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Earlier activity of *Drosophila suzukii* in high woodland landscapes but relative abundance is unaffected

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Abstract Natural habitats can affect the population dynamics of mobile insects, and the spatial and temporal effects on agricultural pest species may be especially relevant for tailoring management strategies to the farm context. *Drosophila suzukii* Matsumura (Diptera: Drosophilidae) is suspected to utilize woodland habitat for wild hosts and overwintering with possible adverse effects of woods on adjacent fruit crops. A two-year study in the Upper Midwest, USA examined if the amount of woodland in the landscape affects early season activity and relative abundance of *D. suzukii* in raspberry fields. Thirty-five farms were selected to span a gradient of low-to-high woodland area at the 1.5 km scale. The first capture of *D. suzukii* occurred earlier at farms in high woodland landscapes. However, woodland area was not correlated with metrics of *D. suzukii* abundance in raspberry (growth rate, peak, fall, or total fly catch) suggesting similar crop infestation risk across landscapes. However, woodland area was negatively correlated with fall fly catch in the adjacent woods and significantly more flies were captured in the woods than raspberry. This study suggests woodland landscapes affect early season crop risk and the high numbers of *D. suzukii* in the woods have implications for understanding overwintering.

Keywords Wild host · Overwintering · Invasive · Spotted wing drosophila

Key message

- A 2-year field study in the Upper Midwest, USA found that high amounts of woodland are correlated with earlier activity of *D. suzukii*, but does not affect population levels in raspberry.
- High numbers of *D. suzukii* in the woods suggest that these habitats are providing resources such as wild hosts and overwintering sites.
- Growers with fields adjacent to woods should monitor for *D. suzukii* earlier, but overall pest pressure is unaffected by woodland in the surrounding landscape.

Introduction

Landscape composition has the potential to affect the population dynamics of mobile insect species (Tscharntke et al. 2005; Gardiner et al. 2009). The amount of natural habitat in the landscape can be an important driver if it provides resources such as food, nesting, or overwintering sites. In agroecosystems, these resources may be limited spatially or temporally by management practices and the monoculture of plant resources. The positive correlation between the proportion of natural habitat and insect population size has been well documented for beneficial guilds such as native bees,

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which provide critical pollination services in apple orchards (Mallinger and Gratton 2015) and in predator species such as native ladybird beetles, which provide biocontrol services to surrounding soybean fields (Gardiner et al. 2009). However, natural habitat can also be a source of insect pest populations (Rusch et al. 2013a, b). This study aimed to examine the influence of woodland habitat on the newly arrived invasive species in the USA, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), known commonly as spotted wing drosophila. Woodlands may affect *D. suzukii* populations by providing resources such as wild host plants and overwintering habitat. By understanding the drivers of *D. suzukii* timing of early season activity and population abundance, growers may be better able to make effective management decisions.

Drosophila suzukii is a major agricultural pest in Japan, Europe, and North America and significant economic losses in berry and tree fruit crops have been sustained (Bolda et al. 2010; Goodhue et al. 2011; De Ros et al. 2015). Current insecticide management recommendations for *D. suzukii* are problematic for use in integrated pest management programs because they consist of mainly broad-spectrum insecticides (Bruck et al. 2011; Van Timmeren and Isaacs 2013). Effective insecticides are non-selective with negative implications for natural enemies (Musser and Shelton 2003; Roubos et al. 2014) and pollinators (Wu et al. 2011), but many growers rely on these products to produce a marketable yield. Effective insecticide regimes require frequent sprays (Van Timmeren and Isaacs 2013) and increased labor and chemical costs are estimated at 6–8 % of farm gate value (Bolda et al. 2010). Management options for organic growers including organically approved insecticides are generally more costly and less effective (Van Timmeren and Isaacs 2013) and cultural methods such as field sanitation are labor-intensive. By understanding the phenology and abundance of *D. suzukii* in different landscapes, growers will be better able to tailor management spatially and temporally to lower environmental, economic and human health impacts while protecting their fruit crop.

Recent studies have identified the fly's host range to include not only its cultivated fruit crop hosts such as strawberry (*Fragaria* × *ananassa*) and blueberry (*Vaccinium* spp.) (Lee et al. 2011), but also wild hosts such as dogwood (*Cornus* spp.) and honeysuckle (*Lonicera* spp.) (Lee et al. 2015). Many of these wild hosts grow in woodland habitat in the Upper Midwest, USA raising the potential that farms with greater amounts of woodland in the surrounding landscape may have higher risk of infestation by *D. suzukii*. While the potential for many wild plants to be hosts of *D. suzukii* has been established (Lee et al. 2015), their relative contribution to the seasonal arrival and severity of fruit crop infestation remains unknown.

Little is known about the overwintering success of *D. suzukii* in the Upper Midwest. Trapping over the winter (2012–2013) in Wisconsin detected no activity between December and June (Guédot and Pelton, unpublished data). Recent studies simulating overwintering conditions suggest only a small proportion of adults could survive overwintering (Dalton et al. 2011) and most likely in a winter-morph form (Stephens et al. 2015). A field study in Italy suggests that successful overwintering occurs in protected microclimates (Zerulla et al. 2015) and woodland leaf litter may create suitable conditions. If the protection provided by woodland habitats improves overwintering survival, proximity to overwintering habitat may contribute early season *D. suzukii* activity and larger early season population size in crop fields.

Drosophila suzukii is an emerging pest in the Upper Midwest (initial detections in 2010–2012) and thus early season activity and dispersal are still poorly understood (Asplen et al. 2015). Spring wild hosts and woodland microclimates may provide additional resources and protection to build up local populations early in the season which can then move into susceptible fruit crops. In the fall, wild hosts may provide late-season resources which build up populations before the winter and suitable microclimates may increase survival rates.

The presence and quantity of wild hosts in the woodland may determine the relative contribution to local population levels. When both wild hosts and fruit crops are available, the total amount of resources available to ovipositing females would be higher than crops alone. The use of both wild hosts and fruit crops in the same area by *D. suzukii* has been documented in Florida with wild blackberry (*Rubus* spp.) and adjacent blueberry crops (Iglesias et al. 2014) and in Oregon with wild blackberry and cultivated raspberry (*Rubus* spp.; Klick et al. 2015). As *D. suzukii* is multivoltine in temperate climates, these additional resources of wild hosts may lead to higher overall populations.

The main question addressed in this study was whether the amount of woodland in the landscape affects early season activity and population abundance of *D. suzukii*. To examine this question, we conducted a two-year, season-long monitoring study of *D. suzukii* in raspberry crop fields and adjacent woods in three states in the Upper Midwest, USA in landscapes spanning a low-to-high woodland gradient at the 1.5 km scale. We predicted that at farms in highly wooded landscapes, *D. suzukii* would appear earlier and relative abundance would be greater compared with those with lower amounts of woodland.

Materials and methods

Site selection

To test the hypothesis that the amount of woodland in the landscape affects the early season activity and population abundance of *D. suzukii*, we conducted adult and larval monitoring at raspberry farms ranging across a low-to-high woodland gradient in the Upper Midwest, USA. Raspberry was used as the focal crop because it is widely grown and one of the most susceptible crops to *D. suzukii* (Lee et al. 2011; Bellamy et al. 2013). In 2013, we monitored *D. suzukii* adults and larvae at 18 farms in Southern Wisconsin. In 2014, we repeated adult monitoring at 17 farms over a wider geographic range (six farms in Southern Wisconsin, six farms in Southeast Minnesota, and five farms in Southwest Michigan). The amount of woodland in the landscape was estimated at the 1.5 km radius scale around raspberry farms. Although the dispersal capacity of *D. suzukii* is currently unknown, the species are suspected to disperse when resources are scarce (Mitsui et al. 2010). Additionally, the 1.5 km scale was chosen because landscape composition is typically found to have the greatest effect on moderately mobile insects at scales between 1 and 2 km (e.g., Gardiner et al. 2009).

Landscape composition surrounding raspberry field sites was evaluated using satellite-derived land cover imagery from the Cropland Data Layer (USDA NASS 2013). Land cover maps were imported into ArcGIS version 10.1 software (ESRI, Redlands, CA) and the composition of landscape around each field site was calculated for a circular buffer with a 1.5 km radius, centered on the raspberry crop field. Percent woodland area was calculated by combining all woodland classifications and dividing by total area of all landscape classifications in the 1.5 km buffer. Cropland Data Layer classifications included as woodland were forest, deciduous forest, evergreen forest, mixed forest, and woody wetland. In 2013, the sites in Wisconsin ranged from 5 to 60 % woodland area; in 2014, sites across the Upper Midwest ranged from 5 to 67 %, with five farms repeated both years in Wisconsin. This range of low-to-high woodland composition approximates the naturally occurring range of relative woodland area in the main agricultural regions of Minnesota, Michigan, and Wisconsin.

Raspberry fields within each farm ranged in size from a single 75 m row to 8 hectares, and pest management strategies included certified organic, no-spray, and conventional. The majority of the farms in the study cultivate a variety of crops including vegetables and other fruit crops including early-bearing strawberries and fall-bearing apples and grapes (*Vitis* spp.) which may also be susceptible to *D. suzukii*. Self-reporting of management and spray dates were collected from cooperating growers. The majority of farms did not report any insecticide use and farms that did spray reported a maximum of four insecticide applications including the use of spinosyns, pyrethroids, organophosphates, and neonicotinoids to target *D. suzukii* and other insect pests.

Habitat sampling

To determine if the surrounding woodlands contained potential sources of wild hosts, habitat sampling was conducted at farms each year of the study in June or July. In the woodland edge closest to the raspberry crop, a 100-m-long transect was established 5 m in and parallel to the woodland edge. Every 5 m, a 1 × 1 m quadrat was randomly placed on the ground for a total of 20 quadrats per farm. The presence of all plants which bear soft-skinned fruit (making them a potential host for *D. suzukii*) was recorded and identified to genus or species.

Adult monitoring

To understand how *D. suzukii* populations varied between farms with different landscapes, we conducted monitoring of adults using yeast-sugar baited traps in both the raspberry crop and adjacent woods at each farm. Traps consisted of a clear 946 mL plastic cup (Webstaurant Store, Lancaster, Pennsylvania, USA) and lid with ten 5 mm holes placed along the top rim of the cup. Bait consisted of 3.5 g dry active baker's yeast (Red Star, Milwaukee, Wisconsin, USA), 14 g granulated white cane sugar, and 177 mL water per trap. A drop of unscented dish soap (Seventh Generation, Burlington, Vermont, USA) was added to each trap to break surface tension and increase adult *D. suzukii* capture. Bait and trap design were chosen based on the capture reliability in multiple fruit crops and regions of the USA (Burrack et al. 2015); however, the relative attractiveness of the bait varies through the season based on the availability of nearby fruit crops.

Three traps were placed 1–2 m into the woods from the edge and within 300 m of the raspberry crop. Three additional traps were placed in the raspberry crop in the fruiting zone, suspended from canes or trellising. The traps were placed at least 2 m apart within the crop and at least 10 m from any woodland trap. Monitoring was conducted weekly from mid-June through October in 2013 and from late-May through early November in 2014. Each week, the yeast-sugar bait was replaced, and the contents of the three traps in each trap type (woods or raspberry) were pooled. Samples were assessed for the total number of female and male *D. suzukii* adults in the laboratory under a dissecting microscope. Samples were subsampled if the numbers of *D. suzukii* were >400 (in 2013) or >200 (in 2014) by counting 20 % of cells in a gridded tray and then estimating a sample total. In 2013, only 60–95 % of samples collected between late-July and mid-October were counted (a minimum of one sample every other week at each site). To standardize the data, all sample counts were divided by the number of traps and number of days the sample represented, then multiplied by seven for a weekly average of *D. suzukii* adults per trap.

From the catch data, we calculated six metrics of *D. suzukii* populations which represent risk to the raspberry crop and fall woods populations: (1) week of first detection, defined as the first week an adult was trapped in either the raspberry or woods trap at a farm; (2) raspberry population growth rate, defined as the change in abundance from the second week of non-zero trap catches through peak fly capture (transformed by $\log_{10}$) divided by the number of weeks for the raspberry traps; (3) raspberry peak population, defined as the highest adult catch recorded in the raspberry traps; (4) woods fall population, defined as the sum of every other week's trap catches from mid-August through October; (5) raspberry fall population, defined as the sum of every other week's trap catches from mid-August through October; and (6) total raspberry population, defined as the sum across all weeks' adult catches from mid-June through October. For weeks in 2013 without counts, an average of the preceding and following week was used.

Larval monitoring

To determine whether adult *D. suzukii* presence and abundance were correlated to crop infestation, the raspberry crop was sampled in 2013 to determine larval abundance. Fruit was sampled for larvae six times between late-July and early October in order to assess infestation in both summer and fall-bearing raspberry varieties. Each sample consisted of 65–100 g of ripe, marketable fruit collected from both the edges and center of rows. Fruit was placed in a sealed plastic bag in the field before being transferred to a refrigerator in the lab. Within 48 h, all fruits were subject to a fruit dunk-test. Fruit was lightly crushed to break the skin and then placed in the salt water solution (consisting of 72 g salt dissolved in 946 mL warm water per sample) for a minimum of 1 h before examination. Fruit samples were placed in a shallow glass tray with white paper underneath and a bright light shined on top in order to maximize visibility of larvae which floated to the surface. Larvae were confirmed as *Drosophila* larvae based on the presence of spiracles and larval form characteristics.

While *D. suzukii* are one of the only drosophilids able to oviposit in ripening fruit (Atallah et al. 2014), additional fruit samples were reared to adulthood to confirm that larvae present in fruit were *D. suzukii*. Samples were taken twice in 2013 (August and September) at all farms ($n = 18$) and once in 2014 (August) at a subset of farms ($n = 9$). Fruit samples were placed in plastic containers with a screen mesh bottom and slightly elevated so excess liquid could drain in order to minimize larval drowning. After 7–9 days, pupae (up to 40 per sample) were removed and placed on lightly moistened filter paper in a sealed Petri dish for 2 weeks when emerged adults were identified.

Statistical methods

To assess the hypotheses that the amount of woodland area affects *D. suzukii* timing and population abundance, we fitted multiple linear regressions for six metrics of the populations: (1) week of first detection; (2) raspberry growth rate; (3) raspberry peak population; (4) woods fall population; (5) raspberry fall population; and (6) raspberry total population. In each analysis, we modeled each population metric separately with relative amount of woodland area, year, and state as fixed effects. A paired t test was used to compare woods fall population and raspberry fall population for each farm. To determine if adult catch in raspberry was a reliable proxy for fruit infestation, larval abundance in raspberry was correlated to adult *D. suzukii* catch (from both the concurrent week's catch and the previous week's) as well as date and amount of woodland area using linear regression. All statistical analyses were performed in R (R Development Core Team 2012).

Results

Habitat sampling

In 2013, habitat sampling was conducted at 13 of the 18 farms; in 2014, at 15 of the 17 farms. At five farms, there was no substantial woodland (greater than 2 m wide) within 300 m of the raspberry crop or the adjacent woodland was not owned by the participating grower and therefore was not accessible, and no habitat sampling was conducted. A total of nine genera or species of plants confirmed as *D. suzukii* hosts were identified across all farms. Each farm in the study had at least two plant genera present. Percent cover of wild hosts (i.e., percent of quadrats with at least one host) ranged from 10 to 95 % between farms, with a mean of 60 ± 5 %. The most common potential host plants for *D. suzukii* were wild caneberries (*Rubus* spp.) and gooseberries (*Ribes* spp.). Common shrubs included European buckthorn (*Rhamnus* spp.), honeysuckle (*Lonicera* spp.), and dogwood (*Cornus* spp.). Other plants found rarely included elderberry (*Sambucus racemosa*), wild blueberry (*Vaccinium corymbosum*), bittersweet nightshade (*Solanum dulcamara*), and aronia (*Aronia melanocarpa*).

Adult monitoring

Drosophila suzukii was detected at all farms within a 5 week window from mid-June through mid-July in both 2013 and 2014. In 2013, mean first detection occurred on July 5th in Wisconsin; in 2014, mean detection occurred on June 26th in Michigan, July 1st in Minnesota, and July 9th

Table 1 Parameter estimates (±SE) of four multiple linear regressions for *D. suzukii* adult catches in 2013 and 2014 in Michigan, Minnesota, and Wisconsin as a function of the proportion of Woodland Area (evaluated at 1.5 km around a raspberry farm), state and year (as fixed effects)

Metric	Woodland area	State	Year	R^2	$F_{3,31}$	p
Date of 1st detection	−0.02 (0.01)	−0.79 (0.27)	0.37 (0.38)	0.379	6.32	<0.01
	$p = 0.05$	$p < 0.01$	$p = 0.34$			
Raspberry growth rate	−0.002 (0.002)	−0.23 (0.07)	0.15 (0.09)	0.354	5.65	<0.01
	$p = 0.29$	$p < 0.01$	$p = 0.11$			
Raspberry peak population	3 (11)	−488 (332)	87 (474)	0.105	1.21	0.32
	$p = 0.76$	$p = 0.15$	$p = 0.07$			
Raspberry fall population	−6 (15)	−207 (436)	−11 (622)	0.02	0.26	0.86
	$p = 0.69$	$p = 0.64$	$p = 0.99$			
Woods fall population	−56 (23)	−1066 (690)	−119 (984)	0.318	4.82	<0.01
	$p = 0.02$	$p = 0.13$	$p = 0.90$			
Total population (Raspberry)	−11 (32)	−897 (949)	421 (1355)	0.045	0.48	0.70
	$p = 0.73$	$p = 0.35$	$p = 0.76$			

Adult *D. suzukii* metrics included (1) week of first detection, defined as the first week an adult was trapped in either the raspberry or woods trap at a farm; (2) raspberry population growth rate, defined as the change in abundance from the second week of non-zero trap catches through peak trap catch (transformed by $\log_{10}$) divided by the number of weeks for the raspberry traps; (3) raspberry peak population, defined as the highest adult catch recorded in the raspberry traps; (4) woods fall population, defined as the sum of every other week's trap catches from mid-August through October; (5) raspberry fall population, defined as the sum of every other week's trap catches from mid-August through October; and (6) total raspberry population, defined as the sum across all weeks' adult catches from mid-June through October

in Wisconsin. Across both years and states, median and mean first detection occurred in the first week of July. The dominant phenology of the raspberry crop varied between farms at date of first detection: bud stage or flowering (20 % of farms), unripe fruit (34 %), unripe and ripe fruit (14 %), and ripe fruit (31 %). There was no pattern between phenology stage and date of first detection or amount of woodland in the surrounding landscape.

The week of first detection of *D. suzukii* in Wisconsin in 2013 was negatively associated with woodland area (parameter estimate: -0.028 ± 0.011, $p = 0.02$) and, across both years and all states, had a similar negative relationship that was significant ($p = 0.05$, Table 1). The results are qualitatively similar when the trap types are assessed separately. This model predicts that a farm with 60 % woodland in the surrounding landscape would detect *D. suzukii* one week earlier than a farm surrounded by 10 % woodland. There were also significant differences in the date of first detection among states ($F_{2,14} = 5.6$, $p = 0.02$) and *D. suzukii* was detected in Michigan earlier than Wisconsin (Tukey's HSD: $p = 0.01$).

The amount of woodland surrounding sampling areas was not associated with any other indices of *D. suzukii* population in raspberry including raspberry growth rate, raspberry peak population, raspberry fall population, and raspberry total population (Table 1). Population growth rate ranged from 0.364 to 1.145 (log *D. suzukii* change/week) and varied significantly among the three states, with populations increasing more slowly in Michigan than Wisconsin or Minnesota (Table 1; Figs. 1, 2). In 2013,

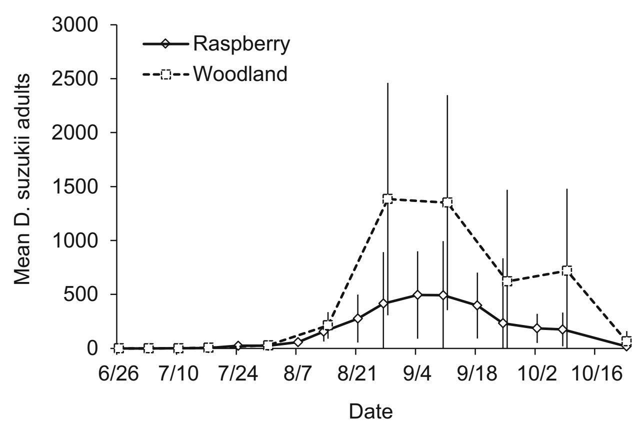

Fig. 1 Phenology of *D. suzukii* adults (±SE) captured per trap per week in raspberry crop fields and in adjacent woodlands from mid-June through October 2013 at 18 Wisconsin farms

population growth rate was 0.778 (±0.040) in Wisconsin; in 2014, population growth rate was 0.344 (±0.060) in Michigan, 0.852 (±0.081) in Minnesota, and 0.846 (±0.117) in Wisconsin. Peak population in raspberry ranged from 103 to 2,637 adults with no significant differences between state and year. In 2013, mean peak population was 685 (±134) in Wisconsin; in 2014, mean peak population was 229 (±76) in Michigan, 1767 (±851) in Minnesota, and 1229 (±375) in Wisconsin. For the five farms that were sampled in both years of the study in Wisconsin, peak fly captures varied by as few as 15 adults and as many as 1961 adults (an order of magnitude difference), despite similar management practices and landscape composition between

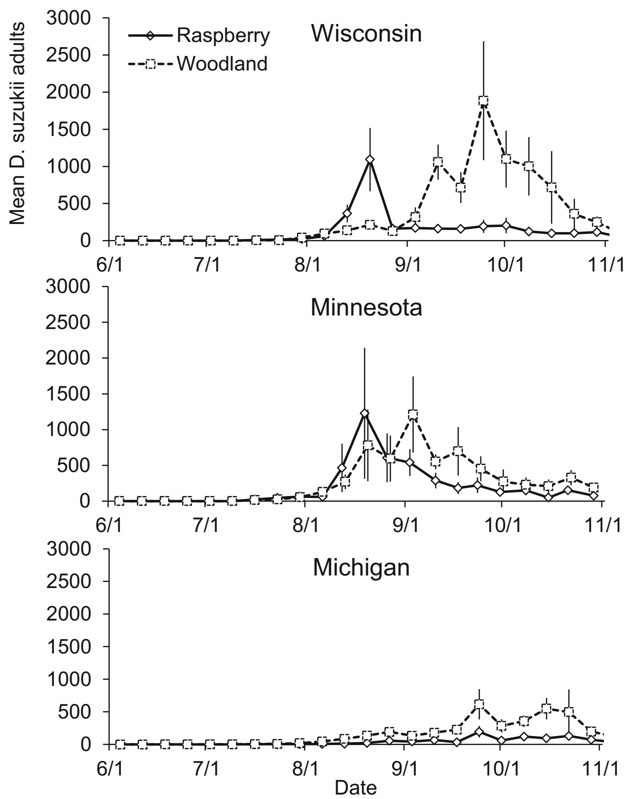

Fig. 2 Phenology of *D. suzukii* adults (±SE) per trap per week in the raspberry crop and in adjacent woodlands June through early November 2014. Trapping consisted of six farms in Wisconsin, six farms in Minnesota, and five farms in Michigan

years. *Drosophila suzukii* captures in raspberry reached a peak between mid-August and late-September (Figs. 1, 2) with no significant differences between years or state (Table 1). Mean raspberry fall population was 1226 (± 230) and mean raspberry total population was 3017 (±506) adults with no significant differences between years or states. Mean woods fall population was 3409 (±435) and woods fall trap catches were significantly higher than raspberry fall trap catches ($t = -4.80$, $df = 34$, $p < 0.0001$). Moreover, the amount of woodland area in the surrounding landscape was negatively associated with woods fall population (Table 1).

Larval monitoring

Drosophila larvae were present in all raspberry crop fields in 2013 and in 79 % of the 65 fruit samples assessed. Densities ranged from 0 to 3 larvae per gram of fruit with a mean of 0.40 (±0.07) larvae per gram over the fruiting season. Between both 2013 and 2014, 99 % of *Drosophila* larvae reared from raspberry samples ($n = 40$) were confirmed to be *D. suzukii.* Larval abundance was positively correlated with concurrent week adult trap catch within the raspberry crop ($r = 0.246$, $p = 0.048$), but there was no correlation of larval abundance with the previous week's adult trap catch ($r = 0.121$, $p = 0.33$). An additional model including date and woodland area along with concurrent week adult trap catch showed no significant effect of either on larvae numbers ($r = 0.308$).

Discussion

We hypothesized that as the amount of woodland in the landscape increased, *D. suzukii* flies would appear earlier and would achieve greater population abundance. In support of this hypothesis, we found that *D. suzukii* adults appear earlier in the season at farms in landscapes with higher amounts of woodland. This pattern was particularly pronounced in Wisconsin in 2013, but was also observed when combining results across states in the second year of the study. Farms surrounded by relatively high amounts of woodland (e.g., 60 % of area within 1.5 km of a farm) had flies first collected in traps 1 week earlier on average than farms surrounded by low amounts of woodland (10 % woodland). The stronger patterns when the study was conducted only in Wisconsin may be due to reduced variability in other factors, such as climate or other characteristics of the woodland habitat. However, whether the pattern of earlier arrival is consistent in other geographic areas needs to be examined in more detail since there was a spatial variation in this study, with stronger patterns with woodland area in Wisconsin in 2013 and earlier detections in Michigan.

One possible reason for earlier activity of *D. suzukii* may be that woodlands provide fall-bearing wild hosts or overwintering habitat. The presence and abundance of wild hosts immediately adjacent to raspberry farms were similar across farms and states, with each site containing at least two different genera of potential host for the flies and on average a similar relative abundance of potential hosts in these woodlands. Most of these hosts have ripe fruit during mid-to-late summer, so they have the potential to provide resources for *D. suzukii* at a time that coincides with cultivated summer and fall-bearing raspberries. However, unlike cultivated fruits, wild host fruits are not harvested and may persist longer into the fall. We collected flies in woods traps into early November (Figs. 1, 2), suggesting they are utilizing woodland habitat. Recent studies focused on *D. suzukii* overwintering (Dalton et al. 2011; Jakobs et al. 2015; Stephens et al. 2015; Zerulla et al. 2015) have suggested that *D. suzukii* overwinter as adults. The Upper Midwest has cold and relatively long winters with average temperatures below 0 °C for four to 5 months. This may cause high mortality of *D. suzukii* as laboratory simulations (Dalton et al. 2011; Jakobs et al. 2015) and the lack of adults found in winter trapping (Guédot and Pelton, unpublished data) have suggested. However, if some flies survive, they may be the first to start recolonizing and cause earlier arrival on farms in landscapes with high amounts of woodland. Another possibility is that wild hosts are utilized by adults for food in the fall rather than oviposition sites. To meet overwintering energy needs, females may need to build up sufficient fat reserves through feeding or, if lacking, be required to reabsorb eggs. Dissections of adults after a typical winter found indiscernible ovaries in 90 % of females and in 50 % of females after a mild winter (Zerulla et al. 2015). These results raise the possibility that wild hosts may provide much needed food resources for females to overwinter successfully in cold climates. Higher fat reserves, in turn, could lead to a higher proportion of females with mature eggs in the spring.

The patterns of *D. suzukii* arrival and population growth rate varied across the three states. In particular, the dynamics of *D. suzukii* in Michigan appeared to be different than Wisconsin and Minnesota. In Michigan, flies were detected earlier than in Wisconsin and increased more slowly than Minnesota or Wisconsin. It is unclear whether this pattern is broadly representative of the state due to the limited sample size of each state in 2014 ($n \leq 6$). However, there are differences in abiotic factors such as temperature that may explain the differences between states on either side of Lake Michigan. Michigan farms were located in Southwest and Southcentral parts of the Lower Peninsula, which experiences relatively warmer spring temperatures and could favor earlier spring populations. Additionally, higher levels of snow cover during the winter in Michigan may provide protection that enhances winter survival compared to Minnesota and Wisconsin. *Drosophila suzukii* activity and reproduction slows at high temperatures (Tochen et al. 2014), but whether or not this explains the slower growth rate recorded in Michigan was not assessed. It is more likely that the very active management of this pest using insecticides at the farms in Michigan reduced the growth rate compared with the other states. The degree to which abiotic and management factors influence *D. suzukii* population trends is an active area of investigation (Wiman et al. 2014) and will help better understand crop risk in different regions.

All other indices of *D. suzukii* population size in raspberry fields, including population growth rate, peak population, total abundance in the late-season (fall), and overall population (total) size were not associated with the amount of woodland in the surrounding landscape. In the Upper Midwest, most species confirmed as wild hosts (e.g., wild caneberries, honeysuckle, and dogwood) bear fruit in mid-to-late summer. For example, honeysuckles typically fruit in late-June through the end of September. This phenology suggests that wild hosts in the Upper Midwest could provide resources at the same time as the availability of raspberries and other commonly grown fruit crops susceptible to *D. suzukii* which may be present at a farm (e.g., blueberry). Raspberry is a highly preferred fruit (Bellamy et al. 2013) and, in a cultivated field, is available to *D. suzukii* in high quantity and density. A synchronized phenology between abundant fruit crops and relatively sparse wild hosts may explain the lack of relationship between *D. suzukii* populations in raspberry and amount of woodland in the landscape.

It is also possible that wild hosts could influence *D. suzukii* populations at a finer scale than this study examined, as the flies have been shown to utilize both wild hosts and crops at field edges (Iglesias et al. 2014; Klick et al. 2015). Therefore, using total woodland area within the landscape as an index of woodland resource abundance may be at too coarse of a scale to find associations with patterns in fly abundance. The distance *D. suzukii* adults forage is unknown, but if local resources are abundant, foraging distance may be quite short and fine scale effects of wild hosts may be most noticeable in crops within meters of woodland, not kilometers.

In warmer geographic regions, wild hosts in woodland landscapes may be more important to *D. suzukii* populations, and therefore crop risk, by providing temporal continuity of resources. If fly populations are not reduced by high winter mortality, wild hosts can create temporal resource continuity (e.g., with citrus crops in California and the southeastern USA). *Drosophila suzukii* has been detected year-round in California (Hamby et al. 2014; Harris et al. 2014) and North Carolina (Burrack et al. 2012) and woodland may affect the abundance of spring populations more acutely in these regions due to lower overwintering mortality.

We predicted a positive correlation between woodland area and fall populations of *D. suzukii*, but interestingly the relationship was the opposite in the woods, with fewer flies trapped in woods traps where there was a high proportion of woodland in the landscape. One possible explanation for this pattern is a resource dilution effect. That is, at farms with low amounts of woodland adjacent to the raspberry field, the woodlands present may serve as the only refuge for overwintering or source of wild hosts. When there are high amounts of woodland in the landscape, adults emerging from the raspberry crop can disperse across a larger area on the farm-scale. Adults may be able to select from a much larger area to find the ideal microclimatic habitat for overwintering (Zerulla et al. 2015). Baited taps in the woods may also be relatively more attractive at farms with minimal woodland due to the reduced availability of wild host fruits. Further work is required to understand the nature of the relationship between *D. suzukii* and woodland landscapes which rests on a better understanding of all the habitats and hosts in which flies develop over the course of a year and dispersal dynamics among habitats.

One insight gained from this study includes the continued value of sampling of fruit for larvae rather than relying on adult fly catches to assess risk. While larval infestation and concurrent adult abundance were positively correlated, the previous week's trap catch was highly variable and a weak predictor of infestation. Other studies have also found adult trap catch to be a weak predictor of larval infestation (Hamby et al. 2014; Burrack et al. 2015). Moreover, once larvae are found in fruit, management options are limited although some insecticides can limit further development of larvae (Wise et al. 2014) and culling fruit may be required if mature larvae are detected. The timing of early season *D. suzukii* activity may be important for growers to focus monitoring and could lead to cultivar selection for varieties which ripen during periods of low *D. suzukii* populations, such as early-ripening blueberries in Rhode Island (Hampton et al. 2014). Despite adult fly activity earlier in the season in high woodland landscapes, this study found that raspberry crops are at no greater risk for high *D. suzukii* populations in such landscapes. This suggests that integrated pest management within the crop field may be sufficient to effectively manage *D. suzukii* populations, which is good news for growers due to the relative immutability of landscape composition beyond the borders of their farms (i.e., 1.5 km scale).

This study is the first to examine the link between *D. suzukii* phenology and populations in cultivated crops and the amount of natural area at a landscape level. We found that *D. suzukii* are active earlier in the season in landscapes with high amounts of woodland area but overall risk to raspberry crops is similar across landscapes. *Drosophila suzukii* are present in high numbers in resource-rich woodlands bordering crop fields throughout the summer and fall. Our findings contribute to the growing understanding of the overwintering of *D. suzukii* and early season crop risk.

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Author contributions EP and CGratton conceived and designed the research. AB, EP, and SVT conducted field and laboratory research. EP and CGratton analyzed data. EP wrote manuscript. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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