The effects of non-crop habitat on spotted wing drosophila (Drosophila suzukii) abundance in fruit systems: a meta-analysis

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Received: 28 February 2022 | Accepted: 14 July 2022

DOI: 10.1111/afe.12531

ORIGINAL ARTICLE

Agricultural and Forest Entomology

The effects of non-crop habitat on spotted wing drosophila (*Drosophila suzukii*) abundance in fruit systems: A meta-analysis

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Funding information
BerryWorld; BBSRC Waitrose Collaborative Training Partnership

Abstract

1. *Drosophila suzukii* (SWD) poses a threat to soft and stone fruit globally. SWD inhabits non-crop areas adjacent to farms from where it moves into crops to cause damage. Effective IPM control strategies, considering both the crop and non-crop area, are needed to control this economically important pest.
2. We conducted a meta-analysis to quantify the impacts of different non-crop habitats around fruit farms on SWD populations, comparing abundance of SWD trapped in crop and non-crop habitats.
3. Overall, SWD abundance was greater in non-crop habitats than in cropped areas and this difference was greatest in farms adjacent to woodland, or field margins containing known SWD host plants.
4. The difference in SWD abundance between crop and non-crop habitats was not affected by crop type but was greatest in the winter months and in conventional compared to organic farms, indicating conventional approaches can reduce relative SWD abundance.
5. *Drosophila suzukii* overwinter in non-crop habitats which provide refuge outside the cropping season. However, certain habitats support greater relative abundance of SWD than others and this is also affected by farm management. We discuss what these findings mean for effective control of SWD.

KEYWORDS
grapes, host potential, integrated pest management, land management recommendations, overwinter, refugia, season, spotted wing drosophila

INTRODUCTION

Spotted Wing Drosophila (SWD), *Drosophila suzukii* (Matsumura), poses a threat to fruit growers globally. Originating in Asia, *D. suzukii* was first recorded in North America on berries in the coastal areas of California in 2008 (Asplen et al., 2015). The same year, *D. suzukii* was found in Europe near the Rasquera municipality in Spain (Calabria et al., 2012). It is now widespread across Europe, Asia, North and South America and a pest of fruit systems around the world (Asplen et al., 2015; Cini et al., 2012). *D. suzukii* is a pest of many soft fruit and some top fruit crops because it can lay eggs in unripe fruit (Karageorgi et al., 2017). The larval feeding degrades the fruit flesh, reducing its marketability (Grassi & Pallaoro, 2012) and the resulting damage acts as a pathway for secondary infection by pathogens such as fungi or bacteria, which further reduces marketability of affected fruit (Cini et al., 2012).

Damage from *D. suzukii* can result in substantial economic loss, particularly for areas of fruit production that have high climate suitability for *D. suzukii*. For example, in California, Washington, and Oregon which accounted for all US commercial production of blackberries and raspberries in 2008–2009, a study showed there was a 20% yield loss to *D. suzukii*, equivalent to $421.5 million (Bolda et al., 2010). In 2017, Minnesotan fruit growers experienced a median yield loss of 20% due to *D. suzukii*-related damage, equating to $2.36 million in sales (DiGiacomo et al., 2019).

Alongside climate factors, non-crop habitats which border fruit farms can also exacerbate fruit damage by *D. suzukii*, especially when left unmanaged (Briem et al., 2016). While growers are often advised to increase the area of semi-natural habitats for conservation biocontrol and other ecosystem services (Martin et al., 2019; Schellhorn et al., 2014), these habitats may also act as a reservoir for pests by providing them with feeding, shelter, and nesting resources (Karp et al., 2018; Santoiemma et al., 2019).

Non-crop habitats can act as a source of *D. suzukii* populations adjacent to fruit farms (Diepenbrock et al., 2016; Santoiemma et al., 2019; Urbaneja-Bernat et al., 2020). The adaptability of *D. suzukii* to reproduce on a wide range of wild hosts such as those in the *Cornus*, *Prunus*, *Rubus*, *Sambucus*, and *Vaccinium* genera (Kenis et al., 2016) likely aids its ability to persist year-round on farms in adjacent non-crop habitats (Kenis et al., 2016; Lee et al., 2015; Poyet et al., 2015; Schmidt et al., 2019). One study showed earlier detection in soft fruit farms adjacent to woodland areas (Pelton et al., 2016), while another study showed a decrease in *D. suzukii* activity in the crop with increasing distance from the woodland margin (Tonina et al., 2018). This supports the hypothesis that semi-natural habitats, such as woodlands, foster *D. suzukii* populations when the neighbouring cropping system is out of season.

A variety of methods are currently used to control *D. suzukii* in and around fruit systems. For example, plant protection products can provide effective control of *D. suzukii* adults (Shawer et al., 2018; Smirle et al., 2017). Physical barriers such as insect exclusion mesh also limit crop damage by *D. suzukii* (Chouinard et al., 2016; Leach et al., 2016; Santoiemma et al., 2020), as does frequent fruit picking (Leach et al., 2018), and stringent waste management (Noble et al., 2017). Biocontrol by natural enemies is not widely exploited (Giorgini et al., 2018). Integrated Pest Management (IPM) strategies in soft fruit production can reduce yield losses caused by *D. suzukii* from 13% to 7% (de Ros et al., 2015). Despite this, each control method has limitations. Repeated application of plant protection products increases the risk of resistance, residues in fruit, and operator exposure (Diepenbrock et al., 2017). More frequent picking and waste management increase crop management costs with a higher demand on labour, and the installation of mesh may be costly and impede spray and picking operations (Kuesel et al., 2019). Consequently, control strategies should be based on risk level, combined with *D. suzukii* monitoring to gain an understanding of when action is necessary to prevent damage. A better understanding of the role of non-crop habitat on *D. suzukii* abundance and how this is influenced by crop and management factors is therefore required to develop a fully integrated approach.

We used a meta-analysis of published research to compare *D. suzukii* populations in different crop and non-crop habitats and to explore how this is influenced by crop types, farm management and seasonality. This study provides a greater understanding of the factors influencing *D. suzukii* pressure on crop plants, and provides evidence to better inform management decisions in developing a comprehensive pest management programme for *D. suzukii* on fruit farms.

METHODS

Literature search

A comprehensive, global literature search was carried out using the search engine Web of Science to identify studies that had collected data on *D. suzukii* populations using traps in crops and surrounding non-crop habitats. The search string ((ALL = [Drosophila suzukii OR Spotted Wing Drosophila]) AND (ALL = [habitat OR non-crop]) AND (ALL = [bait OR traps])) was used to generate a list of relevant studies from 1970 to 21 November 2021 all of which were screened. An additional search of literature with relevant data on Web of Science was performed with the same search words without inputted Boolean operators to find additional relevant studies; these returned studies were ordered by relevance and the first 1000 were screened (see S1 for full literature search description and Figure S5 for a PRISMA diagram). Studies were only included in our analysis if (a) they reported numbers of adult *D. suzukii* caught in traps on a farm, orchard, or vineyard in comparison to surrounding non-crop habitat, (b) they reported mean, SD or a convertible variability measure, and sample size. In a third literature search step, the reference lists of all included studies were screened for additional studies. In total, 25 studies published between 2016 and 2021 met our inclusion criteria.

Data extraction

For this meta-analysis, the response variable was the standardized mean difference in abundance of *D. suzukii* caught in traps in non-crop habitats (treatment) and in the crop (control). To understand the role of different factors on the relative abundance of *D. suzukii* in crop and neighbouring habitats, several factors were compared. Habitat types consisted of woodland (areas surrounding fruit farms dominated by trees, identified as woodland or forest, also including woodland edge), urban (gardens and unmanaged areas such as brownfield sites), crop edge (outermost part of the crop which meets the surrounding non-crop habitat), host margin (hedgerows, grassy margins or riparian strips containing known hosts of *D. suzukii*), and non-host margin (hedgerows, grassy margins or riparian strips containing no known *D. suzukii* hosts). Management approach (conventional vs. organic or low input, defined here as little or no application of synthetic inputs), crop type (blueberry, blackberry, cherry, citrus, grape, raspberry, strawberry or mixes of these), broader crop group (soft fruit, top fruit, grape/vineyard or a mix), production system (closed, such as glasshouses or open, which included open orchards, vineyards and crops covered with open-ended polytunnels), and the season in which the survey was carried out (spring, summer, autumn [fall], winter) were the other factors assessed. Means, standard deviation (SD) and replicate number (n) were extracted for crop and non-crop sites in each study. When SD was not provided, it was calculated from the standard error (SE) or raw data where available.

Data were extracted from tables and figures in the manuscripts or their supplementary materials. Data were extracted from figures using the ImageJ application. Where figures had a logscale, the software WebPlotDigitiser was used.

When *D. suzukii* abundance data was presented from several timepoints within one season, only the highest value of abundance was used (see below for between-season comparisons). When different habitat types showed different peaks in abundance, the point at which the total peak abundance across all habitats was highest was used. The highest trap catch point over the surveyed period was used because this represents the peak in *D. suzukii* abundance in the different systems and regions. Two studies tested the effect of different trap designs and baits on their attractiveness to *D. suzukii* adults. For both studies, the most widely used trap type of those tested was selected (liquid traps baited with apple cider vinegar), to match the traps used in other studies.

To explore the effects of season on *D. suzukii* abundance in crop and non-crop habitats, additional data were collected from relevant studies which included data for different seasons. Abundance data in studies which presented records for multiple sampling periods were extracted separately for spring, summer, autumn and winter. For each seasonal sampling period, the same approach for selecting peak abundance, as described in the previous section, was used. Of the original 25 studies meeting our inclusion criteria, eight contained seasonal data.

Where studies presented data with comparisons of more than one crop type or non-cropped habitat, data were extracted for these separately, comparing each crop type with each non-crop habitat to maximize data acquisition. This led to some studies providing more than one datapoint but each datapoint was considered independent from one another because they were collected from different locations and habitat types. Where two or more measurements in non-crop habitat were compared to a single measurement in a crop habitat (e.g., shared controls), the sample size of the control group was divided evenly across the shared comparisons prior to calculation of the effect size (Higgins et al., 2019). Overall, 25 studies provided 57 data points with the addition of 53 datapoints from eight studies available for the seasonal analysis.

When mean, SD and n were not provided and had to be calculated from raw data, different approaches were used depending upon the experimental design. When data were presented from multiple survey sites within a study, the mean and SD were calculated using sites as replicate. In studies which were carried out at a single site with no site level spatial replication, distinct sampling periods or years were used as replicates. Where studies provided multiple spatial and temporal replicates, spatial replicates were used for calculations. Of the 25 total studies used, six were carried out at a single site.

Statistical analysis

A random-effects model was used to quantify an overall estimate of the difference in *D. suzukii* abundance between crop and non-crop habitats. The random-effects model assumes there is variability in effect sizes between studies. The Standardized Mean Difference (Hedges, 1981) was calculated for each comparison of *D. suzukii* abundance in crop and non-crop habitat. The Hartung-Knapp-Sidik-Jonkman (HKSJ) estimator was used as it produces a more robust estimate of variance in the random-effects model (Inthout et al., 2014). The model estimated the overall Standardized Mean Difference across studies as well as 95% confidence intervals and measures of variability of effect size among studies. Additional analyses were used to investigate effects of moderator variables (e.g., habitat type, crop type, management system etc.) on the abundance of *D. suzukii*. If the 95% confidence intervals for a given Standardized Mean Difference estimate did not incorporate zero, we assumed the effects were significant. Datapoints where SD $= 0$ were omitted from the analysis. All statistical analysis was carried out in RStudio 3.6.1 with the "meta", "metafor" and "dmetar" packages (see S3 for full list of packages used).

Sensitivity analyses

Sensitivity analyses were conducted to identify datapoints that may have exerted a high influence on the overall pooled effect size estimate. We used the Leave-One-Out method, in which the meta-analytic model is re-run leaving out each datapoint in turn to identify influential data points (Viechtbauer & Cheung, 2010). The sensitivity analyses identified a datapoint that exerted a strong influence on the overall pooled effect size estimate. As the effect size estimate showed little change when this datapoint was removed, it was deemed appropriate to report the models without this influential case (Viechtbauer & Cheung, 2010) (see S15–19).

Publication bias

To assess publication bias, we produced a funnel plot and used Egger's test (Egger et al., 1997), to identify the presence of a 'true' effect size. The P-curve assessment was also carried out (Head et al., 2015) to identify the presence of skewness and a 'true' effect, an effect not influenced by publication bias. Little to no evidence of publication bias was found in this meta-analysis. As a result of these findings, it was deemed the original datasets acquired were fit to use.

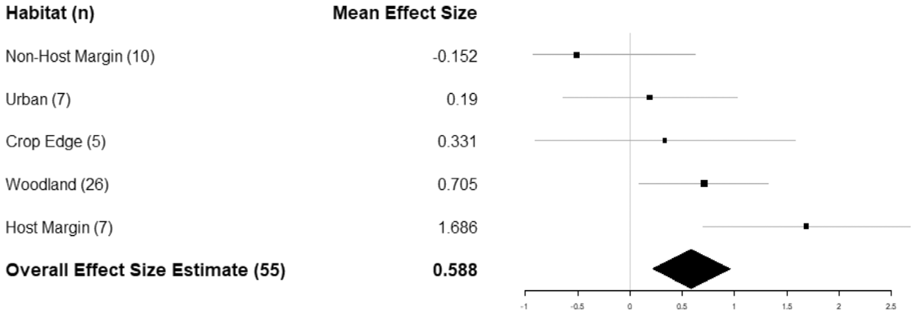

FIGURE 1 Mean effect sizes for *D. suzukii* trap catches in non-crop habitats compared to crops (n = number of datapoints for each habitat type) surrounding fruit farms. The effect sizes estimates for each habitat are indicated by black boxes, while the 95% CI is represented by dark grey horizontal lines. The overall effect size estimate and 95% CI of the random-effects-model are indicated by the black diamond

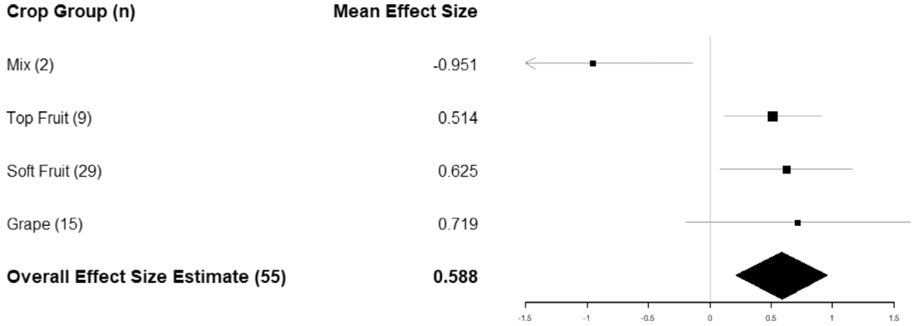

FIGURE 2 Mean effect sizes for *D. suzukii* trap catches in crop and non-crop habitats separated by crop group (n = number of datapoints for each crop or crop group)

RESULTS

There were significantly more *D. suzukii* trapped in non-crop habitats compared to crop; the standardized mean difference estimated by the random effects model was 0.588 (95%CI 0.217–0.959). There was high heterogeneity between studies ($I^2 = 70.6\%$).

Influence of habitat type

Differences in *D. suzukii* abundance between crop and non-crop habitat varied significantly between non-crop habitat types ($p < 0.05$). *Drosophila suzukii* trap catches in host margins (hedgerows or field margins containing hosts known to *D. suzukii*, SMD = 1.686) showed the largest effect size, which was statistically significant, followed by woodland (SMD = 0.705), also significant (Figure 1). This indicates significantly more *D. suzukii* were caught in traps in host margins and woodland than in the neighbouring cropped area.

Influence of crop

The data were categorized into broad crop groups: mix, soft fruit, top fruit and grape. There was a significant difference between groups (Q = 102.87, $p < 0.0001$, see S8). Top fruit (comprising cherry, citrus and ‘other stone fruit’, SMD = 0.514) and soft fruit (SMD = 0.625, see Figure 2) were the only categories which showed significantly higher numbers of *D. suzukii* in the non-crop when these crop groups were grown on site. However, the grape category showed an insignificant response while the mix category showed a significantly negative response, indicating higher *D. suzukii* numbers in the crop than non-crop habitat, but this category only had two datapoints.

Influence of management systems

Most of the studies reported whether the focal crop was managed conventionally, organically or with low input. There was no significant difference between groups (Q = 2.92, $p = 0.087$, see S10, Figure 3). While both categories exhibited positive responses, a significantly higher number of *D. suzukii* in the non-crop area compared to cropped area was seen only when the crop was conventionally managed (SMD = 0.922).

Influence of season

The analysis including seasonal variance showed large heterogeneity within groups ($p < 0.05$) with summer ($I^2 = 52.6\%$) showing the highest (see S13). The overall effect size estimate was 0.687

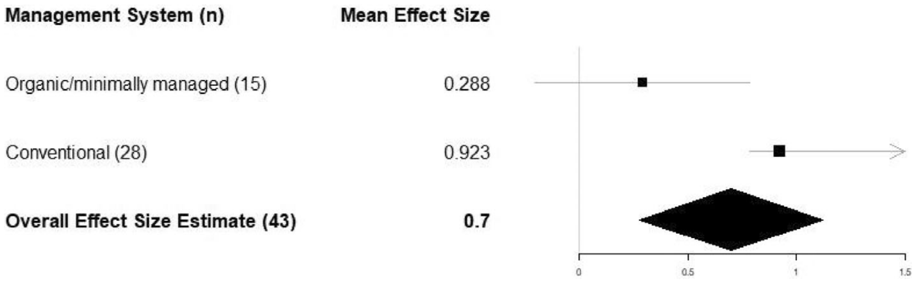

FIGURE 3 Mean effect sizes for *D. suzukii* trap catches in crop and non-crop habitats when separated by management system (n = number of datapoints for each management system)

FIGURE 4 Mean effect sizes for *D. suzukii* trap catches throughout the different seasons. A higher effect size indicates a greater difference in trap catch numbers between farms and their surrounding non-crop habitats

(see Figure 4). There was no statistically significant difference between the groups ($Q = 1.24$, $p = 0.742$, see S13). The winter season showed the greatest number of *D. suzukii* caught in traps in the non-cropped habitat ($SMD = 1.022$), compared to cropped area and this was significant (95%CI 0.237–1.806). This was followed by autumn ($SMD = 0.653$), summer ($SMD = 0.601$) and spring ($SMD = 0.59$), with all of these being significantly different from zero.

DISCUSSION

Effects of habitat type

The abundance of *D. suzukii* in fruit systems compared to non-crop habitats varied between habitat types, crop types and crop groups. Host margins and woodlands, where *D. suzukii* host plants were present, significantly increased adult *D. suzukii* trap catches in non-cropping areas compared to crops. This was not the case for other habitat types which did not contain host plants including non-host margin, urban and crop edges.

Drosophila suzukii are highly polyphagous and utilize wild berries in field margins in temperate climates (Kenis et al., 2016; Poyet et al., 2015). Furthermore, woodland often contains non-crop *D. suzukii* hosts, such as wild berries, and sheltered overwintering habitat for reproductively diapausing *D. suzukii* adults (Fountain et al., 2018), including providing suitable feeding sites into the autumn and winter periods (Briem et al., 2016; Pelton et al., 2016). Polyphagy enables *D. suzukii* to target a wide range of wild and ornamental fruit types, including, unripe, ripe, and fermenting or damaged fruits. Hence, non-crop habitat containing a diversity of these hosts makes *D. suzukii* presence likely (Briem et al., 2016; Kienzle et al., 2020; Lee et al., 2015). Our meta-analysis showed a significantly greater relative abundance of *D. suzukii* in host margins and woodland than the cropped areas. Supporting this, *D. suzukii* abundance assessments conducted in a range of habitats have identified a preference for woodland, with one study showing *D. suzukii* activity density decreasing with an increased sampling distance from a woodland edge (Tonina et al., 2018). The preference for sheltered woodland habitat is likely explained by the favourable conditions they provide over the winter period, such as a higher humidity and warmer temperatures which aid longevity and reproduction (Hamby et al., 2016; Tochen et al., 2016). While margins and woodland may provide out-of-season hosts and ideal microclimatic conditions, they are also a source of natural enemies of other fruit pests (Santoiemma et al., 2018). Management of these areas and resulting negative impacts should be considered in any IPM programme.

Effects of crop

Due to the lack of sufficient data on individual crop types, further research is needed to identify which individual crop types are particularly vulnerable to *D. suzukii* in association with non-crop habitats.

When broader crop groups were compared; there were significantly higher trap catches of *D. suzukii* in the non-crop than cropped areas when soft fruit and top fruit were grown on site. Other research compared suitability and preference between crops for *D. suzukii* oviposition and showed a preference for strawberry and cherry (Cai et al., 2019). In one host suitability and emergence study, where a range of fruit were assessed, *D. suzukii* had the highest reproduction rate in raspberry (Bal et al., 2017). Raspberry is attractive due to semiochemical and/or visual attraction, ease of oviposition in epicarp and/or nutrition which could aid larval growth and survival (Burrack et al., 2013; Kinjo et al., 2013; Little et al., 2019; Silva-Soares et al., 2017). This preference for raspberries was further highlighted in raspberries and blackberries grown outdoors. *Drosophila suzukii* oviposited at a higher rate in raspberries; although host attractiveness likely depends on a variety of factors including sugar content and colour (Burrack et al., 2013), with ripe fruits being the preferred choice to underripe fruits (Lee et al., 2011; Little et al., 2017). However, dropped fruits can act as hosts for *D. suzukii* and support populations if not cleared (Bal et al., 2017), which may have an impact on the results obtained from this assessment. While this research highlights a preference for a variety of soft fruit, our analysis suggests *D. suzukii* abundance is higher in the non-crop habitat regardless of the neighbouring crop group due to the lack of difference in trap catches between studies assessing soft and top fruit sites. This highlights the importance of non-crop habitats in top fruit, soft fruit and grape systems as potential drivers of reproduction due to the shelter and wild hosts they provide out of season.

Effects of production and management systems

Due to the lack of studies in closed systems, a comparison with open systems was not meaningful. However, physical barriers are expected to reduce pest numbers by limiting access to the crop (Chouinard et al., 2016). Soft fruit grown under insect exclusion mesh had fewer *D. suzukii* emerging from fruit and fewer adults in traps compared to crops grown without mesh (Candian et al., 2020; Ebbenga et al., 2019; Kuesel et al., 2019; Stockton et al., 2020). However, one barrier to adoption of mesh installation is the impediment of access to the crops for regular picking and spray operations (Kuesel et al., 2019). More studies comparing open and closed systems are required to explore the extent to which this effects SWD pest pressure.

Most studies in the meta-analysis stated whether the sites assessed were managed conventionally, organically or low input, or both. Only farms that were conventionally managed showed significantly higher *D. suzukii* trap catches in their neighbouring non-crop habitats compared to the crop, suggesting an effect of approved plant protection products on *D. suzukii* survival within the crop. Adult *D. suzukii* trap catches will inevitably be influenced by crop management. This is likely due to an effect of the intense spray regimes on some farms that will limit the number of *D. suzukii* in the growing season which have significantly reduced *D. suzukii* presence in the crop (Civolani et al., 2021; Shaw et al., 2019; Van Timmeren & Isaacs, 2013). While plant protection products such as methomyl, spinosyns, cyantraniliprole, lambda-cyhalothrin and acetamiprid offer good control of *D. suzukii* their efficacies can be impacted by length of exposure and contact with rain (Cuthbertson et al., 2014; Mermer et al., 2019; Shaw et al., 2019; Van Timmeren & Isaacs, 2013). Both conventional and organic farms employ spinosad, which also gives good control of *D. suzukii* (Cuthbertson et al., 2014; Noble et al., 2017). However, due to the risk of resistance of *D. suzukii* to certain products using a single effective product, numbers of applications within a growing season are restricted leaving organic crops more vulnerable to *D. suzukii* egg laying (Gress & Zalom, 2019; Haviland & Beers, 2012). The effectiveness of plant protection products likely explains the difference in effect sizes between conventional and organic farms.

Several biopesticides have been identified and shown to significantly reduce the survival *D. suzukii*, with encouraging implications for control on fruit farms (Fanning et al., 2018). For example, the entomopathogenic fungi *Entomophthora muscae* reduced survival of exposed *D. suzukii* by 27.3% (Becher et al., 2018), while certain *Wolbachia* strains have achieved high sterility levels in *D. suzukii* (Cattel et al., 2018). Blends of yeast and insecticides also show potential for biocontrol and the reduction of *D. suzukii* population numbers (Mori et al., 2017). Combined with other management practices, biocontrol may help to further reduce *D. suzukii* egg laying in fruit (Wiman et al., 2016). Until methods for effective organic control become more widely available, there is likely to be a difference in abundance of *D. suzukii* between organic or low input and conventional systems as illustrated by the findings of this assessment, highlighting the need for further research in this field.

Effect of season

While the difference in *D. suzukii* trap catches between crop and non-crop habitat was not significantly different between seasons, it was highest in the non-crop during the autumn and winter periods. This can be explained by the *D. suzukii* summer morph which undergoes reproductive diapause in the autumn, resulting in a more cold-tolerant winter morph (Hamby et al., 2016, Zhai et al., 2016, Grassi et al., 2018,). The adult winter morphs exhibit significantly lower lethal temperatures than their summer morph counterparts (Stephens et al., 2015) and have increased survival at 1°C compared to the summer morphs (Shearer et al., 2016). As a result, the findings from this seasonal analysis are likely due to *D. suzukii* moving to sheltered habitat such as hedgerows and woodland for the winter to enter reproductive diapause (Fountain et al., 2018; Pelton et al., 2016).

When at-risk crops, such as raspberries and other soft fruit, begin to fruit in the summer, *D. suzukii* population abundance increases within the crop (Tonina et al., 2018), illustrated by our analysis showing increased relative trap catches in the cropped areas in the spring and summer periods. As such this should act as a guide for growers to manage the non-crop habitat surrounding their farms during these periods as *D. suzukii* successfully overwinter in sheltered habitats that provide hosts out of season (Cahenzli et al., 2018; Hennig & Mazzi, 2018; Pelton et al., 2016).

Overall, this analysis highlights the role season has on *D. suzukii* abundance in fruit systems. Because *D. suzukii* retreat to non-crop habitats in the winter period and remain active, we recommend targeted control in host margins and woodland during the autumn and winter periods to reduce numbers adjacent to crops the following spring.

Land management recommendations

This meta-analysis highlights the potential for non-crop habitats such as woodland and host margins to support higher numbers of *D. suzukii*, especially throughout the autumn and winter periods. We suggest measures that may further reduce winter *D. suzukii* populations with the aim of decreasing pressure of this pest on growers the following spring and our study highlights when and in which contexts these approaches may be targeted and deployed most effectively.

The potential for non-crop habitats such as host margins and woodland to support winter populations of *D. suzukii* is likely due to the shelter and wild hosts they provide. As there is a lower abundance of fruit for *D. suzukii* in the non-crop areas over the winter period (Fountain et al., 2018), there will be less competition between fruit and mass traps previously shown to be a cause of ineffectiveness of mass traps in cropping areas (Hampton et al., 2014). This is likely aided by *D. suzukii* ovipositing more readily in wild hosts than hosts in the crop. Studies on mass trapping *D. suzukii* have been shown to influence behaviour of the pest towards traps, increase infestation of fruit closer to the traps and highlight the potential for future control (Clymans et al., 2022; Hampton et al., 2014; Wallingford et al., 2018). Mass trapping in these non-crop habitats over winter when less wild hosts are present, may further reduce *D. suzukii* population numbers. However, recently fed *D. suzukii* have shown to fly greater distances than starved individuals (Wong et al., 2018). In addition, the low selectivity of certain trap types and low volatility of substances used could lead to the capture of non-target species. These two points could be considered if planning to mass trap over the winter period. As female *D. suzukii* enter reproductive diapause over the winter (Grassi et al., 2018; Hamby et al., 2016; Wang et al., 2016), the sterile insect technique (SIT) could be exploited in the spring before fecund females enter crops. Consistent releases of sterile males could outcompete fertile males with the aim of reducing populations of *D. suzukii* in the crop. This method has already been shown to significantly reduce numbers of *D. suzukii* in open strawberry polytunnels by 91% throughout the season when compared with untreated control sites (Homem et al., 2022). This technique could be used with repeated releases in non-crop habitats to intercept newly emerged females from wild hosts before they enter the crop (Nikolouli et al., 2018). At this point, the mass traps would need to be removed to prevent sterile male captures. However, as more research and commercial availability is required for this approach, SIT could be a focus for future IPM strategies (Krüger et al., 2021).

Few farms involved in this study employed insect exclusion netting but this can be an effective form of physical protection from incursion of *D. suzukii* into crops (Cormier et al., 2015; Ebbenga et al., 2019). Even in commercial high-tunnel systems, netting reduced *D. suzukii* oviposition and delayed the impact on fruit by up to 3 weeks (Leach et al., 2016). Netting could be deployed as a vertical barrier around the crop margins at the start of the cropping season, limiting entry of low-flying *D. suzukii* from the non-crop habitat while allowing pollinator access over the top (Cini et al., 2012; Groot et al., 2021; Leach et al., 2016). However, without a roof barrier meeting these mesh borders, the effect on *D. suzukii* populations within the crop and related fruit damage can be limited. Insect exclusion netting is expensive but such approaches could be targeted at vulnerable sites such as those associated with woodlands or those with field margins containing SWD host plants identified as particularly vulnerable to SWD in this study.

Recommendations for management of non-crop habitats surrounding fruit crops warrant more research as these areas support natural enemies important for predation and parasitism of a variety of pests (Holland & Fahrig, 2000; Marshall & Moonen, 2002; Veres et al., 2013) and increases biodiversity on the neighbouring farmlands (Garratt et al., 2017; Groot et al., 2021; Haro-Barchin et al., 2018; Montgomery et al., 2020).

We recommend future research on control to focus on organic systems where control is currently less adequate than conventionally managed crops. For example, parasitoids such as *Trichopria drosophilae*, *Ganapsis brasiliensis*, and *Pachycrepoideus vindemmiae* have shown to develop on and reduce numbers of *D. suzukii* (Daane et al., 2021; Miller et al., 2015; Rossi-Stacconi et al., 2018; Wang et al., 2016). These parasitoids, if already established in certain regions, could be released in crop and non-crop habitats to further reduce *D. suzukii* populations prior to the growing period. But future research is needed to incorporate biocontrol measures such as this into an IPM strategy.

Whichever IPM strategy is used, we recommend making the neighbouring non-crop habitat a focus of *D. suzukii* control as our meta-analysis shows abundance is not only highest in host margins and woodland over the autumn and winter periods, but that this is not influenced by the crop type grown on site.

Limitations and further research

The data used in this meta-analysis were taken from assessments carried out in Korea, the US, Canada and Europe. Data from more regions and habitat types would provide better insight into the influences of certain landscape features on *D. suzukii* population abundance, particularly in non-temperate regions. Concerning publication bias, the power of the analyses used to detect bias in the studies used can be limited due to the relatively low number of studies included in this meta-analysis. As the response type was trap catches of mobile adults, the response was dependent on alate individuals being attracted to the bait in the traps. Different baits and trap designs were used across publications highlighting the possibility of bias in *D. suzukii* numbers in some studies (Rossi-Stacconi et al., 2013; Santoiemma et al., 2019; Valerio et al., 2019). However, all studies deployed the same trap type when comparing crop and the non-crop habitat within an individual study. An issue when trapping during crop susceptibility is the dilution effect which suggests *D. suzukii* will be more drawn to their host crop than they are to the trap. As such the trap activity can differ with the development stage of the crop and may have influenced the results. The authors recommend any future work to include fruit preference and oviposition and emergence studies to indicate reproductive success on different hosts. This data may be correlated with the habitat trap catch data to provide insights into the mechanism of why some habitats support a greater relative *D. suzukii* abundance than others giving growers a better indication of the potential of the habitat surrounding their farms acting as a source of *D. suzukii* populations. We have given recommendations for *D. suzukii* control in and around fruit farms but the impact of these controls is likely landscape, location, variety and crop dependent (Asplen et al., 2015; Lee et al., 2015; Little et al., 2021). We therefore recommend future research to focus on the impacts these variables have on the control methods suggested.

CONCLUSIONS

This study provides new evidence to guide land management decisions to control numbers of *D. suzukii* in surrounding habitats both in and out of season. We have identified differences in *D. suzukii* population abundance with field margins containing SWD host plants and woodland showing the highest numbers caught in traps. Winter is the most critical period in which non-crop habitats exhibit the highest numbers of *D. suzukii* relative to the crop. *Drosophila suzukii* control strategies could exploit this knowledge to reduce local populations in non-crop habitats and target in field approaches to the most vulnerable areas.

ACKNOWLEDGMENTS

The research was funded as part of the BBSRC Waitrose Collaborative Training Partnership (BB/S507325/1) and supported by BerryWorld. We thank the authors of the studies used when assessing for eligibility criteria and more specifically those which we extracted data from to be able to conduct this study. We also thank Mathias Harrer, M.Sc. and his respective coauthors for the helpful step-by-step ‘Doing Meta-Analysis in R’ guide.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supporting Information.

How to cite this article: Buck, N., Fountain, M.T., Potts, S.G., Bishop, J. & Garratt, M.P.D. (2022) The effects of non-crop habitat on spotted wing drosophila (*Drosophila suzukii*) abundance in fruit systems: A meta-analysis. *Agricultural and Forest Entomology*, 1–11. Available from: https://doi.org/10.1111/afe.12531