected the larval parasitoids *Asobara japonica* Belokobylskij, *A. leverii* (Nixon) and *A. brevicauda* Guerrieri & van Achterberg (Hym.: Braconidae), *Ganaspis brasiliensis* (Hering), *Leptopilina japonica japonica* Novković & Kimura and *L. j. formosana* Novković & Kimura (Hym.: Figitidae); and the pupal parasitoids *Pachycrepoideus vindemiae* (Rondani) (Hym.: Pteromalidae) and *Trichopria drosophilae* Perkins (Hym.: Diapriidae). From UC Berkeley quarantine records, percentage parasitism ranged from 0 to 17.1 % and varied

by geography, season, and collection methods. *Asobara japonica* was the most common parasitoid species. Higher numbers of parasitoids were reared from field-picked fruit as opposed to traps baited with uninfested fruit. Quarantine bioassays confirmed that *A. japonica*, *G. brasiliensis*, *L. j. japonica*, *P. vindemiae*, and *T. drosophilae* developed from *D. suzukii*. Female individuals of the endoparasitoid, *A. japonica*, were larger when reared on the larger *D. suzukii* larvae compared with those reared on the smaller larvae of *D. melanogaster* Meigen. Larger parasitoid size was associated with longer developmental time. Several of the South Korean parasitoid species have the potential for use in classical biological control and may contribute to the suppression of *D. suzukii* in the newly invaded regions.

Keywords Biological control · Invasive species · Parasitoid · Spotted wing drosophila

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Key message

- Spotted wing drosophila is an invasive fly pest that damages soft- and thin-skinned fruit crops.
- A classical biological control program was initiated by surveys for spotted wing drosophila parasitoids in South Korea during 2013 and 2014.
- Seven known and one new parasitoid species were reared from spotted wing drosophila, with field percent parasitism by larval parasitoids ranging from 0 to 17.1 %.
- Quarantine studies are ongoing to select the most suitable natural enemies for release in North America and Europe.

Introduction

Spotted wing drosophila, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), is a pomace fly distributed natively across eastern China, Japan, the Korean Peninsula, and other regions in Southeastern Asia (Hauser 2011; Kanzawa 1939). In North America, the fly was first detected in 2008 in California (Bolda et al. 2010) and was subsequently reported in most fruit growing regions in the continental United States (US) and Canada (Asplen et al. 2015; Emiljanowicz et al. 2014; Walsh et al. 2011). *Drosophila suzukii* was also detected in Spain and Italy in 2008, and soon thereafter reported in other European countries (Calabria et al. 2012; Cini et al. 2014); most recently, the fly was reported in Brazil (Deprá et al. 2014). *Drosophila suzukii* is considered a key pest of soft- and thin-skin fruits such as blueberries, cherries, figs, raspberries, and strawberries in all of these newly invaded regions (Burrack et al. 2013; Kinjo et al. 2013; Lee et al. 2011; Mitsui et al. 2006; Yu et al. 2013).

The pest status of *D. suzukii* is attributed to the female's serrated ovipositor (Atallah et al. 2014) which enables oviposition in ripening, rather than over ripe or rotting fruit. While *D. suzukii* is unable to oviposit in fruits with thick, hard, or fuzzy skin, it can oviposit and complete development in some of these fruits when the skin is compromised (e.g., pathogen or insect damage, hail) (Lee et al. 2015; Poyet et al. 2014; Steffan et al. 2013; Stewart et al. 2014; Ioriatti et al. 2015). Additionally, *D. suzukii*'s fast development (a generation in ≈ 10 days at 22 °C) and high reproductive potential (>600 eggs per female) (Emiljanowicz et al. 2014; Tochen et al. 2014) can result in an explosive population increase (Wiman et al. 2014) and significant economic losses to commercial crops (Beers et al. 2011; Goodhue et al. 2011; Walsh et al. 2011). Control efforts in North America currently rely on the use of insecticides that target adult *D. suzukii* (Beers et al.

2011; Bruck et al. 2011). However, insecticide-based programs can be limited by the fact that many host fruits in non-crop habitats act as reservoirs for *D. suzukii* and support its reinvasion into commercial fields (e.g., Klick et al. 2014, 2015).

From this perspective, biological control in non-crop habitats may help suppress regional *D. suzukii* population densities and provide a new tool for reduced risk and environmentally sound management strategies. Worldwide, over 50 hymenopteran parasitoid species attack drosophilid species. In most cases, these parasitoids attack their host in the late-larval or pupal developmental stages (Carton et al. 1986). The majority of the larval parasitoids are braconids in the genus *Asobara* and figitids in the genera *Leptopilina* and *Ganaspis*, and they predominantly attack host fly species found in fermenting substrates (Asplen et al. 2015). There are also two common pupal parasitoids, *Pachycrepoideus vindemiae* Rondani (Pteromalidae) and *Trichopria drosophilae* Perkins (Diapriidae). These larval and pupal parasitoid species undoubtedly play a role in population suppression of some drosophilid species. The effectiveness of these parasitoids against *D. suzukii* in its invaded regions has, however, not been adequately studied and, where surveys have been conducted, there appears to be limited parasitism rates of *D. suzukii* in terms of economic suppression (Miller et al. 2015).

Kacsoh and Schlenke (2012) studied 24 strains or populations of parasitoid species for their effectiveness against *D. suzukii*, and report that among 12 larval parasitoid species tested, only *Asobara japonica* Belokobylskij (from Japan), *A. citri* (from Ivory Coast), and two strains of *Ganaspis* sp. (from Hawaii and Florida) could complete development on *D. suzukii*. Of the tested larval parasitoid species, *A. japonica* had the highest rate of successful development. In most cases, the larval parasitoid species' failure to develop in *D. suzukii* was explained by the host's immune resistance (Kacsoh and Schlenke 2012; Poyet et al. 2013). Similarly, in another laboratory study, Chabert et al. (2012) trialed five parasitoid species that are commonly found in Europe attacking drosophilids (*A. tabida* Nees, *Leptopilina heterotoma* (Thomson), *L. bouvardi* Barbotin et al., *T. cf. drosophilae*, and *P. vindemiae*) and found that only the two pupal parasitoids (*T. cf. drosophilae* and *P. vindemiae*) successfully developed on *D. suzukii*. Field surveys also suggest that parasitoids attacking drosophilid species resident in the US and Europe have not readily adapted to the invasive *D. suzukii*. Typically in field surveys, only the pupal parasitoids *T. drosophilae* and *P. vindemiae* have been reported to attack *D. suzukii* in Italy (Rossi Stacconi et al. 2013), Spain (Gabarra et al. 2015), and the US (Miller et al. 2015; Wang et al. 2016). One exception is a strain of *L. heterotoma* from northern Italy that was recovered from *D. suzukii* (Rossi Stacconi et al. 2015).

The lack of effective biological control in the newly invaded range of *D. suzukii* led to the initiation of a classical biological control program. Genetic analyses suggest that East Asia is the region of origin for *D. suzukii* populations that invaded North America (Adrion et al. 2014; Chiu et al. 2013; Ometto et al. 2013), and this is the focal region for our initial and planned collections. Information on parasitoids associated with *D. suzukii* and other drosophilids in Asia is however limited to reports from Japan. For example, Mitsui et al. (2007) reported 15 parasitoid species collected from fruit-baited traps, these included *A. japonica*, *A. tabida*, *A. rossica* Belokobylskij, *A. rufescens* (Forster), *A. pleuralis* (Ashmead) *A. leverii* (Nixon), *L. heterotoma*, *L. victoriae* Nordlander, *Ganaspis xanthopoda* (Ashmead), and *P. vindemiae*. Among the 15 species, only *A. japonica*, *A. tabida*, and *G. xanthopoda* emerged from *D. suzukii*. The aim of this study was to determine the presence and biological suitability of Asian parasitoids of *D. suzukii* to be considered for quarantine examination and potential field release in North America and Europe. In South Korea, no reports of *D. suzukii*-related damage have been made and this species has not been considered a pest (Asplen et al. 2015). We describe herein the first collection efforts in South Korea and the initial quarantine studies on the imported material.

Materials and methods

Collection sites and methods

The South Korean sample locations were selected based on a pre-collection exploration in 2011 (J. Miller, H. Riedl and Y. Song, pers. comm.). Surveys for frugivorous *Drosophila* parasitoids in South Korea were conducted at 10 locations and three provinces during August 2013 (J. Miller, B. Miller, H. Riedl and P. Shearer), and at 18 locations and four provinces from June to July 2014 (J. Miller and B. Miller), aided in each year by collaborators in South Korea (Fig. 1).

During the expeditions, parasitoids were field-surveyed using uninfested-fruit-baited traps deployed for 4–7 days and via the collection of commercial or wild host fruits with a high probability of infestation as determined primarily by the presence of adult flies. The uninfested-fruit-baited traps were based on previous collections by Rossi Stacconi et al. (2013). For each trap, 100–200 g of mixed fruits (banana, blueberry, fig, melon, and peach) was placed in a 162-mL plastic cup. Each cup was fitted with a lid and ten 0.8-cm diameter entrance holes along the cup rim to allow entry of ovipositing flies and parasitoids, but prevent the entry of other animals or larger insects. The plastic cup was placed inside a 500-mL plastic square tub

and the ‘cup-in-tub’ set-up was then placed inside an orange delta trap (Suterra, LLC, Bend, OR). The cup-in-tub method provided a dry microhabitat for larvae to pupate when the fruit started decaying. Upon collection of the baited traps, the square tub was covered with a screened lid and the tubs were kept at room temperature (22–28 °C) until pupation. Field-collected fruits were separately placed in 162-mL cups on filter paper inside a 500-mL plastic tub until pupation.

In 2013, we primarily used the uninfested-fruit-baited traps, deployed at inland or coastal forests or along the perimeter of crop fields (Table 1). At each collection site, 8–12 traps were hung at shoulder height (1.5 m) from sturdy branches and deployed for 4–7 days. Commercial blackberries (approximately 10 L), damaged pears, apples, peaches, or split grapes were also sampled in four different locations (Table 1). In 2014, we predominantly used fresh-fruit collections of 2–10 L of wild *Rubus* fruits per collection site, as these fruits were still available in these unmanaged habitats during June and July (Table 1). In addition, commercial blackberries were collected from one location (Geochang) and 10 uninfested-fruit-baited traps were placed at another location (Boriamsa) where wild *Rubus* fruits were also collected (Table 1).

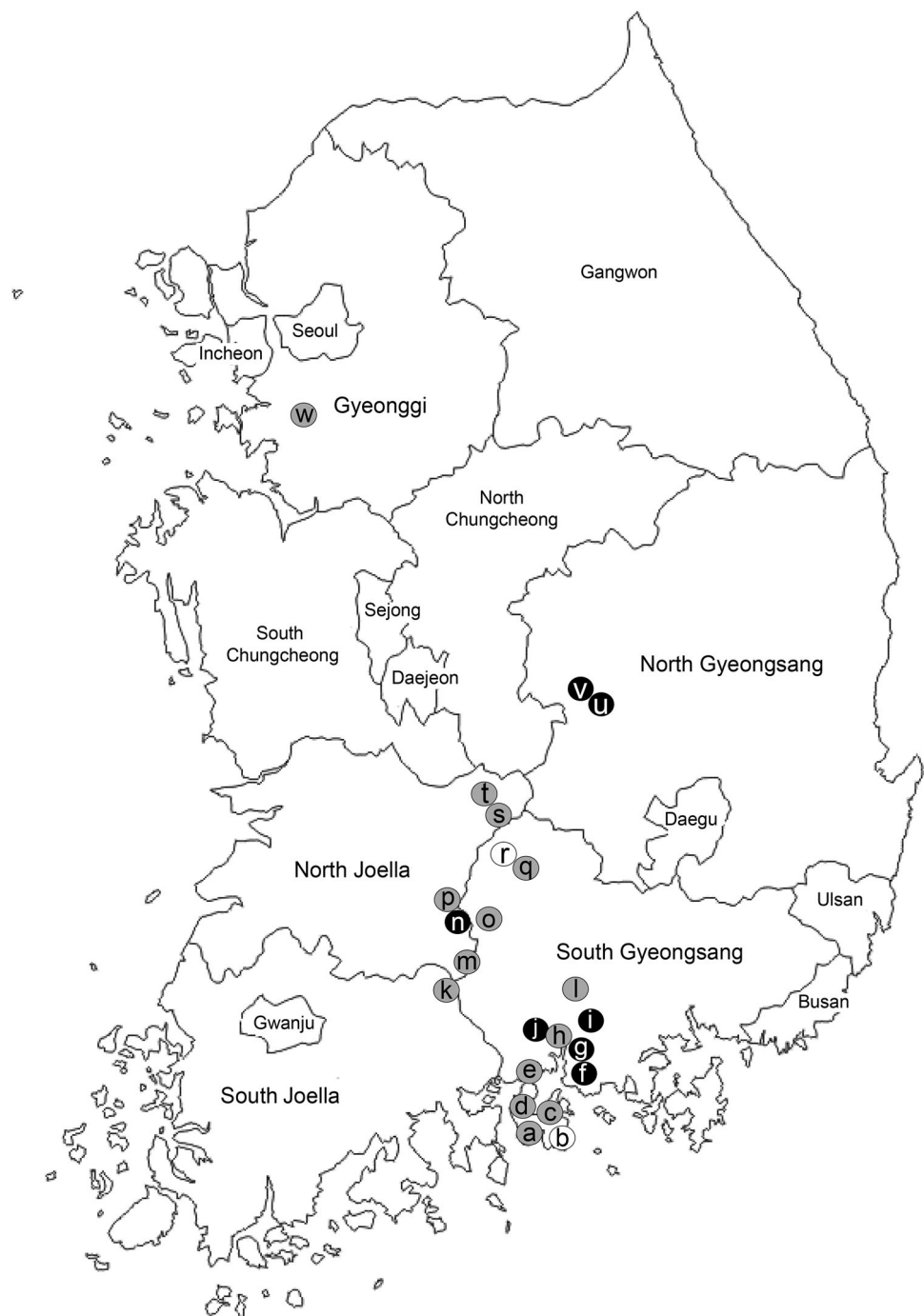
Drosophilid pupae that developed from the field-collected larvae were sorted according to collection or trap location and placed on moist filter papers in 5-cm diameter Petri dishes. The dishes were kept at 4 °C before being packaged for hand-carry to the US. During transportation, the puparia were placed inside a Styrofoam box and kept cool with packaged ice.

Quarantine of imported puparia

Once the Styrofoam box passed through US Homeland Security at San Francisco International Airport, and inspection at the USDA, APHIS, PPQ Plant Inspection Station (permit: P526P-11-03867), imported puparia were processed under controlled conditions (22 ± 3 °C, 12L:12D, 40–70 % RH, and natural light) in quarantine facilities at the University of California, Berkeley. Hosts for imported parasitoid colonies and quarantine evaluation of imported parasitoid species were obtained from laboratory colonies of *D. suzukii* and *D. melanogaster* Meigen (a common host for most parasitoid species attacking drosophilids). The fly colonies originated from field collections in Parlier, California and were maintained on standard corn-meal diets using methods similar to Dalton et al. (2011).

Upon arrival into quarantine, the puparia were sorted to separate those bearing visible signs of parasitism, i.e., visible parasitoid pupae inside the fly puparia. Individual puparia were placed in Eppendorf tubes with a streak of

Fig. 1 Collection locations for drosophilid parasitoids in 2013 (black), 2014 (gray) or both years (white) in South Korea: **a** Namhae Marina; **b** Boriamsa; **c** Ungbongsan; **d** Mangunsan; **e** Kumosan; **f** Sacheon; **g** Guam-Imdo; **h** Jinju city and Gyeongsang; **i** Jinju; **j** Uigoksa and Jinju Heights; **k** Munsusa; **l** Jagulsan; **m** Jeongryeongchi; **n** Namwon; **o** Baekyeonsan; **p** Poyeongsa; **q** Gamaksan; **r** Geochang; **s** Deogyusan; **t** Jeoksangsan; **u** Sangju; **v** Namjangsa; **w** Gunjae Bong and Ban Suk San. Close locations (<5 km) for both years were merged



honey-water provided for emerging adults. Emerged flies were killed and preserved with 95 % alcohol along with empty pupal cases in Eppendorf tubes for later species identification. Emerging female parasitoids were individually placed into vials containing artificial diet and larvae or pupae of *D. suzukii* or *D. melanogaster*. Male wasps emerging from the same location-based samples were coupled with their respective females. Honey-water droplets were provided for the parasitoids and host larvae/

pupae were renewed every 2–3 days. Upon death, individuals of the parental generation of parasitoids were preserved in 95 % alcohol along with their pupal case. Pupae of *D. suzukii* were distinguishable from other *Drosophila* pupae by the presence of a pair of distinct respiratory tubes on the anterior end that was used as a diagnostic character (Kanzawa 1939). Vouchers of the figitids are deposited with the U.S. National Entomological Collection (Washington, D. C.), while other species are deposited in the

Table 1 Number of *D. suzukii* and other drosophilids collected during August 2013 and June to July 2014 explorations in South Korea using different collections methods (fruit-baited traps or collection of fruit from crops or wild habitats) and in different geographic locations

Year	Location ^a	Host habitats	Collection method	Total no. of fly pupae collected	No. of <i>D. suzukii</i> emerged	No. of other drosophilids emerged	
2013	Namjangsa (v)	Inland forest	Fruit bait	477	5	96	
	Sacheon (f)	Hedgerow of rice field	Fruit bait	158	0	111	
	Boriamsa (b)	Coast forest	Fruit bait	433	0	54	
	Geochang (r)	Blackberry farm	Blackberry	826	227	0	
			Fruit bait	467	0	200	
	Uigoksa (j)	Blackberry farm	Blackberry	53	15	0	
			Fruit bait	21	0	7	
	Jinju heights (j)	Peach/ <i>Rubus</i> farm	Fruit bait	446	0	359	
	Guam-Imdo (g)	Coast forest	Fruit bait	11	0	4	
	Jinju (i)	Small farm	Mixed fruit	71	7	9	
	Namwon (n)	Grape farm	Split fruit	293	0	197	
	Sangju (u)	Peach farm	Fallen fruit	21	0	13	
	2014	Gunjae Bong (w)	Inland forest	Wild <i>Rubus</i>	0	0	0
		Bansuksan (w)	Inland forest	Wild <i>Rubus</i>	0	0	0
Baekyeonsan (o)		Inland forest	Wild <i>Rubus</i>	111	0	38	
Poyeongsa (p)		Inland forest	Wild <i>Rubus</i>	2208	648	179	
Jeongryeongchi (m)		Inland forest	Wild <i>Rubus</i>	4374	531	0	
Munsusa (k)		Inland forest	Wild <i>Rubus</i>	516	86	0	
Boriamsa (b)		Coast forest	Wild <i>Rubus</i>	79	29	1	
			Fruit bait	2072	0	246	
Ungbongsan (c)		Coast forest	Wild <i>Rubus</i>	0	0	0	
Namhae (a)		Coast forest	Wild <i>Rubus</i>	0	0	0	
Mangunsan (d)		Coast forest	Wild <i>Rubus</i>	2331	147	21	
Kumosan (e)		Coast forest	Wild <i>Rubus</i>	831	187	0	
Gyeongsang (h)		Inland forest	Wild <i>Rubus</i>	81	35	0	
Jagulsan (l)		Inland forest	Wild <i>Rubus</i>	2855	1002	50	
Gamaksan (q)		Inland forest	Wild <i>Rubus</i>	2124	1222	94	
Deogyusan (s)		Inland forest	Wild <i>Rubus</i>	2198	717	0	
Jeoksangsan (t)		Inland forest	Wild <i>Rubus</i>	24	15	0	
Baekyeonsan (o)		Inland forest	Wild <i>Rubus</i>	0	0	0	
Geochang (r)	Blackberry farm	Blackberry	350	106	0		

^a Collection locations are coded by letters in parenthesis and are shown in Fig. 1

Institute for Sustainable Plant Protection (Portici, Italy) or in the Essig Museum at the University of California (Berkeley, California). Guerrieri et al. (2016) identified all *Asobara* species using both morphological and molecular methods, while all other species were confirmed or identified by ML Buffington.

Additionally, all dead (no adult emergence) pupae were first reconstituted in water and then dissected under the microscope to assess the presence or absence of recognizable fly or parasitoid cadavers. However, it was often difficult to distinguish parasitized pupae from unparasitized pupae when they died at early stages, and in these cases the pupae were classified as ‘unknown.’ The parasitism rate

was estimated as the sum of emerged parasitoids and dead parasitized pupae divided by the sum of emerged flies and parasitoids plus dead parasitized and unparasitized pupae.

Quarantine bioassays

Three parasitoid species, later identified as *A. japonica*, *T. drosophilae*, and *P. vindemiae*, from the collections in 2013, and two additional larval parasitoid species, *Lep-topilina japonica japonica* Novković & Kimura and *G. brasiliensis*, obtained during the 2014 sampling (see Results section), were briefly tested to confirm their ability to attack and develop from *D. suzukii* or from *D.*

melanogaster, chosen as a common alternative host. Two or three-day old larvae (for *A. japonica*, *L. j. japonica*, and *G. brasiliensis*) or two or three-day old pupae (for *T. drosophilae* and *P. vindemiae*) were offered to the parasitoids for 2 days. For each parasitoid species, one female and one male were released into ventilated plastic vials (40 mL) containing hosts infesting artificial diet, or on plastic cups (330 mL) with three *D. suzukii*-infested fruits (blueberries or cherries). Fruits were infested by exposing them, in groups of ten, for 3 h into fly rearing cages containing several adult flies; fruits were then observed under the microscope and the number of eggs per fruit was standardized to three by removing excess eggs using a needle probe. The host density in diet vials varied between 10 and 30 for *D. suzukii* and 40–80 for *D. melanogaster*. Exposed hosts were reared until the emergence of flies or parasitoids.

The most common parasitoid species (see “Results” section), *A. japonica*, was subjected to a no-choice test to determine the parasitoid’s performance on two different-sized hosts. One-week-old mated female wasps were individually exposed to 15 young larvae of either host species in vials with artificial diet for 2 days. The number, sex, and developmental time of emerged parasitoids were recorded. A sub-sample of emerged females was also measured for body size (ovipositor and hind tibia length). Tests consisted of 14 and 24 replicates for *D. suzukii* and *D. melanogaster*, respectively.

Data analyses

Infestation percentages by *D. suzukii* or other drosophilids (estimated as number of emerged adults), and parasitism rates in sampled fruits or in fruit-baited traps were subjected to Analysis of Variance (ANOVA) separately for each collection year. The effect of host species on *A. japonica*’s juvenile development, fertility, and body size was also compared with ANOVA. Prior to the Analysis of Variance (ANOVA), percentage data were logit transformed as needed to normalize the data distribution. All analyses were performed using JMP V11 (SAS 2011, Cary, NC, USA).

Results

Field collections

In 2013, a total of 3266 *Drosophila* puparia were collected in South Korea and imported to the quarantine facilities at Berkeley (Table 1). *Drosophila suzukii* adults emerged mainly from collected blackberries, whereas the uninfested-fruit-baited traps primarily captured other

drosophilid species (Table 1). There were 97 dead parasitized puparia, 728 dead unparasitized puparia, and 1,085 dead puparia for which parasitism status was unknown. Seven parasitoid species (44 individuals) were recovered from drosophilids collected during 2013: *A. japonica* (45.5 % of the recovered parasitoids), *A. leverii* (25 %), *L. j. japonica* (9.1 %), *L. j. formosana* Novković & Kimura (2.3 %), *L. boulandi* (2.3 %), *P. vindemiae* (6.8 %), and *T. drosophilae* (9.1 %). Among these, *L. j. formosana* and *L. j. japonica* emerged only from *D. suzukii*; *A. japonica*, *A. leverii*, and *T. drosophilae* emerged from both *D. suzukii* and other drosophilids; and *L. boulandi* and *P. vindemiae* emerged from other drosophilids (Table 2).

In 2014, a total of 20,358 puparia were collected from a variety of habitats, including wild *Rubus* located in inland forests and blackberries at one commercial farm (Table 1). Collections of wild *Rubus* in five of the locations yielded no drosophilid pupae (Table 1). *Drosophila suzukii* comprised the majority of flies that emerged from *Rubus* but no *D. suzukii* emerged from fruit-baited traps in the same localities (Table 1). From this material, there were 116 dead parasitized puparia, 5271 dead unparasitized puparia, and 8383 dead puparia for which parasitism status was unknown. A total of 181 wasps emerged, representing six species of larval parasitoids: *A. japonica* (60.2 % of the recovered parasitoids), *A. leverii* (2.2 %), *A. brevicauda* (2.8 %), *L. j. japonica* (14.9 %), *L. j. formosana* (1.7 %), and *G. brasiliensis* (18.2 %). Among these, *A. brevicauda* is a new species. Most important for this survey is that *A. brevicauda*, *L. j. japonica*, and *G. brasiliensis* emerged only from *D. suzukii*, whereas *A. japonica* and *A. leverii* emerged from both *D. suzukii* and other drosophilids, and *L. j. formosana* emerged only from other drosophilids (Table 2). The two northern Korean locations (Munsusa and Baekyeonsan) yielded no parasitoids (Table 2). Both the braconids and figitids co-existed in seven locations, but the figitids also occurred in another two locations (Table 2). Up to four different larval parasitoids were reared from *D. suzukii* in a single geographic location.

The percentage of *D. suzukii* among all emerged flies was higher from fruit samples than from fruit-baited traps in both 2013 ($F_{1,76} = 68.7$, $P < 0.001$) and 2014 ($F_{1,192} = 1545$, $P < 0.001$) (Fig. 2a). In 2013, mean parasitism of *D. suzukii* in natural fruit samples (range: 0–17.4 %) was significantly lower than in fruit-baited traps (range: 0.0–33.3 %) ($F_{1,34} = 4.5$, $P = 0.042$), but mean parasitism of other drosophilids was similar between these two sampling methods (range: 0–33.3 % in fruit samples, and 0–39.1 % in fruit traps) ($F_{1,46} = 1.3$, $P = 0.26$) (Fig. 2b, c). In 2014, parasitism of *D. suzukii* was 2.8 ± 0.4 % ($n = 171$) (range: 0–23.5 %) in fruit samples (no *D. suzukii* was found in fruit traps). Parasitism of *D. suzukii* in fruit samples highly varied among locations, but

Table 2 Total number and number of female (in parenthesis) parasitoid species that emerged from collected *D. suzukii* and other drosophilids in South Korea in different geographic locations

Year	Location	Total parasitoids (females)	Parasitoid species ^a	Host	Sampled fruits	
2013	Geochang	8 (8)	<i>A. japonica</i>	Other drosophilids	Banana, fig, and peach bait	
		4 (1)	<i>A. leverii</i>	Other drosophilids	Commercial blackberries	
		3 (1)	<i>L. j. japonica</i>	<i>D. suzukii</i>	Commercial blackberries	
	Jinju	1 (1)	<i>L. j. formosana</i>	<i>D. suzukii</i>	Commercial blackberries	
		2 (1)	<i>A. japonica</i>	<i>D. suzukii</i>	Fallen apple	
		1 (1)	<i>L. j. japonica</i>	<i>D. suzukii</i>	Fallen apple	
	Uigoksa	1 (1)	<i>L. boulandi</i>	Other drosophilids	Fallen apple	
		2 (0)	<i>P. vindemiae</i>	Other drosophilids	Banana, fig, and peach bait	
	Boriamsa	2 (1)	<i>A. leverii</i>	Other drosophilids	Banana, fig, and peach bait	
		10 (10)	<i>A. japonica</i>	Other drosophilids	Banana, fig, and peach bait	
	Namwon	1 (0)	<i>P. vindemiae</i>	Other drosophilids	Grape	
	Namjangsa	1 (0)	<i>A. leverii</i>	<i>D. suzukii</i>	Honeydew, banana, blueberry bait	
		2 (1)	<i>T. drosophilae</i>	Other drosophilids	Honeydew, banana, blueberry bait	
		1 (0)	<i>T. drosophilae</i>	<i>D. suzukii</i>	Honeydew, banana, blueberry bait	
		4 (2)	<i>A. leverii</i>	Other drosophilids	Honeydew, banana, blueberry bait	
	Sangju	1 (0)	<i>T. drosophilae</i>	Other drosophilids	Fallen peach	
	2014	Poyeongsa	3 (0)	<i>A. brevicauda</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>
			1 (1)	<i>A. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>
			2 (1)	<i>G. brasiliensis</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>
Jeongryeongchi		8 (3)	<i>L. j. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
		9 (5)	<i>L. j. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
		2 (1)	<i>G. brasiliensis</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
Boriamsa		2 (2)	<i>A. japonica</i>	<i>D. suzukii</i>	Melon and peach bait	
		87 (86)	<i>A. japonica</i>	Other drosophilids	Melon and peach bait	
		1 (1)	<i>A. leverii</i>	Other drosophilids	Melon and peach bait	
		3 (3)	<i>L. j. formosana</i>	Other drosophilids	Melon and peach bait	
Mangunsan		16 (16)	<i>A. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
		11 (8)	<i>G. brasiliensis</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
Kumosan		1 (1)	<i>A. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
		1 (0)	<i>L. j. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
Gyeongsang		1 (1)	<i>A. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
		4 (2)	<i>G. brasiliensis</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
Jagulsan		1 (1)	<i>A. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
		1 (1)	<i>A. leverii</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
		1 (0)	<i>L. j. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
Gamaksan		2 (1)	<i>G. brasiliensis</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>	
Geochang	6 (5)	<i>L. j. japonica</i>	<i>D. suzukii</i>	Commercial blackberries		
	6 (4)	<i>G. brasiliensis</i>	<i>D. suzukii</i>	Commercial blackberries		
Deogyusan	2 (1)	<i>A. leverii</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>		
	2 (0)	<i>A. brevicauda</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>		
	2 (2)	<i>L. j. japonica</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>		
	6 (4)	<i>G. brasiliensis</i>	<i>D. suzukii</i>	Wild <i>Rubus</i>		

^a Parasitoid families (genus and species) are Braconidae (*Asobara japonica*, *A. leverii*, and *A. brevicauda*); Figitidae (*Leptopilina japonica japonica*, *L. j. formosana*, *G. brasiliensis*); Pteromalidae (*Pachycrepoideus vindemiae*); and Diapriidae (*Trichopria drosophilae*)

the overall parasitism by braconids (range: 0–10.5 %) was similar to that by figitids (0–8.8 %) (Fig. 3). Mean parasitism of other drosophilids was higher in fruit traps (range: 0–33.3 %) than in fruit samples (range: 0–12.5 %) ($F_{1,48} = 22.0$, $P < 0.001$) (Fig. 2b, c).

Quarantine rearing and *Asobara japonica* performance

Of the eight parasitoid species, we were able to establish colonies of five species for further testing in quarantine: *A. japonica*, *L. j. japonica*, *G. brasiliensis*, *T. drosophilae*, and *P. vindemiae*. We were unable to develop colonies of *A. leverii*, *L. j. formosana*, and *A. brevicauda*, because we either did not collect any females (*A. brevicauda*) or collected too few females during any single collection period (*A. leverii*, and *L. j. formosana*) (Table 2). We additionally reared some males and one female *L. boulandi* from

drosophilids other than *D. suzukii*. The limited reared material prevented the development of a colony.

Each of the five tested parasitoid species (*A. japonica*, *L. j. japonica*, *G. brasiliensis*, *T. drosophilae*, and *P. vindemiae*) was able to attack and develop from both *D. suzukii* and *D. melanogaster* cultured on artificial diet or fruits (Table 3). Detailed quarantine studies are ongoing, but initial screening showed that the numbers of offspring produced per *A. japonica* female were similar between *D. suzukii* (8.0 ± 0.7) and *D. melanogaster* (6.9 ± 0.7) ($F_{1,37} = 1.1$, $P = 0.311$). However, female parasitoids developed faster on *D. melanogaster* (27.1 ± 0.2 days) than on *D. suzukii* (25.9 ± 0.1 days) ($F_{1,303} = 19.5$, $P < 0.001$), but perhaps as a consequence females reared from *D. melanogaster* larvae were smaller than those reared from *D. suzukii* (hind tibia length: $F_{1,50} = 28.4$, $P < 0.001$; ovipositor length: $F_{1,50} = 21.6$, $P < 0.001$, Fig. 4).

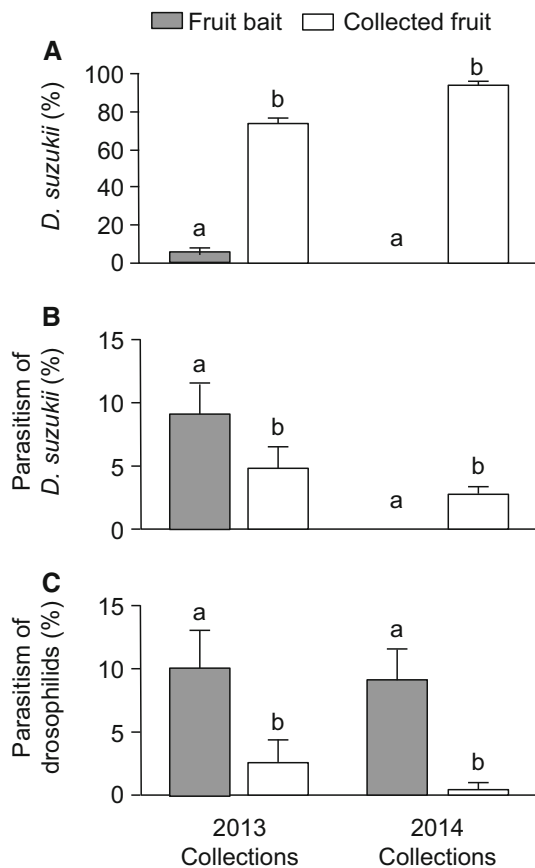


Fig. 2 Effect of sampling methods (fruit trap vs. fruit sample) on (a) the percentage of *D. suzukii* that emerged, (b) parasitism of *D. suzukii* or (c) other drosophilid species during the 2013 and 2014 exploration in South Korea. Data were pooled from all locations; values are mean \pm SE and different letters above the bars indicate significant difference between the two different methods within each year (ANOVA, $P < 0.05$)

Discussion

The current study is the first report of a foreign exploration effort for Asian parasitoids of *D. suzukii* in part of its native range. Six species of larval parasitoids (*A. brevicauda*, *A. japonica*, *A. leverii*, *L. j. japonica*, *L. j. formosana*, and *G. brasiliensis*) and one pupal parasitoid (*T. drosophilae*) were recorded from *D. suzukii* in South Korea. Another pupal parasitoid species, *P. vindemiae*, was field-collected from drosophilid species other than *D. suzukii* in South Korea, but it was able to attack and develop on *D. suzukii* in quarantine. Colonies of five out of eight parasitoid

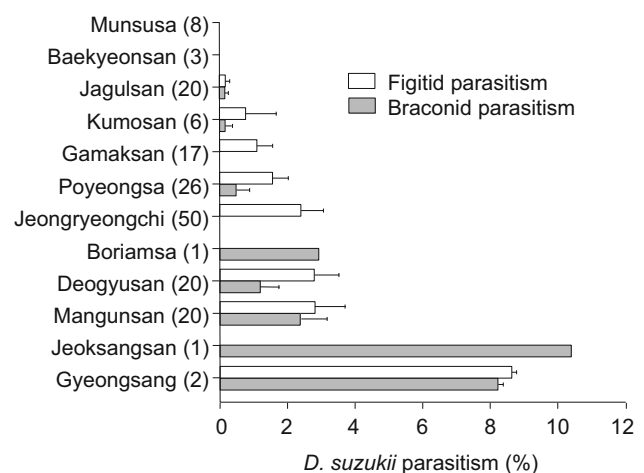


Fig. 3 Mean (\pm SE) parasitism of *D. suzukii* by braconids (*Asobara*) and figitids (*Leptopilina* and *Ganaspis*) from wild *Rubus* in different locations during the 2014 exploration in South Korea; numbers in brackets after each collection site refer to number of samples collected

Table 3 Numbers of host flies and parasitoids emerged in quarantine rearing of three larval parasitoids (*A. japonica*, *L. j. japonica*, and *G. brasiliensis*) and two pupal parasitoids (*P. vindemiae* and *T.*

drosophilae) imported from South Korea when exposed to hosts in different media (artificial diet or different fruit species, *n* is the number of replicates for each parasitoid, host and media combination)

Parasitoid species	Host species	Host medium	<i>n</i>	Emerged flies	Emerged parasitoids	Wasps per vial
<i>A. japonica</i>	<i>D. melanogaster</i>	Diet	6	195	40	1♀1♂
	<i>D. suzukii</i>	Blueberry	11	3	7	1♀1♂
	<i>D. suzukii</i>	Diet	9	7	16	1♀1♂
<i>L. j. japonica</i>	<i>D. melanogaster</i>	Diet	7	197	29	1♀1♂
	<i>D. suzukii</i>	Cherries	10	17	31	1♀1♂
	<i>D. suzukii</i>	Diet	9	154	34	1♀1♂
<i>G. brasiliensis</i>	<i>D. melanogaster</i>	Diet	7	258	19	1♀1♂
	<i>D. suzukii</i>	Cherries	10	31	17	1♀1♂
	<i>D. suzukii</i>	Diet	9	190	20	1♀1♂
<i>P. vindemiae</i>	<i>D. melanogaster</i>	Diet	3	58	28	1♀
	<i>D. suzukii</i>	Blueberry	2	0	2	1♀
	<i>D. suzukii</i>	Diet	2	3	3	1♀
<i>T. drosophilae</i>	<i>D. melanogaster</i>	Diet	8	205	90	1♀1♂
	<i>D. suzukii</i>	Blueberry	4	14	3	1♀1♂
	<i>D. suzukii</i>	Diet	4	1	22	1♀1♂

species were successfully established using *D. suzukii* as host. *G. brasiliensis* was recently re-described as a new combination by Buffington and Forshage (2016).

The estimated parasitism rates varied largely without any clear pattern of location, sampling method, or site. However, parasitism by these larval parasitoids could be underestimated for several reasons. First, at the time when fruits were field-collected, parasitized larvae could have already left the fruits and pupated in the soil, while eggs and young larvae may not have yet been attacked. When these fruits were brought to the South Korean laboratories

where the pupae were isolated for shipment to California, there would have already been a bias against pupal parasitoids because many of the larval-pupal parasitoids might have already exited the host fruit. A more precise estimate of the parasitism would be to collect only those pupae that pupated within 1–2 weeks (i.e., when they were at the suitable larval stages at the time of collection) following the collection. Second, mortalities of the imported pupae were high, partly because all collected materials had to be completely sealed during the transposition resulting in mold growth within the Petri dishes and our observation of numerous dead pupae from unknown factors.

In our South Korean collections, *A. japonica* was the most commonly recovered parasitoid. It was collected in four South Korean provinces and in particular it was recovered in 3 of 10 sampled sites in 2013 and 6 of 18 sampled in 2014. Moreover, 128 *A. japonica* specimens were obtained out of the 141 total *Asobara* spp. that emerged in the quarantine laboratory. These results agree with those obtained in the few previous studies of Asian drosophilid parasitoids, *A. japonica* is the most common and widespread parasitoid and is capable of parasitizing a number of *Drosophila* species (Ideo et al. 2008; Mitsui et al. 2007; Mitsui and Kimura 2010). Nomano et al. (2015) investigated the host use of eight Japanese *Asobara* species; six of these species (*A. japonica*, *A. tabida*, *A. rossica*, *A. rufescens*, and two unidentified *Asobara* spp.) emerged from *D. suzukii* breeding on wild *Cerasus* and *Vaccinium* fruits. In our survey, *A. japonica* was commonly collected from *D. suzukii* in wild *Rubus*. Interestingly, based on adult

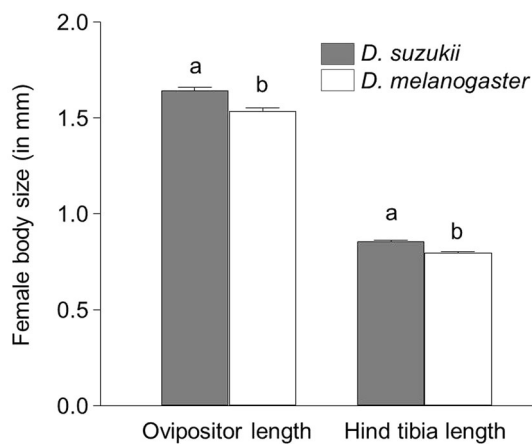


Fig. 4 Body size of developed female *A. japonica* from *D. suzukii* and *D. melanogaster*: different letters above the bars indicate significant difference between different host treatments (ANOVA, $P < 0.05$)

emergence in the quarantine, the *A. japonica* populations collected in our study were 99.8 % female. Similarly, populations of *A. japonica* on the main islands of Japan were parthenogenetic, whereas those in the subtropical islands were sexually reproducing (Mitsui et al. 2007). However, earlier work by Mitsui et al. (2007) and our study may not be directly comparable as the earlier Japanese survey used banana fruit-baited traps, which tend to attract numerous drosophilids in general, but fewer *D. suzukii* (XG Wang pers. observ.). On the other hand, recent studies reported variations in genetic, physiological, or ecological traits among different geographic populations of *A. japonica*, showing a high degree of geographic adaptations to various host habitats (Murata et al. 2009).

With the exception of *A. japonica*, there is little information on the parasitoid species reared in terms of their geographic distribution in Asia or their host species range. Kasuya et al. (2013) reported three species (*L. japonica*, *Ganaspis* sp., and one unidentified *Asobara* species) from *D. suzukii* on wild cherry fruit (*Prunus donarium* Sieb.). The *Ganaspis* sp. strain obtained from *D. suzukii* exhibits a high level of specificity for *D. suzukii* and was referred to *suzukii*-associated type of *G. xanthopoda* (Kasuya et al. 2013), while other stains do not appear to have the same level of specificity (Mitsui and Kimura 2010). The two generalist pupal parasitoids *T. drosophilae* and *P. vindemiae* are cosmopolitan (Carton et al. 1986; Chabert et al. 2012; Gabarra et al. 2015; Kacsoh and Schlenke 2012; Rossi Stacconi et al. 2015). As expected, these parasitoid species were found in South Korea and readily developed on *D. suzukii* in the quarantine. In the current study, all three species of figitids were collected in South Korea from *D. suzukii* collected in fruit samples, especially *G. brasiliensis*, which was found in multiple locations. We also report one new species (*A. brevicauda*) and two other species (*A. leveri* and *L. j. formosana*) with new host-association records on *D. suzukii*. It must still be verified whether or not the new species are the same as one of those undescribed species in Japan (Kasuya et al. 2013; Nomano et al. 2015).

Interestingly, we did not recover *A. tabida* or *G. xanthopoda*, which were reported to occur over a relatively wide range of the Japanese islands (Mitsui et al. 2007; Nomano et al. 2015). In earlier surveys, a few individuals of *A. tabida* were collected from *D. suzukii* in Japan (Mitsui et al. 2007; Nomano et al. 2015) and this host was the focus of our collection efforts in South Korea. However, several laboratory experiments have showed that *A. tabida* could oviposit but did not survive in *D. suzukii* (Chabert et al. 2012; Kacsoh and Schlenke 2012). Nomano et al. (2015) suggested several possible causes for this inconsistency in *A. tabida* and *G. xanthopoda* host use across different geographic ranges with relatively similar

environmental conditions, including misidentification of host species in the earlier collections, host stage influence on parasitoid survival, and kleptoparasitism. Previous studies have shown that host age affected the survival of *A. tabida* in *D. melanogaster* (Van Alphen and Janssen 1982), and *A. tabida* survived better in *D. simulans* (Sturtevant) previously parasitized by *L. bouhardi* (Kraaijeveld 1999). It is also possible that geographic variations occur in the flies' immune resistance against parasitoids or in parasitoid species for their preference or effectiveness against flies (Rossi Stacconi et al. 2015).

While uninfested-fruit-baited traps provided a quick means of monitoring the presence of adult parasitoids that attack frugivorous *Drosophila*, it appeared in our collections to be relatively unattractive to South Korean *D. suzukii*. We found that the uninfested-fruit-baited traps captured mainly other drosophilid species, thus disrupting the search for specialist parasitoid species. In contrast, our collections of field-infested fresh fruits yielded primarily *D. suzukii* and with this more host-specific parasitoids, which was similar to previous collections in Japan (Kasuya et al. 2013; Mitsui et al. 2007; Nomano et al. 2015), although the authors did not always emphasize the differences in collection methods. In Japan, Kasuya et al. (2013) reported that *D. suzukii* was the only fly species breeding on wild cherry fruit. Both the host-specific *Asobara* species (Nomano et al. 2015) and *D. suzukii*-associated type of *G. xanthopoda* (Kasuya et al. 2013) were collected from wild fruits. Fruit traps could also influence the estimated rate of parasitism as both entering flies and parasitoids could reside in the traps for considerable periods of time, permitting repeated oviposition by the same species.

In the Berkeley quarantine, *A. japonica*, *L. j. japonica*, *G. brasiliensis*, *T. drosophilae*, and *P. vindemiae* readily attacked *D. suzukii*. This assessment was important to verify that, at least in the laboratory, the North American strain of *D. suzukii* (from Parlier, CA) did not show complete resistance to the five tested parasitoid species, as was shown in earlier studies (Kacsoh and Schlenke 2012; Poyet et al. 2013). In these preliminary quarantine studies, we also used *D. melanogaster* as a potential alternative and widespread host. This host was physiologically suitable for all the tested parasitoid species, thus potentially increasing the chances of these parasitoids to survive in the wild even without the availability of the pest. We also found a positive correlation between the host size and the size of emerged *A. japonica*, thus potentially favoring *D. suzukii* over other drosophilids as a preferred host. However, a more accurate assessment of the ecological suitability of *D. melanogaster* for these parasitoid species is needed before predicting its real potential as an alternative host species in the field (Desneux et al. 2012). To this goal of finding specialized parasitoid species that exclusively attack or

strongly prefer *D. suzukii*, future extensive quarantine work is designed to test host preference on a series of non-target fly species. *A. japonica* was the more common parasitoid reared from *D. suzukii* (Table 2). If strains of this, or other species, have clearly better performance on or preference for *D. suzukii* compared with other fly species, an argument could be made for their release in some regions.

In conclusion, some specialized *D. suzukii* parasitoids in the genera of *Asobara*, *Leptopilina*, and *Ganaspis* seem to be present in South Korea and their specialization may be preferable as biological control candidates for *D. suzukii* populations that occur in North America and Europe. However, further detailed evaluations are needed to determine their effectiveness and safety with regard to non-target risk in order to obtain release permits in the US and/or in Europe. Moreover, the highest levels of *D. suzukii* parasitism recorded in South Korea were by the more generalist parasitoid species, particularly *A. japonica*. Therefore, this initial collection shows promise for improved biological control of *D. suzukii* in some of its invaded regions. Furthermore, additional collections in Asia will likely result in novel species and species associations with *D. suzukii*. For example, in 2013 collections in South Korea (K. Hoelmer, E. Guerrieri, M. Giorgini, D.S. Choi) using banana-baited traps infested by *D. suzukii* yielded *A. japonica*, *A. leverii*, *G. xanthopoda*, and one new species *Asobara brevicauda* Guerrieri and Van Achterberg (Guerrieri et al. 2016), while collections in Yunnan Province, China using uninfested-banana-baited traps yielded *A. japonica*, *A. leverii*, *G. xanthopoda*, one undescribed *Leptopilina* sp. and four *Asobara* species that have been described as new including *A. brevicauda*, *A. elongata* Guerrieri and Van Achterberg, *A. mesocauda* Guerrieri and Van Achterberg, *A. unicolorata* Guerrieri and Van Achterberg and *A. triangulata* (Guerrieri et al. 2016). While the material was not processed in quarantine and screened for effectiveness against *D. suzukii*, these collections highlight the need for further exploration and quarantine screening, as well as more detailed studies of parasitoid-host associations in situ in the native range of *D. suzukii*. The wide geographic distribution of *D. suzukii* in Asia also suggests that surveys in other regions of Asia, habitats, and over longer periods and throughout the seasons will be needed to fully discover the diversity of its natural enemies.

Author contribution

KMD, XGW, JCM, PWS, KAH, and VMW conceived and designed the project. KMD and XGW wrote the initial manuscript, all co-authors helped editing the manuscript thereafter. XGW and AB analyzed the data and conducted the quarantine work. JCM, BM, PWS, YS, TK, CJ, DWL, BC, and HR conducted the foreign exploration in South

Korea. EG, MG, and KvA identified all *Asobara* species, while MB identified all other parasitoid species. All authors read, revised, and approved the manuscript.

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