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RESEARCH

Preliminary evidence of *Drosophila suzukii* parasitism in Southeast England

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Abstract

Controlling the invasive fruit pest, *Drosophila suzukii,* relies on a range of complimentary pest management approaches. However, increasing external costs (e.g., labour, exclusion mesh and fuel), are limiting the ability to control the pest via non-chemical means. Extant UK parasitoids could be exploited for the suppression of *D. suzukii* populations, but there is currently a lack of knowledge of the UK species utilising *D. suzukii* as a host or their lifecycle requirements. Between 2017 and 2020, we identified parasitoids developing in *D. suzukii*, in Southeast England.

Sentinel traps, containing laboratory reared *D. suzukii* larvae/pupae in fruit, were deployed within the vicinity of commercial crops and semi-natural areas. Six generalist parasitoid species were recovered from *D. suzukii* sentinel traps. These included two species of larval parasitoids (*Leptopilina heterotoma* Thomson (Hymenoptera: Figitidae) and *Asobara tabida* (Nees) (Hymenoptera: Braconidae) and four pupal parasitoids (*Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae), *Spalangia erythromera* (Forster) (Hymenoptera: Pteromalidae), *Trichopria modesta* (Ratzeburg, 1848) and *T. prema* Nixon (both Hymenoptera: Diapriidae)).

The performance of the first four species as *D. suzukii* parasitoids was further tested in the laboratory and then in the field to assess rates of parasitism. *Pachycrepoideus vindemiae* was the most abundant species recovered from field collections and had in increasing rate of population rate in the laboratory. Other species were not successful at parasitising *D. suzukii*. In the field, adult *D. suzukii* emergence from sentinel traps was reduced by ~ 21% where parasitoids could access *D. suzukii* larvae and pupae.

Parasitoids of *D. suzukii* are understudied in the UK, and this research indicates where future efforts could be made in understanding the interaction between host and parasitoid and the opportunities to exploit extant parasitoids for the control of *D. suzukii.* We also evaluate the prospects for classical and augmented control and discuss how they may fit with current regional integrated pest management options.

Keywords Biological control · Invasive pest · Spotted wing drosophila · Integrated pest management · Parasitism

Introduction

Spotted Wing Drosophila, *Drosophila suzukii* Matsumura, was first detected in the UK in 2012 (Harris and Shaw 2014) and resulted in economic losses to the soft and stone-fruit industry within 2 years of detection. While research has focused on Integrated pest management (IPM) strategies to target *D. suzukii*, including high standards of crop hygiene, more frequent picking, canopy management and exclusion mesh (Leach et al. 2017; Noble et al. 2017; Schöneberg et al. 2020; Ebbenga et al. 2019), the increase in labour and cost attached to these approaches (Del Fava et al. 2017) are unobtainable for some growers. Hence, pest management, which

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Key message

- This study is the first to explore possible parasitoids of *D. suzukii* in the British Isles.
- Six Hymenopteran species were identified as potential parasitoids of *D. suzukii* in the Southeast of England.
- *Pachycrepoideus vindemiae* can parasitise *D. suzukii* in the English landscape.
- *Pachycrepoideus vindemiae* could increase its population size on *D. suzukii* in the laboratory.
- *D. suzukii* emergence was reduced by ~ 21% in the field when extant parasitoids could access larvae and pupae.

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requires little input, including fostering existing parasitoids, could play a role in reducing *D. suzukii* numbers and hence yield losses.

The use of biological options to control *D. suzukii* has been explored in native and invaded ranges as it offers an Integrated pest management (IPM) compatible approach. An extensive review of biological control by Wang et al. (2020b) concluded that combining conservation, classical and augmentative biological control is optimum for *D. suzukii* suppression. The benefit of using macro-organisms over micro-organisms is that larger biocontrols can disperse more widely, actively seeking out *D. suzukii*, while micro-organisms generally rely on the pest orientating towards the agent (Wang et al. 2020b). Of the generalist natural enemies investigated, earwigs, spiders and predatory bugs predate various life stages of *D. suzukii* in laboratory and field-based experiments (Wolf et al. 2018). Promising parasitoids from the native range of *D. suzukii* include the larval parasitoid, *Ganaspis brasiliensis* (Ihering) (Hymenoptera: Figitidae) (Nomano et al. 2017), proposed as a viable option for classical biological control, due to its narrow host range and relatively high parasitism rate (31% on average) in the field (Giorgini et al. 2019). The pupal parasitoid *Trichopria drosophilae* (Perkins) (Hymenoptera: Diapriidae) has received much attention due to its large range throughout continental Europe and the USA (Wang et al. 2020b). *Trichopria drosophilae* is attracted to *D. suzukii* over other species due to its larger pupal size (Wang et al. 2016) and reportedly reduces *D. suzukii* infestation in the field by 34% in augmented releases, compared to untreated areas (Rossi Stacconi et al. 2019). Within the last decade, several pupal and larval parasitoids have been highlighted as options for use as biological control (see, Tait et al. (2021)). However, the efficacy of parasitoid species to reduce *D. suzukii* populations differs between studies and geographical origins (Wang et al. 2020b; Rota-Stabelli et al. 2020).

Drosophila suzukii has a high level of resistance to some larval parasitoids due to an ability to 'encapsulate' parasitoid eggs, resulting in the death of the parasitoid (Kacsoh and Schlenke 2012). Encapsulation is where *Drosophila* haemocytes (cells) bind to the parasitoid egg and cause death of the parasitoid juvenile by asphyxiation or cellular toxins (Fellowes and Godfray 2000; Kim-Jo et al. 2019). *Drosophila suzukii* has a high haemocyte load compared to other *Drosophila* species, with eight times the amount of *Drosophila melanogaster* (Meigen) (Poyet et al. 2013). Hence, even if Drosophila parasitoids co-exist with *D. suzukii*, they may not be capable of successful development in the host and not contribute to a reduction of *D. suzukii* populations. The number of hemocytes also varies between *D. suzukii* populations. For example, French *D. suzukii* populations had four times more haemocytes than those in Japan (Poyet et al. 2013), likely the cause of varying reports of efficacy in some field- and laboratory-based research studies (Kruitwagen et al. 2018). Resistance to larval parasitoids is also a contributing factor in the invasion success into new territories where generalist larval parasitoids are unsuccessful in their attempts to exploit *D. suzukii* as a host. Pupal parasitoids are not affected by encapsulation but their survival and ability to cause mortality in the host is variable. Both *T. drosophilae* and *Pachycrepoideus vindemiae* (Rondani) had significantly different parasitism success depending on temperature, with significantly lower success of both species in 15 °C compared to 20, 25 and 30 °C (Rossi Stacconi et al. 2017). It is clear from the published research that the interaction between parasitoids and *D. suzukii* as a host are not consistent between regions, and results are dynamic requiring each area to assess efficacy independently.

The aim of this research was to (1) identify extant UK parasitoids utilising *D. suzukii* as a host, (2) identify which habitats they are most prevalent in, (3) determine the phenology of parasitoid species, (4) investigate the impact excluding parasitoids had on *D. suzukii* emergence in the field and (5) test the reproductive performance of these parasitoids on *D. suzukii* in the laboratory. An increased awareness of which species are contributing to *D. suzukii* parasitism and where they are most prevalent could help growers make informed IPM decisions regarding crop and semi-natural habitat management. In addition, the documentation of species in England could simplify the registration of augmented releases of biological controls in the future.

Methods

Detection and identification of UK extant *D. suzukii* parasitoids

Drosophila suzukii originally collected in 2013 from Trento, Italy, were used as the inoculum of the sentinel traps deployed in 2017, 2018 and 2020. *Drosophila suzukii* were cultured on a Bloomington Stock Centre Diet (distilled water 1 L, agar 10 g, table sugar 90 g, pre-cooked maize 90 g, baker's yeast 20 g, soya four 10 g, malt extract 50 g, nipagin 3 g (dissolved in 70% ethanol), propionic acid 3 g) poured into 90-mm petri dishes (Fisherbrand™ Polystyrene). Adults were held in 30 × 30 × 30 cm cages (Watkins & Doncaster BugDorms) kept humid by covering each cage with clear polyethylene and damp blue laboratory roll. Cultures were maintained at 23 °C under a 16:8 light:dark cycle, and Petri dishes with new diet were added to the cages weekly, and old dishes were removed after 5 weeks.

To harvest juvenile *D. suzukii*, strawberries (mixed cultivars grown at NIAB, East Malling, Kent, UK and untreated with plant protection products) were frozen for 48 h and defrosted prior to use. This ensured fruit was free from live *D. suzukii* and parasitoids. After de-frosting, the strawberries were exposed to *D. suzukii* adults at 23 °C under a 16:8 light:dark cycle to allow egg laying to occur for 4 days. Adult flies were then removed from the fruit, which was stored in the same conditions and checked daily until puparium formation was first observed, resulting in both larvae and pupae being present in the fruit. At this point, a 90-mm Petri dish containing 160 g of the *D. suzukii* inoculated fruit was added to a 10×10×20 cm clear Perspex box lined with blue laboratory roll (Fig. 1). The blue roll absorbed unwanted liquid from the base of the box and prevented larvae drowning. A smaller 7×7×7 cm ventilated (0.2 mm mesh) Perspex box was added containing additional fresh strawberries to maximise olfactory stimulus to attract parasitoids (Fleury et al. 2009). Ventilated lids were sealed to the Perspex boxes with electrical tape. For the large box with the immature *D. suzukii*, a 2-mm mesh size was used to allow parasitoids to enter while preventing the entry of larger insects and the exiting of *D. suzukii* that developed to adult (Fig. 1). For the smaller box, a 0.2-mm mesh size was used ensuring parasitoids were unable to access the olfactory stimulus fruit. The large Perspex box was then inserted into a red delta trap (Agralan Ltd. www.agralan.co.uk) to protect the sentinel fruit from rain and direct sunlight (Fig. 1). The sentinel traps were replaced every 2 weeks in 2017, 2018 and 2020.

In 2017, 288 sentinel traps were deployed across 61 locations including urban (private gardens), semi-urban (packhouse yards), commercially managed and semi-natural habitats, from June to September.

In 2018, 280 sentinel traps were redeployed at 14 locations between March and November which yielded parasitoids in 2017 resulting in no urban or semi-urban location deployments.

In 2020, only 2 locations were surveyed between July and September. Sites consisted of a hedgerow beside an abandoned cherry orchard and a woodland next to a strawberry crop. Six sentinel traps were deployed at each site with a total of 72 sentinel traps deployed over this time. These two environments were used as they yielded the highest number of parasitoids in 2018.

Sentinel traps were collected and replaced every 10–14 days. Once collected, sentinel fruits were transferred to the environmental conditions stated above. The large Perspex lid was replaced with a 0.2-mm mesh ventilated lid to prevent the escape of any emerging parasitoids. Sentinel traps were then examined weekly for 6 weeks to ensure all emerging parasitoids were recorded. All parasitoids were recorded and identified to species. Unidentified specimens were placed into vials of 70% ethanol and sent to the Natural History Museum, London and/or the Swedish Museum of Natural History, for identification.

Impact of parasitism on *D. suzukii* emergence in the field

In 2020, additional sentinel traps containing *D. suzukii* pupae and larvae were deployed alongside the survey traps. These traps regarded as ‘controls’ were inaccessible to parasitoids due to the mesh lid preventing parasitoid entry (< 0.2 mm). Methodology prior to deployment in the field followed the process above and the only variable was the addition of the parasitoid-excluding lid. Control traps were deployed so that comparative natural *D. suzukii* emergence could be recorded in the field in the absence of parasitoids. Six pairs of sentinel traps were deployed at the two sites, with 5 m between each pair of the parasitoid accessible (treatment) and inaccessible (control) traps. These were left in situ for 14 days, after which, they were replaced with new traps. Sentinel traps were replaced on six occasions from July to September.

After collection, all traps were treated as above and incubated for 6 weeks for parasitoid emergence and identification. In addition, all *D. suzukii* were recovered, stored in 70%

Fig. 1 Left: fruit-baited sentinel trap box containing inoculated strawberries within a Petri dish (right) and non-inoculated fresh fruit in a ventilated small Perspex box (left). Right: sentinel fruit box inserted into red delta trap for deployment in the field

ethanol and counted. *Drosophila suzukii* were removed from the boxes every 2 days for 3 weeks with those emerging after 3 weeks not counted to prevent counting second-generation adults. Numbers of *D. suzukii* emerging from the control fruit, which was inaccessible to parasitoids, were compared with the number of *D. suzukii* emerging from the parasitoid accessible traps to give an indication of the impact parasitoids had on *D. suzukii* emergence. For the percentage parasitism, *D. suzukii* emergence between treatment and control boxes was analysed using generalised linear models (GLM) in R version 4.0.3 (R core Team 2013). The model was fitted with a Poisson distribution with a 'log' link function and the total number of *D. suzukii* as the response variable. Differences were compared using Tukey's honest significant difference (HSD) test in the package 'emmeans' (Lenth 2021) at a 95% confidence level.

Preliminary laboratory evidence of *D. suzukii* as a parasitoid host

The performance of the parasitoid species that emerged from the sentinel traps was assessed following the Gabarra et al. (2015) method for culturing parasitoids using *D. suzukii* as the host species. A ventilated Perspex box (10 × 10 × 20 cm, < 0.2 mm mesh) was lined with moist paper towel. A Petri dish containing *Drosophila* quick mix media (Blades Biological, UK) infested with *D. suzukii* larvae and pupae was placed on top of the paper towel. This media was used instead of fruit to prevent the growth of moulds from hindering the parasitoid survival. The number of introduced *D. suzukii* larvae and pupae was unknown in this experiment; however, all Petri dishes were exposed to an estimated 100–300 *D. suzukii* adults for 4 days to ensure an even number of eggs were laid initially. Petri dishes were then removed and monitored for pupa formation. Parasitoids of the same species that had emerged from the sentinel traps in 2018 were transferred into the *D. suzukii* inoculated box. Parasitoids were provisioned with a honey-water-soaked cotton ball as a food source. After 4 days, parasitoids were removed, and the boxes transferred to 23 °C under a 16:8 light:dark cycle for 6 weeks. Boxes were checked weekly for emerging parasitoids, which were transferred to 70% ethanol for future species verification. Numbers of *D. suzukii* were not assessed in this experiment.

Results

Identification of Southeast England extant *D. suzukii* parasitoids

In 2017, 218 of the 288 sentinel traps yielded parasitoids. A total of 1358 parasitic wasps emerged from 41 of the 61 sites sampled (Table 1). Four species were identified; two pupal parasitoids, *Pachycrepoideus vindemiae* (Rondani) (Hymenoptera: Pteromalidae) and *Spalangia erythromera* (Forster) (Hymenoptera: Pteromalidae) and two larval parasitoids (*Leptopilina heterotoma* Thomson (Hymenoptera: Figitidae) and *Asobara tabida* (Nees) (Hymenoptera: Braconidae) (Fig. 2). The two pupal parasitoids accounted for the largest percentage of individuals (*P. vindemiae* 83.2% and *S. erythromera* 15.0%), while low numbers of the two larval parasitoids were recovered (*L. heterotoma* 1.1% and *A. tabida* 0.7%).

In 2018, 1165 parasitic wasps emerged from all 14 sites sampled (Table 1). Five species were identified, including the four species identified in 2017 and an additional pupal parasitoid: *Trichopria prema* Nixon (Hymenoptera: Diapriidae) (Fig. 2). As for 2017, the two pupal parasitoids, *P. vindemiae* and *S. erythromera*, accounted for the highest numbers of individuals. Minimal numbers of the two larval parasitoids, *L. heterotoma* and *A. tabida* and of the third pupal parasitoid, *T. prema* (0.5, 0.2 and 0.1% of total individuals caught, respectively) were also collected (Table 1).

In 2020, 62 parasitic wasps emerged from the 72 traps and included three previously recovered species (*S. erythromera* (56 individuals), *A. tabida* and *L. heterotoma* (2 individuals each)) (Table 1 and Fig. 2). An additional pupal parasitoid, *Trichopria modesta* (Ratzeburg, 1848) (Hymenoptera: Diapriidae), was also recovered in 2020 (2 individuals). *Pachycrepoideus vindemiae* was not recovered in 2020 (Fig. 3).

The only recorded species of Drosophila, not *D. suzukii*, was *D. melanogaster* and *D. simulans* from a trap (F60) with a hole in the ventilated lid, recovered on 08/10/2018 from a vineyard. No parasitoids emerged from this trap.

Mean monthly temperature data, from the survey period throughout the 3 survey years and 2019, is shown in Fig. 4. Overall total numbers of parasitoids were lower per trap in 2019 than 2017 and 2018.

Habitats in which parasitoids were found

The highest parasitoid-yielding habitat in 2017 was woodland centres (410 parasitoids). However, woodlands did have the highest number of traps deployed (Table 1and was the only habitat from which four species of parasitoid were recovered (Table 1). Sentinel traps deployed in commercial strawberry yielded the highest number of parasitoids per trap in managed crops (10 individuals per trap); however, only the pupal parasitoids, *P. vindemiae* and *S. erythromera*, were recovered. *Asobara tabida* was recovered from woodland edges and woodland centres. *Leptopilina heterotoma* was only recovered from the centre traps in woodlands.

Table 1 The total number of parasitoid species that emerged from *D. suzukii* inoculated replicate sentinel fruit traps in Southeast England in different habitats in 2017, 2018 and 2020. Data includes the number of sentinel traps deployed per habitat which yielded parasitoids, the total number of parasitoids per habitat, and the number of parasitoids per trap

Habitat	*Pachycrepoideus vindemiae*	*Spalangia erythromera*	*Leptopilina heterotoma*	*Asobara tabida*	*Trichopria prema*	*Trichopria modesta*	Total traps/ habitat	Total individuals/ habitat	Number of parasitoids/ trap
2017									
Woodland centre	374	16	15	5	0	0	42	410	9.8
Strawberries edge	143	77	0	0	0	0	22	220	10.0
Raspberries edge	193	11	0	0	0	0	30	204	6.8
Hedgerow	108	89	0	0	0	0	40	197	4.9
Wild cherry orchard	95	3	0	0	0	0	38	98	2.6
Vineyard	86	0	0	0	0	0	20	86	4.3
Woodland edge	56	8	0	4	0	0	19	68	3.6
Packhouse yard	39	0	0	0	0	0	3	39	13.0
Elderberry	32	0	0	0	0	0	1	32	32.0
Brambles	4	0	0	0	0	0	6	4	0.7
Total per sp.	1130	204	15	9	0	0	-	1358	-
2018									
Woodland centre	218	142	3	1	0	0	76	364	4.8
Strawberries edge	70	72	0	2	0	0	57	144	2.5
Raspberries edge	85	1	2	0	0	0	57	88	1.5
Hedgerow	161	8	0	0	2	0	57	171	3.0
Wild cherry orchard	258	102	1	0	0	0	38	361	9.5
Vineyard	0	37	0	0	0	0	19	37	1.9
Total per sp.	792	362	6	3	2	0	-	1165	-
2020									
Woodland centre	0	35	2	1	0	0	36	38	1.1
Wild cherry orchard	0	21	0	1	0	2	36	24	0.7
Total per sp.	0	56	2	2	0	2	-	62	-

In 2018, the unmanaged cherry orchard yielded higher parasitoid numbers per trap compared to 2017 (mean individuals per trap; 9.5 in 2018; 2.6 in 2017, Table 1). Two *T. prema* were recovered from sentinel traps in hedgerows. *Asobara tabida and L. heterotoma* were more typical in woodland but also collected from the edges of strawberry and raspberry crops and the wild cherry orchard, respectively.

In 2020, the survey focused on the two locations with the highest number of parasitoids in 2018: the wild cherry orchard and woodland centre. More parasitoids emerged from the woodland sentinel traps than those in the cherry orchard.

Phenology of the parasitoids

Over the 3 study years, sentinel traps were deployed for different durations with 2018 spanning the longest period from March to November. *Spalangia erythromera* was found from May through to October in 2018. *Pachycrepoideus vindemiae* was present in the sentinel traps from June to October and the larval parasitoids, *A. tabida* and *L. heterotoma*, were recovered between June and August. Two *T. modesta* were detected in September 2020 and two *T. prema* in June 2018.

During the 6-week *D. suzukii* laboratory incubation period, the greatest numbers of parasitoids emerged 3 weeks after collection from the field (2017 and 2018, Fig. 3).

Impact of parasitism on *D. suzukii* emergence in the field

From the sentinel traps which parasitoids were able to access, four parasitoid species emerged in 2020. Three species had been detected in previous years (*S. erythromera* (total = 65), *A. tabida* (total = 2), and *L. heterotoma* (total = 2)). The first record of *Trichopria modesta* emerging from *D. suzukii* in the UK was also recorded (total = 2). Interestingly, the parasitoid most prevalent in previous years, *P. vindemiae*, was not recovered in 2020.

Significantly fewer ($F\ [1141] = 155.96$, $p < 0.001$) *D. suzukii* emerged from sentinel fruit which parasitoids were

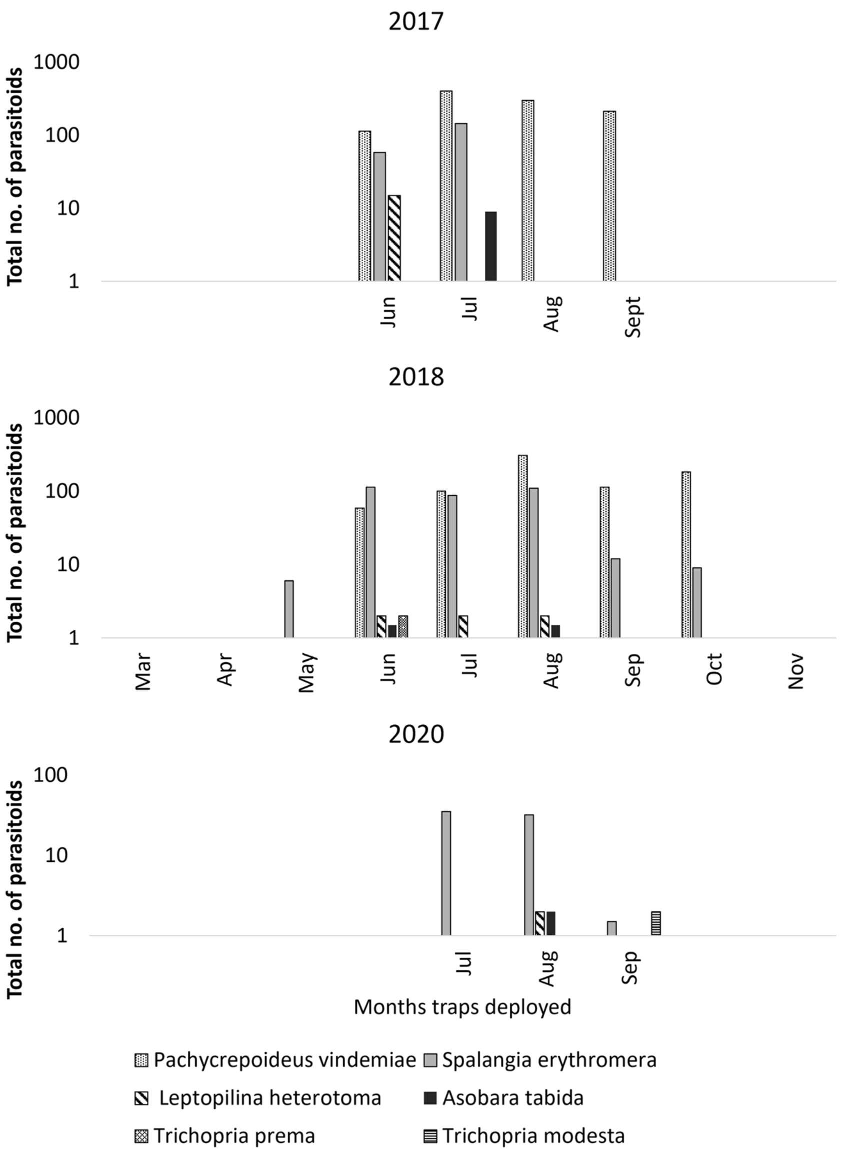

Fig. 2 The total number of parasitoids recovered from *D. suzukii* inoculated fruit-baited sentinel traps deployed in the field (top) June–September 2017, (middle) March–November 2018 and (bottom) July–September 2020. The totals were taken from all habitat types. Note that the *x*- axis is on a log scale and starts at 1; therefore, 0.5 was added to counts of 1 to enable visibility on the graphs

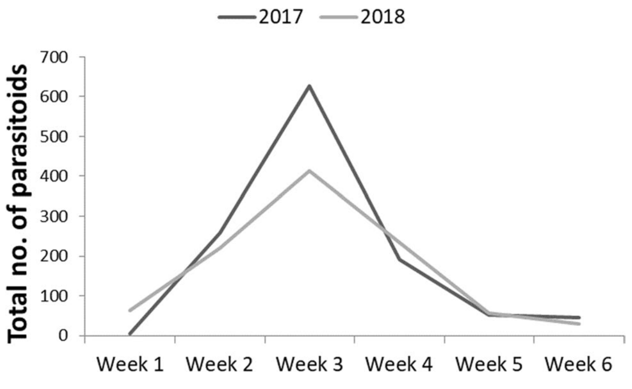

Fig. 3 The total numbers of parasitoids (all species combined) emerging from *D. suzukii* sentinel fruit boxes incubated at 23 °C under a 16:8 light:dark cycle for 6 weeks in the laboratory during the 2017 and 2018 surveys peaking 3 weeks after collection from the field

able to access in the field (cherry orchard: 63.1 ± 1.11, woodland: 74.3 ± 1.24) in comparison to sentinel fruit from which parasitoids were excluded (cherry orchard: 80.0 ± 1.30, woodland: 94.2 ± 1.44, Fig. 5), a 21% decrease in *D. suzukii* emergence when exposed to extant parasitoids.

Preliminary laboratory evidence of *D. suzukii* as a parasitoid host

Of the four parasitoid species introduced to laboratory reared *D. suzukii*, three successfully produced adult offspring; *P. vindemiae*, *S. erythromera* and *L. heterotoma* (Table 2). Of the pupal parasitoids, only *P. vindemiae* increased in population size, producing more than one offspring per adult (Table 2). A total of 291 offspring resulted from 82 adults (3.5 offspring per adult), compared to only

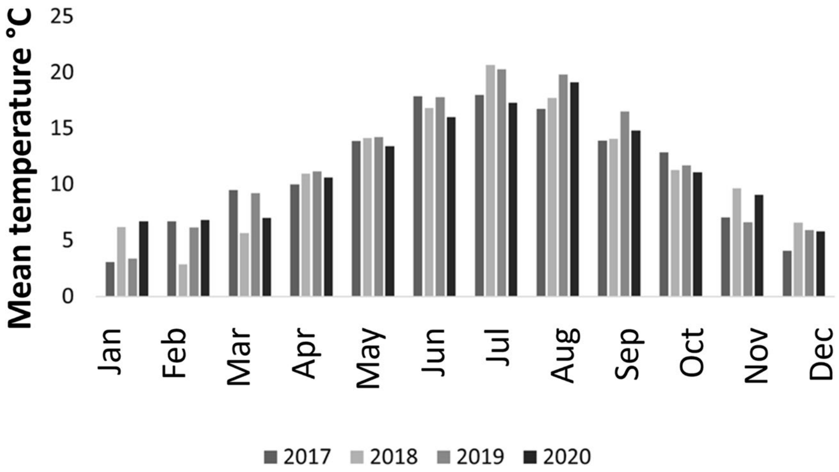

Fig. 4 The mean monthly temperature recorded from East Malling weather station, Kent, UK in 2017, 2018, 2019 and 2020

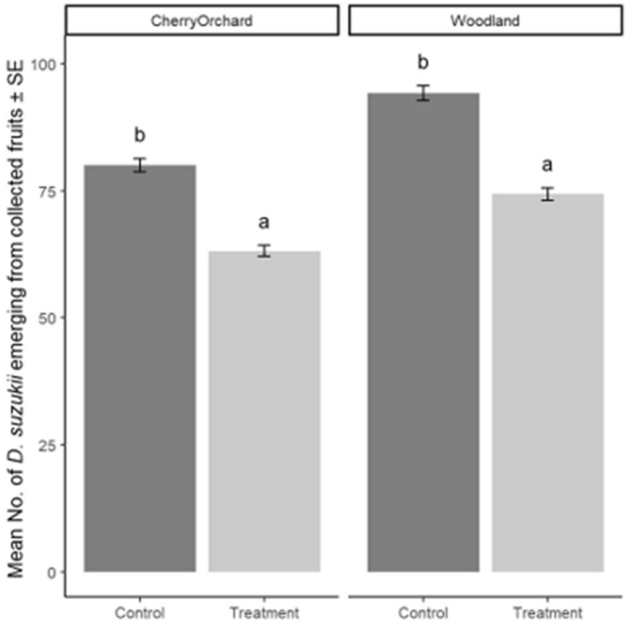

Fig. 5 Mean (±SE) numbers of adult *D. suzukii* emerging from control (parasitoid excluded) and treated (parasitoid accessible) strawberry sentinel fruit traps deployed in a cherry orchard and a woodland in Southeast England between July and September 2020. Different letters signify a significant difference between treatment and control within each habitat type. Figure produced in R

11 from 46 adult *S. erythromera* (0.3 offspring per adult), after 6 weeks of incubation.

Three live female *A. tabida* were recovered from the survey in 2018; however, they did not produce offspring in the laboratory bioassay. Although *T. prema* was recovered from the field, adults died soon after emergence and were not tested for reproduction on *D. suzukii*.

Discussion

Detection and identification of Southeast England extant *D. suzukii* parasitoids

This study documents the first records of six Southeast England parasitoids actively utilising *D. suzukii* as a host in the landscape. Two species of larval parasitoids (*A. tabida and L. heterotoma*) and four pupal parasitoids (*P. vindemiae*, *S. erythromera*, *T. prema* and *T. modesta*) were recorded from *D. suzukii* between 2017 and 2020. All six species are generalist parasitoids of *Drosophila* (Carton et al. 1986, Notton 2014).

We also report the first record of *T. prema* and *T. modesta* potentially parasitising *D. suzukii*, but more records are needed to confirm this. There is very little literature on the behaviour and biology of these species although, in the laboratory, *T. modesta* is reported to be less adapted to parasitise *D. suzukii* compared to other *Drosophila* species, due to a requirement for a longer developmental time (Trivellone et al. 2020). It should also be noted that sentinel fruit traps can be contaminated with species of Drosophilidae other than *D. suzukii* (see, e.g. Abram et al. (2022)), hence the less abundant species of parasitoid in our study would need more evidence for true *D. suzukii* parasitism. However, we observed only one incidence of contamination from other *Drosophila* species from a trap where there was a damaged lid.

Pachycrepoideus vindemiae was the most numerous species in 2017 and 2018 and has the widest host range of the four pupal parasitoids found in our surveys. It has been reported to attack over 60 fly species, including many tephritids and several *Drosophila* (Wang and Messing 2004). *Pachycrepoideus vindemiae* is widely distributed and recorded in America, Africa and Europe (Carton et al. 1986). Surprisingly, *P.*

Table 2 The total numbers of parasitoid offspring emerging from inoculated *D. suzukii* laboratory cultures in 2018 in 23 °C 16:8 light:dark cycle after 6 weeks incubation. The number of *D. suzukii* larvae and pupae were not assessed prior to parasitoid inoculation, but oviposition media Petri dishes were inoculated with the same numbers of *D. suzukii*

Replicate no	Species	Stage of *D. suzukii* host	No. adult parasitoids introduced	No. emerged offspring	No. offspring per adult
1	*Leptopilina heterotoma*	Larvae	10	1	0.1
1	*Asobara tabida*	Larvae	3	0	0.0
1	*Spalangia erythromera*	Pupae	11	3	0.3
2	*Spalangia erythromera*	Pupae	10	5	0.5
3	*Spalangia erythromera*	Pupae	12	2	0.2
4	*Spalangia erythromera*	Pupae	13	1	0.1
1	*Pachycrepoideus vindemiae*	Pupae	25	80	3.2
2	*Pachycrepoideus vindemiae*	Pupae	10	45	4.5
3	*Pachycrepoideus vindemiae*	Pupae	14	41	2.9
4	*Pachycrepoideus vindemiae*	Pupae	8	11	1.4
5	*Pachycrepoideus vindemiae*	Pupae	9	67	7.4
6	*Pachycrepoideus vindemiae*	Pupae	16	47	2.9

vindemiae was not recovered in our 2020 survey even though it was present at the same sites in the previous years. While *P. vindemiae* was not able to parasitise at constant 15 °C in the laboratory in one trial (Rossi Stacconi et al. 2017), other researchers found successful parasitism at temperatures as low as 12 °C for this species (Wang et al. 2018). In 2020, temperatures for May–July were lower in comparison to 2017 and 2018 (average of 0.5–0.7 °C lower, 0.8–1.9 °C lower and 0.7–3.4 °C lower in May, June and July, respectively); however, *P. vindemiae* were recovered through to October in 2018 in average temperatures of 11.3 °C. Average temperatures for June and July 2020 in our survey were 16 and 17.3 °C, respectively indicating that temperature range was unlikely to have caused an absence of *P. vindemiae* in 2020.

Spalangia erythromera was recovered in all 3 years of our survey and found in 80% of the habitats surveyed in 2017, and all habitats in 2018 and 2020. This generalist pupal parasitoid can parasitise many Hymenoptera and Diptera species in Palearctic regions and is common in Western Europe (Boucek 1963, Gibson 2009, Graham 1969). It is associated with habitats with a high density of grassy vegetation (Boucek 1963) and was not found in bramble hedgerows, vineyards or packhouse yards in our survey. *Spalangia erythromera* primarily parasitises house flies (*Musca domestica* L.) (Hall and Fischer 1988), but also species in several other common fly families in Europe, including the Anthomyiidae, lance flies (Lonchaeidae), scuttle flies (Phoridae) and blow flies (Sepsidae) (Gibson 2009).

The low numbers of larval parasitoids were found in the sentinel fruit traps, although *L. heterotoma* (peak of 15 in 2017) and *A. tabida* (peak of 9 in 2017) were identified in all 3 study years. The low numbers of *L. heterotoma* might be explained by the lack of young *D. suzukii* larvae in the traps as *L. heterotoma* prefers to parasitise young instar larvae (up to about 48 h) (Bakker et al. 1967). While a mixture of larval instars and pupae were deployed in the field, numbers of 1st instar larvae would have been small in comparison to later-stage larvae due to the time taken to prepare and deploy the traps in the field. In addition, there is a high immune response produced by *D. suzukii* against this species. Only three adult *L. heterotoma* emerged from 180 parasitised eggs (Chabert et al. 2012), indicating the difficultly this species has developing in *D. suzukii*. *Leptopilina heterotoma* can overcome immunological response by *D. suzukii* under standard laboratory conditions (Rossi Stacconi et al. (2015) although these conditions are somewhat removed from those found in the field. Various populations of *L. heterotoma* have been tested on *D. suzukii* but few parasitoids complete development in *D. suzukii* (Chabert et al. 2012; Kacsoh and Schlenke 2012; Poyet et al. 2013), except a northern Italian population (Rossi Stacconi et al. 2015). Later, it was confirmed that the northern Italian *L. heterotoma* only developed from *D. suzukii* artificial diet and *D. suzukii* in infested fruit (Ibouh et al. 2019). Future studies should separate puparia from field collected samples and sort by puparial morphology, to distinguish *D. suzukii* from other species of Drosophilidae (Abram et al. 2022; Fellin et al. 2023).

Asobara tabida is reportedly a parasitoid of *Drosophila* larvae that occurs throughout Europe in different ecological niches depending on region and availability of resources (Janssen 1989). Adult *A. tabida* in North-Western Europe feed on tree sap, whereas in Southern Europe they feed on fermenting fruit (Ellers and Van Alphen 1997). Within our survey *A. tabida* were recovered from habitats with trees (cherry orchards, woodland centre, woodland edge). *Asobara tabida* has been reported emerging from field samples of *D. suzukii* in Japan (Mitsui et al. 2010); however, few individuals emerged from *D. suzukii* occurring in natural fruits (Nomano et al. 2015), and *A. tabida* may occasionally develop from *D. suzukii* after it has been parasitized by more suitable parasitoids, e.g. *Ganaspis brasiliensis* and *Leptopilina japonica* to suppress the host immunity (Kraaijeveld and Godfray 1999). To date, *A. tabida* have not been collected from *D. suzukii* in other studies other than the two Japanese studies and the current study.

No *T. drosophilae* were identified in our survey. This species is approved for augmented biological control in continental Europe. If identified in the UK, the process for registration as a biocontrol product would be greatly simplified. *T. drosophilae* will utilise other *Drosophila* sp. as hosts, ensuring sufficient host availability in a wide range of ecological niches (Mazzetto et al. 2016), and surveys should continue to attempt to find this species in the UK.

The susceptibility of *D. suzukii* to parasitoids can vary between geographic location, strain and climatic conditions (Poyet et al. 2013; Rossi Stacconi et al. 2017). Within this study, a laboratory strain originally collected in 2013 from Trento, Italy, was used as the inoculum of the sentinel traps and subsequent laboratory trials. It would be beneficial to repeat this study with a genetically younger, UK-collected stain of *D. suzukii* to confirm whether the parasitoid species identified within this study are capable of utilising UK *D. suzukii.*

Impact of parasitism on *D. suzukii* emergence

In 2020, we assessed the impact of parasitism by extant parasitoids on *D. suzukii* emergence from fruit under field conditions. Fruit containing *D. suzukii* which could not be reached by parasitoids (controls) were compared to sentinel fruits where wild parasitoids could access immature *D. suzukii.* While we inoculated fruit with the same numbers of parent *D. suzukii*, the number of pupae and larvae in each replicate trap was unknown. Even so, significantly fewer *D. suzukii* emerged from sentinel fruits which could be accessed by parasitoids. There was a 21% reduction in *D. suzukii* emergence where parasitoids could gain access to pupae and larvae. However, the total number of individual parasitoids that emerged from these assessments did not reflect this reduction. For *L. heterotoma*, *A. tabida* and *T. modesta*, only 2 individuals emerged from the treatment sentinel traps and 62 individual *S. erythromera*. Using emergence of parasitoids from the sentinel fruit appears to greatly underestimate the impact parasitoids have on *D. suzukii* survival. Using direct counts of emerging parasitoids does not account for the reduction in *D. suzukii* survival due to parasitoids that failed to emerge (or be recovered), or stings from parasitoid oviposition. For comparison, during laboratory experiments testing *T. drosophilae* parasitisation of *D. suzukii* pupae, the daily mean parasitisation rate was recorded at 9.47% per female when 30 host pupae were provided daily. In that instance, the parasitisation rate was calculated as the total number of pupae used by parasitoids (including those successfully emerging and failing to emerge) divided by the total number of host pupae available (Chen et al. 2018). While this is not directly comparable with our investigation, it does indicate that calculating the rate of parasitism requires consideration of other behaviours, more than adult parasitoid emergence.

Performance of parasitoids using *D. suzukii* as a host in the laboratory

Parasitoid survival and efficacy in suppressing target pests is dependent on their ability to complete their lifecycle within the host. Partial or low success rates could lead to parasitoid population crashes if dependent on less than optimum hosts, or in cases where the host has a level of resistance (Kraaijeveld and Godfray 1999). Due to a high haemocyte load, *D. suzukii* is not an optimum host for many generalist *Drosophila* larval parasitoids, because they are unlikely to survive through to the next generation. We were unable to test the reproductive capabilities of *A. tabida* as only three females emerged from the sentinel traps. In laboratory trials, Knoll et al. (2017) found that *A. tabida* was unable to reproduce in *D. suzukii*, with eggs failing to survive through to adult emergence. In addition, they found no significant reduction in *D. suzukii* emergence when offered to *A. tabida* indicating that although detected in all 3 years of our surveys, it is an unlikely species for *D. suzukii* control.

In our laboratory tests, *P. vindemiae* produced more offspring per parent (mean = 3.5) compared to *S. erythromera* (mean = 0.3 and *L. heterotoma* (mean = 0.1), when allowed to parasitise *D. suzukii*. Augmented releases of *P. vindemiae* to control *D. suzukii* could help control populations in cropping habitats. However, the limited ability of *L. heterotoma* to increase in population size makes these less effective for augmented release options. The low survival rate of *L. heterotoma* in our laboratory bioassay was not unexpected due to the prior awareness of the encapsulation process in *D. suzukii* (Iacovone et al. 2018). Concerns of introduced parasitoids becoming conditioned to alternative species have been mitigated to some extent in laboratory and semi-field bioassays by Wolf et al. (2020a). The pupal parasitoid, *T. drosophilae*, preferred *D. suzukii* over two native *Drosophila* species in choice tests (*Drosophila subobscura* Collin and *D. melanogaster*) even though cultures had originally been maintained on *D. melanogaster*. *Drosophila melanogaster* are good alternative host for mass rearing due to their quicker life cycle and stability in laboratory cultures in comparison to *D. suzukii*. Boycheva Woltering et al. (2019) suggested using *D. melanogaster* as the primary host for mass rearing *T. drosophilae*, followed by one generation on *D. suzukii* prior to release into the field. This would need to be confirmed for other parasitoid species. However, Jarrett et al. (2022) explored the adaption of the US native parasitoids using *D. suzukii* as a host in laboratory-based trials with positive results. They found both *P. vindemiae* and *T. drosophilae* increased in development success by 88 and 259%, respectively, after only 3 generations indicating that some pupal parasitoid species could be successfully achieved using *D. suzukii* as the host.

While ample numbers of *S. erythromera* were applied to our *D. suzukii* cultures, the next generation emergence was low (0.3 per parent). This species has a longer emergence time than *P. vindemiae*; 29–40 days compared to 21–24 days (Wang and Messing 2004) but should have had time to develop to adult in our 6 weeks incubation period. Wolf et al. (2020a) also noted low offspring emergence in *S. erythromera* concluding it was not a reliable species for the control of *D. suzukii*. Knoll et al. (2017) observed low offspring survival but gained a 62% reduction in *D. suzukii* emergence when this species was applied to pest cultures. In Southeast England, *S. erythromera* was recovered in all 3 years from sentinel traps, and while it may not be successfully completing its life cycle in this host, it could be contributing to *D. suzukii* suppression.

Factors limiting parasitoids as effective biocontrol

Pachycrepoideus vindemiae is a cosmopolitan species with a broad host range (see Wang et al. (2021) and generally reported as ineffective at providing adequate control of *D. suzukii*, although augmentative releases have shown some potential (Hogg et al. 2022; Rossi Stacconi et al. 2019; Gonzalez-Cabrera et al. 2019; Miller et al. 2015). *Pachycrepoideus vindemiae* can locate *D. suzukii* pupae in dropped fruit (Wolf et al. 2020a), and *T. drosophilae* emerges from fruit which has dropped to the ground 8–14 days post collection ((Rossi Stacconi et al. 2018). However, fruit pickers are encouraged to remove all unmarketable fruit from, not only the crop, but also dropped fruit from the ground (Schöneberg et al. 2021). While this practice removes sources of *D. suzukii*, it unintentionally removes parasitoids in the processes. As strawberries and raspberries are harvested 2–3 times per week, there is little opportunity for parasitoids to complete their long development time. Cherries and other stone fruit have a longer ripening period potentially leaving more opportunity for parasitoids to emerge. In addition, Rossi Stacconi et al. (2018) found no *T. drosophilae* emerged from marketable harvested likely because parasitoids are attracted to decomposing fruit volatiles typically associated with other *Drosophila* species (Kaiser et al. 2009). An additional objective of 2020 was to collect waste fruit from commercial crops and allow parasitoids to emerge in the laboratory (results not shown); however, no parasitoids were recovered using this approach. While waste fruit has been utilised as a method of parasitoid release for other pest flies in laboratory conditions, more research is required to optimise this for *D. suzukii* parasitoids in crops (Desurmont et al. 2022). During the 6-week incubation of sentinel fruits in our study, the greatest numbers of parasitoids emerged 3 weeks after collection suggesting that current hygiene approaches in commercial crops do not support parasitoid populations, although parasitoid stings can cause mortality. As such, deploying or supporting parasitoids in a commercial crop is unlikely to be sustainable and would require frequent re-introductions.

More progress is being made with classical control using Asian larval parasitoids such as *Ganaspis brasiliensis and L. japonica*. Significantly more *G. brasiliensis* (G1 strain) were found to emerge from *D. suzukii* larvae within blueberry fruit on the plant in comparison to *D. melanogaster* within decomposing fruit in replicated cage trials (Seehausen et al. 2022). While these artificial conditions are not representative of a commercial crop (the decomposing fruit consisted of 2-week-old blueberries and the authors highlighted low survival of *D. melanogaster* in control fruit), it is reassuring that *G. brasiliensis* is attracted to ripening fruits and resulted in 15% parasitism of *D. suzukii*. In addition, *G. brasiliensis* has been approval for release as a classical biological control agent in the USA and Italy with pending requests for Switzerland indicating it is likely to gain approval in other territories if pursued. The efficacy of the *G. brasiliensis* strain on the UK *D. suzukii* would need to be verified prior to release as the rate of parasitism varies depending on strain and host interaction (Wang et al. 2020a).

While augmented and classical releases of parasitoids may not be suitable within crops, naturally occurring and introduced parasitoids could be supported in wild habitats. Wild fruit and unmanaged habitats are a source of *D. suzukii* (Wolf et al. 2020b; Kenis et al. 2016; Lee et al. 2015; Buck et al. 2023) and subsequently its parasitoids. There was a significant reduction in *D. suzukii* emergence from common wild host-fruit species when exposed to parasitoids (Wolf et al. 2020b). *Drosophila suzukii* emergence was reduced by 78% in mistletoe (*Viscum album* L. subsp. *album* (Santalaceae)), 67% in snowy mespilus 'Edelweiss' (*Amelanchier ovalis* Medik (Rosaceae)) and 80% in Oregon grape or holly-leaved berberry (*Mahonia aquifolium* (Pursh) Nutt. (Berberidaceae)). Wild fruit are unlikely to be picked or managed as intensely as commercial crops and are not subject to hygiene practices. Hence, wild fruits can support *Drosophila* parasitoids in semi-natural habitats.

However, wild fruit are also likely to support *D. suzukii*. Alternative hosts such as black nightshade (*Solanum nigrum* L.) (Kenis et al. 2016), firethorn (*Pyracantha coccinea*) (Ulmer et al. 2020) and bird cherry (*Prunus padus* L.) (Alhmedi et al. 2019) are classed as dead-end hosts for *D. suzukii* because *D. suzukii* females lay eggs in the fruit, but few offspring survive to adult (Poyet et al. 2015). It would be beneficial to determine parasitoid survival within *D. suzukii* of dead-end hosts as an alternative to promote the development and survival of parasitoids. Currently identified extant parasitoids in Southeast England were active from May to October coinciding with commercial fruit production in this region. Early releases of parasitoids could facilitate *D. suzukii* control before wild parasitoid populations establish, especially in tunnel and glasshouse grown crops where temperatures are generally warmer.

Finally, parasitoids may play an invaluable role in supressing *D. suzukii* populations. However, their efficacy in the field is more likely to be a contribution as part of an IPM programme. Further research is required to better understanding how current parasitoids interact with their native hosts, including *D. suzukii.* This will enable fruit growers and agronomists to optimise habitats and tailor IPM programmes to suit the parasitoids needs, promoting a free contributory pest regulation service.

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Data availability Raw data is provided in the body of the manuscript or in the Figshare repository at https://doi.org/10.6084/m9.figshare.23826675.v1. Please note that location information has been removed due to the sensitivity of disclosing commercial growers' sites.

Declarations

Ethical approval Not applicable.

Competing interests The authors declare no competing interests.

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