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Agricultural landscape affects sex-specific differences in the abundance of *Drosophila suzukii* in raspberry orchards

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Abstract

In recent decades, the spotted wing *Drosophila* (SWD) (*Drosophila suzukii*), an invasive pest, has caused a great deal of damage to fruit crops. There is therefore an urgent need to develop strategies to control the populations of this species. It has been found that the landscape context can buffer or increase the severity of pest outbreaks in agriculture, and it is important to understand how this process works in SWD for all crops. Given this background, we investigated the influence of forest on SWD populations in raspberry orchards and surrounding agricultural land. We selected 10 locations in the central part of Slovenia, five of which were closer than 200 m from the forest edge and five of which were more than 200 m from the forest edge. We collected SWD adults in three habitat types per location from the end of June until the end of October 2020. The results showed that forest harboured a larger SWD population than orchards and agricultural land. Over the season, the number of individuals increased exponentially over time, and the difference between forest and other habitat types increased. The distance from the forest had a negative effect on the abundance of SWD. There was a difference in abundance observed between males and females, with males being less abundant farther away from the forest than females. However, the distance from the forest only had a negative effect on the abundance of females in September. Based on the results, we propose potential measures for the control of SWD in raspberry orchards.

KEYWORDS

agricultural ecosystem, integrated pest management, invasive species, raspberry, spotted wing drosophila

1 | INTRODUCTION

The landscape context is important for understanding pest management (Evans, 2005; Jonsson et al., 2012; Rusch et al., 2013; Thies et al., 2003, 2005). It affects the populations of pests and their natural enemies in different ways at different scales (Evans, 2005; Gardiner et al., 2009; Jonsson et al., 2012; Rusch et al., 2013). The simple agricultural landscapes of intensive farming have the potential to dramatically, but not necessarily, increase pest populations (Chaplin-Kramer et al., 2011; Rusch et al., 2013) while negatively impacting natural enemies (Chaplin-Kramer et al., 2011; Jonsson et al., 2012). Forest patches, bushes, hedgerows and other landscape structures provide hiding places for natural enemies (Garratt et al., 2017; Miñarro & Prida, 2013; Morandin et al., 2014). However, large non-crop areas can also have negative effects such as the spillover of pests from adjacent habitats to crops (Rodriguez-Saona et al., 2018; Tscharntke et al., 2005, but see Chaplin-Kramer et al., 2011; Karp et al., 2018). The habitat requirements of invasive species are often not yet known in the newly introduced environment, especially when there are interactions between habitat types (With, 2002). The management of these species becomes very difficult when the pest is not a priority for the different stakeholders managing these habitat types (e.g. forestry versus. agriculture). In this case, it is even more important for pest management to integrate the landscape into pest management planning (Dent & Binks, 2020).

We investigated the influence of the landscape context on the spotted wing *Drosophila* (SWD) (*Drosophila suzukii* (Matsumura, 1931)), an invasive pest. The native distribution of SWD is in Asia, but it was introduced in Europe and the USA (Calabria et al., 2012; Cini et al., 2012; Hauser, 2011). It causes damage to economically important fruit crops in the EU and the USA (Asplen et al., 2015; Cini et al., 2012). Depending on the year, yield losses have been estimated to be from 30% to 100%. The costs of SWD damage in the USA are estimated at 500 million dollars per year (Bolda et al., 2010).

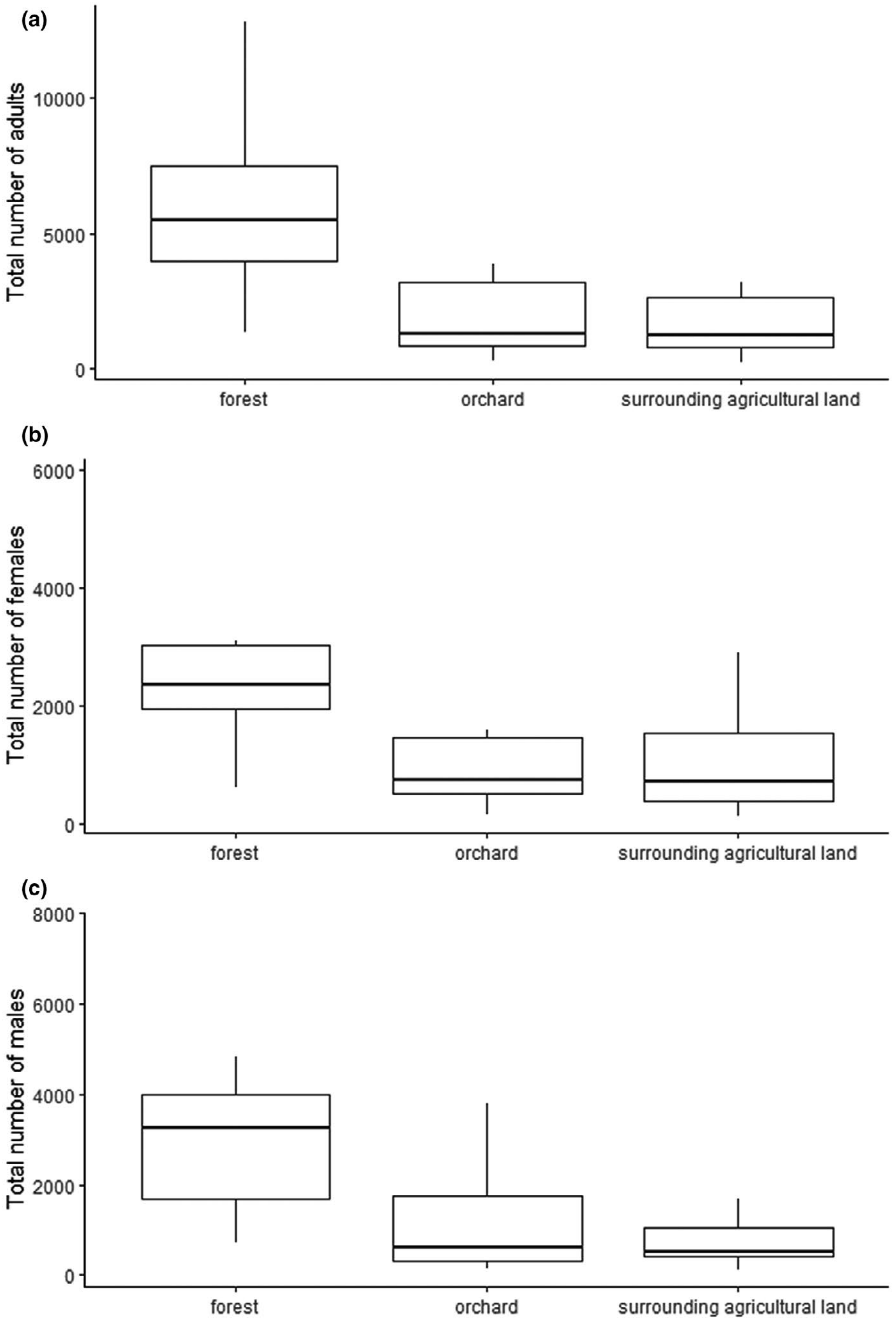

FIGURE 1 Boxplot showing the total number of SWD caught per habitat type: (a) adults, (b) females and (c) males. The data are shown in boxplots with the represented by the median value, 25th and 75th percentile and outliers (black dots)

TABLE 1 Model statistics for the comparison of the trap catch of SWD between different habitat types compared with forest for all specimens and separately for females and males, their estimates, standard error, z value, *p* value and significance (* $p < 0.05$, ** $p < 0.01$, ***$p < 0.001$)

Model	Variable	Estimate	Std. Error	z value	Pr(>|z|)	
Adult	(Intercept)	8.622	0.280	30.83	< 0.001	***
	Habitat type-agricultural land	−1.174	0.305	−3.85	< 0.001	***
	Habitat type-orchard	−1.060	0.305	−3.48	< 0.001	***
Female	(Intercept)	7.833	0.273	28.71	< 0.001	***
	Habitat type-agricultural land	−1.076	0.283	−3.81	< 0.001	***
	Habitat type-orchard	−0.968	0.281	−3.44	< 0.001	***
Male	(Intercept)	8.007	0.292	27.40	< 0.001	***
	Habitat type-agricultural land	−1.251	0.343	−3.65	< 0.001	***
	Habitat type-orchard	−1.132	0.343	−3.30	< 0.001	***

One of the reasons that this species is so invasive is because it is highly polyphagous (Kenis et al.2016; Poyet et al.2015). Additionally, it can have more than 10 generations per year and is able to damage healthy, undamaged fruit with its serrated ovipositor, whereas other fruit flies can only feed on damaged and/or rotting fruit (Atallah et al., 2014; Rota-Stabelli et al., 2013). The main habitat of this species is forest (Santoiemma et al., 2018), which provides breeding (Kenis et al., 2016; Poyet et al., 2015) and overwintering resources (many optimal microclimatic conditions) (Zerulla et al., 2015). Therefore, there should be a better understanding of the effect of forest on nearby agricultural land in relation to pest pressure.

In the last few years, several studies have investigated the impact of the surrounding landscape on the abundance of SWD in small fruit orchards (Haro-Barchin et al., 2018; Santoiemma et al., 2018, 2019; Tait et al., 2020). However, most research has only been done in the vicinity of forest (Tonina et al., 2018) or just for sweet cherry and blueberry crops (Haro-Barchin et al., 2018; Tonina et al., 2018), and some research has been done only early in the season when SWD populations are relatively small (Tonina et al., 2018). However, it has been observed that SWD can disperse naturally up to 9 km (Tait et al., 2018) and that the population dynamics can synchronize over a distance of more than 100 km (Santoiemma et al., 2019). Although Tonina et al. (2018) and Tait et al., 2020) worked on migration of SWD in orchards located near forests in a shorter time frame or focused on daily dispersal, no single study has examined how the distance from the orchard to the forest affects populations over the whole crop growing period and what impact the surrounding agricultural land has on the migration ability of SWD. Additionally, dispersal potential and phenology can be different per species and sex (Mazzi & Dorn, 2012; Zera & Denno, 1997). As females are the main cause of fruit damage, it is important to understand the impact of the distance from the forest on females. This knowledge would be highly beneficial for the development of SWD management strategies.

The aim of the study was therefore to investigate the effect of landscape structure on SWD population structure in the agricultural landscape. We attempted to answer four questions: (a) How far does the spillover effect from forest to raspberry orchards reach? (b) Does the surrounding agricultural land accumulate a higher number of SWD individuals that might affect crops? (c) If there is a difference in the effect of habitat type and distance from the forest, how does this reflect in the abundance of males and females? (d) Does the population dynamics change differently over time for habitat type and distance? We hypothesized that only orchard and other habitat types within 200 m of forests are strongly affected by forest and that the effect dissipates with increasing distance from the forest because of the availability of potential hosts and hibernation resources. Furthermore, we hypothesized that surrounding agricultural land does not have a large number of SWD that could threaten crops because it contains fewer resources for SWD.

2 | MATERIALS AND METHODS

2.1 | Area description

Slovenia is a Central European country that lies at the crossroads of several biogeographic regions: Alpine, Dinaric, sub-Mediterranean and sub-Pannonian. Agricultural land accounts for 33% of the surface area of the country, while 58% is covered with forests. On the landscape scale, the area is very heterogenous with respect to agricultural land and forest, and almost all land is within 1 km of any forest edge. In 2019, there were 264 raspberry orchards registered in Slovenia, covering an area of 36.2 ha and located mostly in the central, temperate part of the country.

2.2 | Survey protocol

SWD were collected on 10 locations in the central part of Slovenia chosen on the basis of their distance from the forest. In five of the locations, the orchard was within 200 m of the forest edge, and in the other five locations, the orchard was more than 200 from the forest edge. These orchards were selected from the GERK database (Ministry of Agriculture, Forestry and Food of Slovenia; Agricultural and Forestry Land Use Database; http://rkg.gov.si/GERK/WebViewer/). Six out of ten of the chosen raspberry orchards were not treated with insecticides against SWD or other pests and diseases. For the other four raspberry orchards, it was not known whether pesticides were used. However, there was no difference in the abundance of individuals of SWD between the untreated orchards and those where the treatment was not known, as shown from a preliminary analysis with a generalized linear model with negative binomial error distribution (total number of adults during the whole season: $\chi^2 = 0.178$, $df = 1$, $p = 0.673$; total number of females of the whole season: $\chi^2 = 0.671$, $df = 1$, $p = 0.413$; total number of males of the whole season: $\chi^2 = 0.002$, $df = 1$, $p = 0.967$). The locations were between 300 and 680 m above sea level and were more than 10 km apart. Within each location, three habitat types were selected: orchard, surrounding agricultural land and forest. The surrounding agricultural land contained bushes, grassland and hedges (which included different grass species, annual herbs, such as *Portulaca oleracea*, *Amaranthus retroflexus*, *Senecio vulgaris*, *Plantago major*, *Sonchus asper*, *Galinsoga quadriradiata*, *Taraxacum officinale*, *Plantago media*, *Trifolium prataense*, *Trifolium* sp., *Veronica* sp., and perennials, such as *Rubus* spp., *Salix* spp., *Prunus* spp., and *Alnus glutinosa*). These sites represented the agricultural land in the study area. SWD sampling in the surrounding agricultural land was performed at the midpoint between the forest and the orchards.

The sampling of SWD was done with Suzukii traps using the Russell IPM attractant (PH-288-1BP)-dry lure (both are manufactured by Russell IPM, integrated pest management) and filled with a mixture of wine vinegar and red wine (Cviček) (3:1). The traps were refilled every sampling day. One trap was placed and sampled every second week within each habitat type. The sampling started before the ripening of raspberries in the third week of June 2020 and ended in the last week of October 2020. The samples were brought to the laboratory, where individuals were sexed and counted for every period per trap.

2.3 | Data analysis

Initially, SWD catches were pooled for the whole period for each trap. One period for two traps each was missing because of mishaps in the field. These data were interpolated by using a prediction line between the prior and subsequent sampling periods. Additionally, the number of adults, females and males was divided by the number of sampling days and multiplied by 14, because we sampled every second week, approximately every 14 days.

We analysed the data using a general linear model (GLM) and generalized linear mixed model (GLMM) using a negative binomial error distribution (Zuur et al., 2009). The independent variable for model 1 was the habitat type (surrounding agricultural land, forest, orchard); for model 2 the week of the year, habitat type and their interaction; for model 3 the habitat type (forest, orchard), distance (more or less

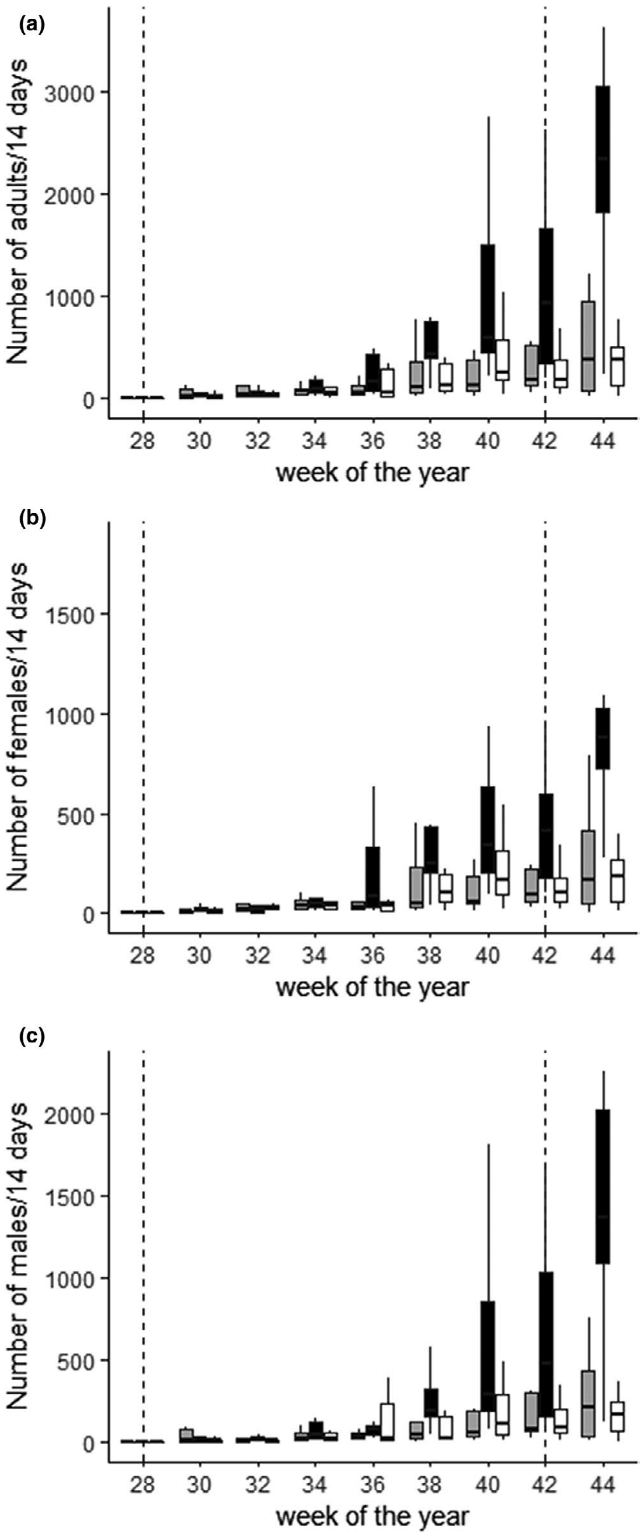

FIGURE 2 Boxplot showing the numbers of adults, females and males collected every 14 days, presented for the different habitat types in the sampled period. Grey shows surrounding agricultural land, black shows forest and white shows orchards. Vertical dotted lines show the raspberry harvest period. The data are represented by the median value, 25th and 75th percentile, and outliers (black dots)

TABLE 2 Model statistics for the comparison of the trap catch of SWD between different habitat types throughout the season from the 28th to the 44th week of 2020 and separately for every 2 weeks. Results are for all specimens and separately for females and males, presented as an estimate, standard error and significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Habitat types were compared with the forest habitat type. Weeks were compared with week 28

	Adults			Females			Males		
Variable	Estimate	Std. Error	Sig.	Estimate	Std. Error	Sig.	Estimate	Std. Error	Sig.
Habitat type-forest	−1.234	0.499	*	−0.577	0.576		−1.603	0.559	**
Habitat type-orchard	−0.877	0.491	.	−0.235	0.556		−1.304	0.552	*
Week 30 * agricultural land	1.676	0.463	***	1.588	0.515	**	1.713	0.502	***
Week 32 * agricultural land	2.025	0.469	***	2.938	0.509	***	1.397	0.511	**
Week 34 * agricultural land	2.148	0.468	***	2.914	0.506	***	1.695	0.512	***
Week 36 * agricultural land	2.297	0.467	***	2.784	0.509	***	2.066	0.508	***
Week 38 * agricultural land	3.480	0.472	***	4.272	0.508	***	3.020	0.516	***
Week 40 * agricultural land	3.388	0.470	***	4.152	0.508	***	2.962	0.512	***
Week 42 * agricultural land	3.586	0.469	***	4.214	0.506	***	3.269	0.511	***
Week 44 * agricultural land	4.034	0.468	***	4.749	0.507	***	3.625	0.507	***
Week 30 * forest	1.424	0.662	*	1.274	0.729	.	1.605	0.738	*
Week 32 * forest	1.514	0.662	*	0.726	0.724		2.013	0.735	**
Week 34 * forest	2.345	0.661	***	1.707	0.724	*	2.676	0.726	***
Week 36 * forest	2.401	0.660	***	2.132	0.725	**	2.355	0.727	**
Week 38 * forest	2.030	0.665	**	1.451	0.723	*	2.283	0.737	**
Week 40 * forest	2.359	0.660	***	1.594	0.719	*	2.843	0.728	***
Week 42 * forest	2.290	0.659	***	1.536	0.718	*	2.761	0.727	***
Week 44 * forest	2.681	0.660	***	1.770	0.719	*	3.286	0.728	***
Week 30 * orchard	0.604	0.653		0.711	0.715		0.650	0.729	
Week 32 * orchard	0.522	0.653		−0.212	0.706		1.052	0.725	
Week 34 * orchard	1.743	0.656	**	1.181	0.706	.	2.029	0.725	**
Week 36 * orchard	1.647	0.654	*	0.990	0.705		2.145	0.719	**
Week 38 * orchard	0.999	0.656		0.305	0.705		1.482	0.724	*
Week 40 * orchard	1.085	0.655	.	0.397	0.705		1.566	0.722	*
Week 42 * orchard	0.571	0.656		−0.035	0.705		0.984	0.723	
Week 44 * orchard	0.634	0.655		−0.120	0.704		1.183	0.721	

than 200 m between orchard and forest) and their interaction; for model 4 the week of the year, habitat type (forest, orchard), distance (more or less than 200 m between orchard and forest) and their interaction; and for model 5 distance (more or less than 200 m between orchard and forest). For models 1, 3 and 5, the dependent variables were the total number of females, total number of males and total number of adults for the whole season, while for models 2 and 3, we used the same dependent variables but per sampling period. For models 1, 2, 3 and 4, location was used as a random effect. Although model 5 had two habitat types per location, the random effect had a very small standard deviation. Therefore, a negative binomial model without random effect was used. The best model was selected on the basis of stepwise backward selection with the help of the Akaike information criterion (Burnham & Anderson, 2002). The LME4 (Bates et al., 2014) and MASS (Venables & Ripley, 2002) libraries in the statistical program R (R Core Team, 2018) were used for the analysis. The data set is stored in the repository Dryad (de Groot et al., 2020).

3 | RESULTS

In total, there were 103,330 adult SWD caught over the whole period: 49,160 females and 54,170 males. On average, there were 395 adults, 188 females and 207 males, per trap per 14 weeks.

Comparison between traps in different habitat types showed that orchards and surrounding agricultural land had a significantly lower number of adults than forests (Figure 1a; Table 1). The same result was found for females (Figure 1b) and males (Figure 1c; Table 1).

The total number of SWD adults caught in traps was influenced by week of the year, habitat type and the interaction between week of the year and habitat type (Figure 2a; Table 2). There was a significant increase in the number of adults in surrounding agricultural land from week 28 onwards. In forests, the number of SWD caught in traps was significantly lower compared with that caught in traps in surrounding agricultural land for week 28. Orchards only had a significantly higher catch than the agricultural land in weeks 32 and

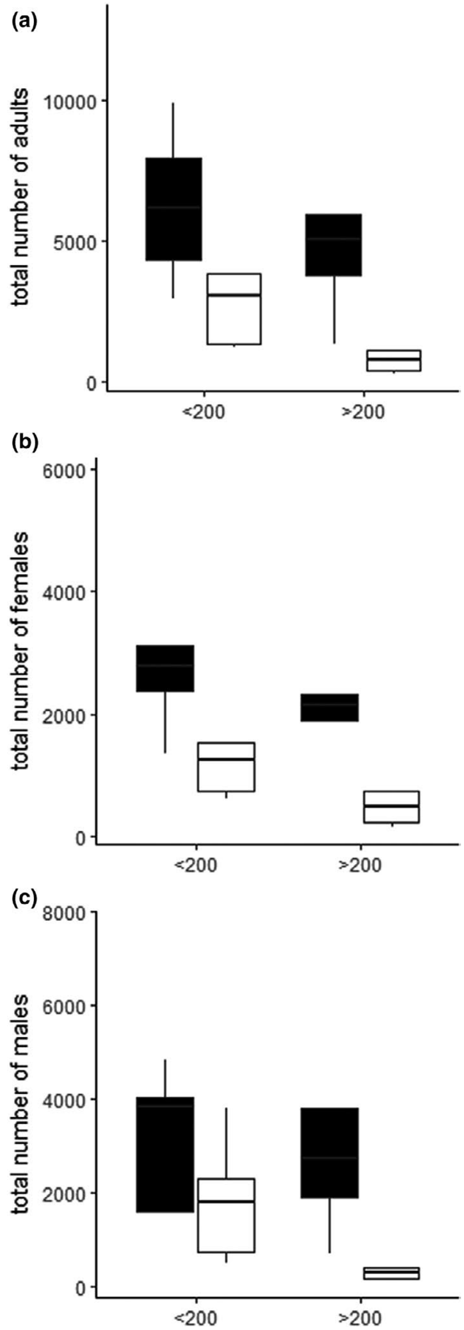

FIGURE 3 Boxplot showing the difference in the number of caught SWD between forest (black) and orchard (white; less than 200 m or greater than 200 m from forest) for (a) adults, (b) females and (c) males. The data are represented by the median value, 25th and 75th percentile, and outliers (black dots)

34 compared with week 28. The number of females was increasingly higher in the other periods in agricultural land compared with week 28 (Figure 2b; Table 2). In week 28, there was no difference in the number of females observed. However, from week 34 onwards, the number of females was increasingly higher in forests, while there was no difference observed for orchards compared with the difference observed in week 28.

Also, the number of males was increasingly higher for agricultural land as the season progressed (Figure 2c; Table 2). In week 28, there was a lower number of males observed in forests and in orchards compared with the agricultural land surrounding the orchards. The number of males in the forest increased over the study period compared with the difference in week 28. For orchards, the number of males was only higher in weeks 34 to 40 compared with the difference between orchards and agricultural land in week 28.

There was no difference in the total number of SWD adults in forest regardless of the distance from the orchard (Figure 3a; Table 3). Generally, fewer SWD were caught in orchards compared with forests, and in orchards more than 200 m from forest, the decrease was even greater. For females there was no difference between forest in both distance categories (Figure 3b; Table 3); however, there were fewer females in orchards compared with forest. For males, there was no difference for forest in the two distance categories (Figure 3c; Table 3) and between forests and orchards, but in orchards more than 200 m from forest, there were significantly fewer males compared with orchards closer than 200 m from forest.

In general, the total number of adults was the same between forests and orchards in week 28 (Figure 4a; Table 4). There was an increase in the total number of adults observed over the following sampling weeks. There was no difference between forests for the different distance categories. The difference in the total number of adults between forests and orchards became larger from weeks 40 to 44. There were significantly fewer adults in orchards that were more than 200 m from forest compared with those that were less than 200 m from forest.

The number of females was the same in forests and orchards, and in forests in the two distance categories in week 28 (Figure 4b; Table 4). There was an increase in females observed over the following sampling weeks. The difference in the number of females between forests and orchards became larger from week 38 to 44. There were significantly fewer females in orchards more than 200 m from forest compared with forests in weeks 38 and 40 compared with week 28.

In general, the number of males was the same between forests and orchards in week 28 (Figure 4c; Table 4). There was an increase in males observed over the following sampling periods. There was no difference in abundancee of males between locations with forests which are further than 200 m and less than 200 m from orchards. The difference in the number of males caught in forests or orchards became larger from week 42 to 44. In general, there were significantly fewer males in orchards more than 200 m from forest compared with those less than 200 m from forest.

The total number of caught adults, females and males in traps had a significant negative relationship with the distance of the orchard and the surrounding agricultural land from the forest (Figure 5; Table 5). The logarithmic correlation shows that SWD abundance drops sharply near forest but decreases with distance from the forest.

TABLE 3 Model statistics for the comparison of the trap catch of SWD between orchards and forests, between orchards with different distances (< 200 m or >200 m) from forest, and for the interaction between them. The results are for all specimens and separately for females, presented as an estimate, standard error, z value, *p* value and significance (**p* < 0.05, ***p* < 0.01, ****p* < 0.001)

Model	Variable	Estimate	Std. Error	z value	Pr(>|z|)	
All adults	(Intercept)	8.729	0.151	57.67	< 0.001	***
	Distance>200	−0.158	0.176	−0.90	0.369	
	Habitat type-orchard	−0.614	0.167	−3.69	< 0.001	***
	Distance>200 * Habitat type-orchard	−1.046	0.186	−5.63	< 0.001	***
Females	(Intercept)	8.197	0.310	26.43	< 0.001	***
	Distance>200	−0.659	0.376	−1.75	0.078	.
	Habitat type-orchard	−1.005	0.285	−3.53	< 0.001	***
Males	(Intercept)	8.054	0.321	25.09	< 0.001	***
	Distance>200	−0.021	0.463	−0.05	0.963	
	Habitat type-orchard	−0.593	0.420	−1.41	0.157	
	Distance>200 * Habitat type-orchard	−1.324	0.593	−2.23	0.026	*

4 | DISCUSSION

Our experiment shows that the abundance of SWD was dependent on the habitat type, the largest SWD population being in the forest, followed by orchards and agricultural land. Distance was an important factor influencing abundance in orchards: abundance was lower in orchards that were more than 200 m from forest. There was a difference in the abundance of males and females. Females showed a decrease between forest and orchard, but no difference between orchards in different distance categories (> or <than 200 m from forest), while males showed a decrease in abundance in orchards that were more than 200 m from the forest. In general, the distance from the forest showed a logarithmic decrease for both males and females.

In this study, we found that the abundance of SWD also depends on the time of the year. The greater abundance in forests is connected with the availability of wild fruits in forests (Kenis et al., 2016; Urbaneja-Bernat et al., 2020). This became even more obvious when checking the temporal pattern, which shows a strong increase towards the autumn months. This is strongly correlated with the availability of forest fruits in Europe (Kenis et al., 2016). Other habitat types showed a less strong increase over time, but in several sampling periods, abundance was greater in orchards than in surrounding agricultural land. During this time, the raspberries in the orchards were ripe and the population of SWD increased. Other studies focusing on other crops found a similar pattern, with greater abundance in forest compared with orchards and other habitat types (Santoiemma, Trivellato, et al., 2019; Tonina et al., 2018). Interestingly, Santoiemma, Trivellato, et al. (2019) found that if the abundance of SWD in vineyards and forests was equal at the beginning of the vegetation period, the abundance was also equal during the ripening period of the crop. We did not find such an overlap, which indicates that forests provided more resources than orchards. Another interesting aspect is that the greatest abundance in all cases was found in forests. Additionally, towards the end of October, abundance was increasingly greater in forest compared with the other habitat types, compared with the situation from Santoiemma, Trivellato, et al. (2019). This might be because the research was carried out in different years, which could mean that there were different climatic conditions or a difference in crop phenology. Tait et al. (2020) for instance found that the daily dispersal of SWD was influenced by temperature and humidity. However, we did not notice a decrease in abundance in the other habitat types throughout the season, which indicates that SWD migrates from crops to forest, as has been observed in other studies (Santoiemma, Trivellato, et al., 2019; Tonina et al., 2018).

The distance to the forest negatively influenced the abundance of SWD. Although we found this to be a general difference for the cumulative number of individuals for the whole year, in orchards less than 200 m from forest, the population increased more in September (up to the numbers found in forest) compared with the population in orchards greater than 200 m from forest. This indicates that the migration of SWD is more pronounced near forest than farther away from forest. Tonina et al. (2018) found that this pattern also holds for cherry orchards near forests. However, most of the studies focused on forest cover in the vicinity of orchards (Haro-Barchin et al., 2018; Santoiemma et al., 2018; Santoiemma, Trivellato, et al., 2019) rather than the distance from the forest. However, distance from the forest and forest cover could arguably be tightly correlated, especially on a smaller landscape scale. In this context, female abundance within orchards also showed a stronger correlation between forest cover and abundance in a certain part of the season (Santoiemma et al., 2018). In this case, the ratio between the population in forests and in orchards was not known, and therefore, we could not gain insight into possible spillover effects. Interestingly, Pelton et al. (2016) found that forest cover surrounding the orchard had no influence, but it was suggested that the surrounding agricultural land might have contained enough wild hosts

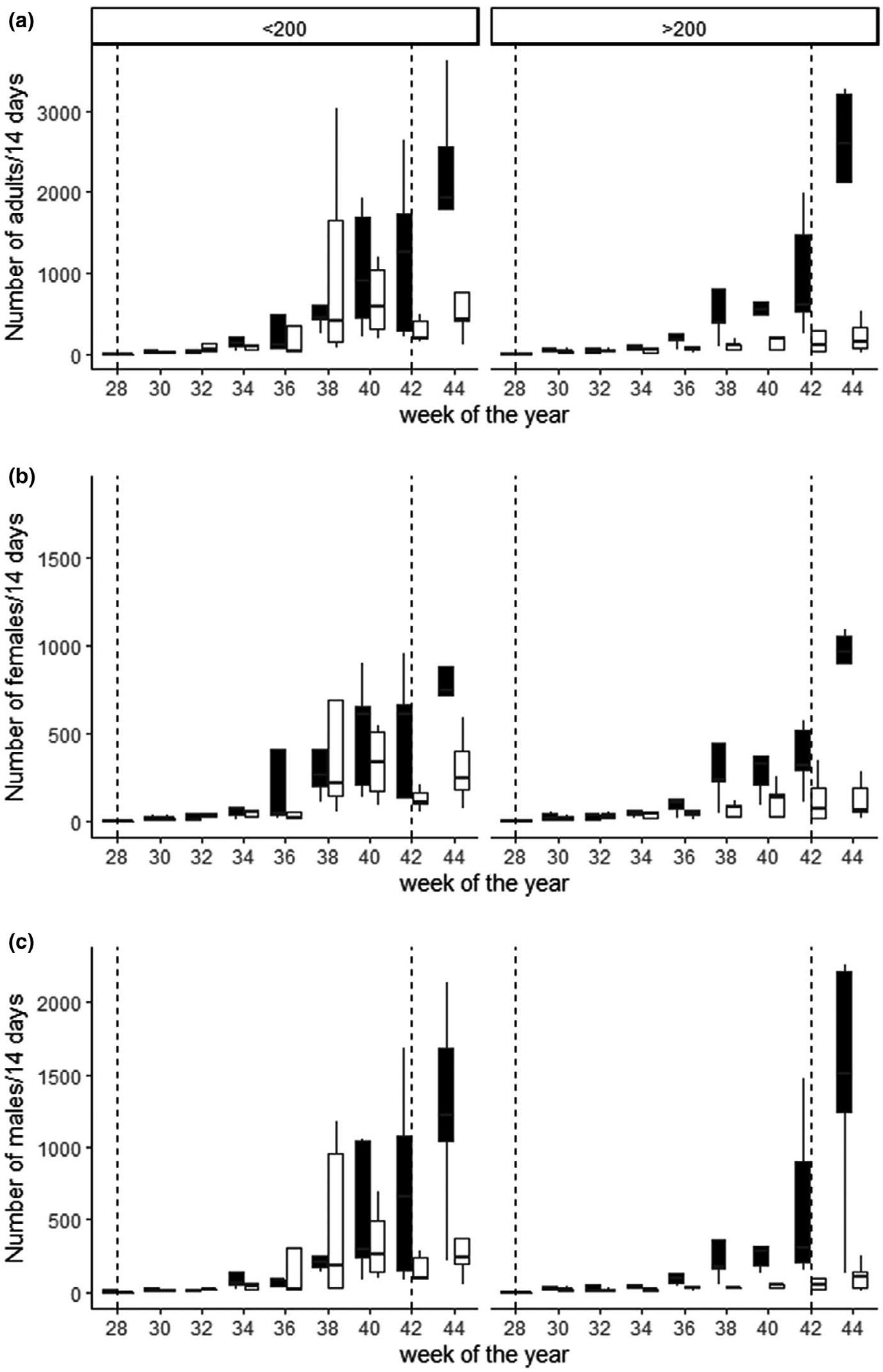

FIGURE 4 Boxplot showing the difference in the number of SWD for (a) total number of adults, (b) females and (c) males in orchards (white) and forests (black) less or more than 200 m apart over time. Vertical dotted lines show the raspberry harvest period. The data are represented by the median value, 25th and 75th percentile and outliers (black dots)

to obscure the pattern. In our study, there was a low abundance of SWD in the surrounding agricultural land because the abundance of the wild hosts in the surrounding agricultural land of the chosen orchards was low, and the species observed were mostly annual weed species, providing few food or shelter resources to SWD (see 'Area description'). Our results show that the facilitation of SWD from forest to orchards is very strong when the populations are equal between habitat types, but that distance also matters. Even though migration may reach up to 9 kilometres (Tait et al., 2018), on a small scale, the abundance diminished markedly over a relatively short distance.

In several aspects, males and females exhibited different migratory responses during our study. It has been shown that in a heterogenous habitat, the number of *Drosophila* flies differs between locations and that dispersal ability differs between males and females (Fontdevila & Carson, 1978). This was confirmed in our study as the numbers of males and females in traps differed in different habitats, and the number of SWD specimens changed during the season. Furthermore, in week 36, the number of females rose more in forests than did the number of males. As a consequence, females may have a head start with dispersion into agricultural land. Lastly, males were more abundant in orchards less than 200 m from forest.

TABLE 4 Model statistics for the comparison of the trap catch of SWD throughout the season from the 28th to the 44th week of 2020 and separately for every 2 weeks. The comparison was made between orchards and forests, between the 28th week and other weeks throughout the season, and between orchards with different distances to forest (< 200 m or >200 m). The results are for all specimens and separately for females and males, presented as an estimate, standard error and significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Additionally, there are data for the interaction between weeks and orchards with different distances from the forest for females, since the interaction was present only for them. Habitat types were compared with the forest habitat type. Weeks were compared with week 28 and Distance >200 was compared with Distance <200

	Adults			Females			Males		
Variable	Estimate	Std. Error	Sig.	Estimate	Std. Error	Sig.	Estimate	Std. Error	Sig.
Orchard	0.684	0.518		0.462	0.569		0.613	0.576	
Distance>200	−0.083	0.37		0.725	0.677		0.045	0.353	
Orchard * Distance>200	−0.643	0.301	*				−0.974	0.329	**
Week 30 versus Week 28	2.971	0.458	***	3.180	0.668	***	2.943	0.519	***
Week 32 versus Week 28	3.448	0.464	***	3.982	0.688	***	3.076	0.513	***
Week 34 versus Week 28	4.512	0.462	***	5.412	0.668	***	4.248	0.504	***
Week 36 versus Week 28	4.61	0.457	***	5.513	0.651	***	4.1	0.506	***
Week 38 versus Week 28	5.504	0.455	***	6.867	0.689	***	5.105	0.502	***
Week 40 versus Week 28	5.887	0.454	***	6.835	0.670	***	5.742	0.502	***
Week 42 versus Week 28	6.016	0.454	***	6.599	0.654	***	5.978	0.502	***
Week 44 versus Week 28	6.733	0.454	***	7.401	0.680	***	6.73	0.502	***
Week 30 * orchard	−0.686	0.639		−0.662	0.712		−0.546	0.72	
Week 32 * orchard	−0.943	0.644		−0.889	0.722		−0.726	0.718	
Week 34 * orchard	−0.733	0.646		−0.716	0.712		−0.657	0.717	
Week 36 * orchard	−0.792	0.644		−1.312	0.711	.	−0.044	0.718	
Week 38 * orchard	−1.168	0.644	.	−1.497	0.721	*	−0.839	0.713	
Week 40 * orchard	−1.485	0.641	*	−1.470	0.708	*	−1.365	0.71	.
Week 42 * orchard	−1.883	0.64	**	−1.853	0.708	**	−1.792	0.711	*
Week 44 * orchard	−2.056	0.643	**	−2.001	0.713	**	−1.986	0.712	**
Week 30 * Distance>200				−0.485	0.720				
Week 32 * Distance>200				−0.586	0.733				
Week 34 * Distance>200				−1.329	0.720	.			
Week 36 * Distance>200				−0.981	0.711				
Week 38 * Distance>200				−1.852	0.732	*			
Week 40 * Distance>200				−1.590	0.723	*			
Week 42 * Distance>200				−1.129	0.725				
Week 44 * Distance>200				−1.361	0.732	.			

However, females were equally abundant in nearby orchards and in distant orchards. This could be explained by the presumably greater ability of females to disperse (Fontdevila & Carson, 1978; Simon et al., 2011). Additionally, SWD can be seen as an income breeder in which feeding and fuel reproductive expenditure occur simultaneously (e.g. Bonnet et al., 1998), as has been shown in the closely related *D. melanogaster* (Min et al., 2006). Thus, females may distribute more evenly in the landscape compared with males. The lower dispersal of males could also be the reason for the significant increase in the number of males in orchards in the period between weeks 34 and 42, correlating well with the number of males in the surrounding agricultural land in the same period. More research is needed to understand the mechanisms underlying the differences in the phenology and dispersal rate between male and female SWD.

There are several other potential factors which could affect the abundance of SWD in our study, such as pesticide use, lower soil quality and reduced chemical inputs (Chaplin-Kramer et al., 2011). Pesticides are not used in Slovenian forests but might be used in orchards in Slovenia. However, pesticides were confirmed to have been used in only one of the raspberry orchards monitored in this study. Regarding the four orchards for which we do not have reliable data on pesticide use, the SWD catches were statistically nondistinguishable from the orchards where insecticides were not used. Furthermore, the distance from the forest did not influence SWD abundance in these four orchards.

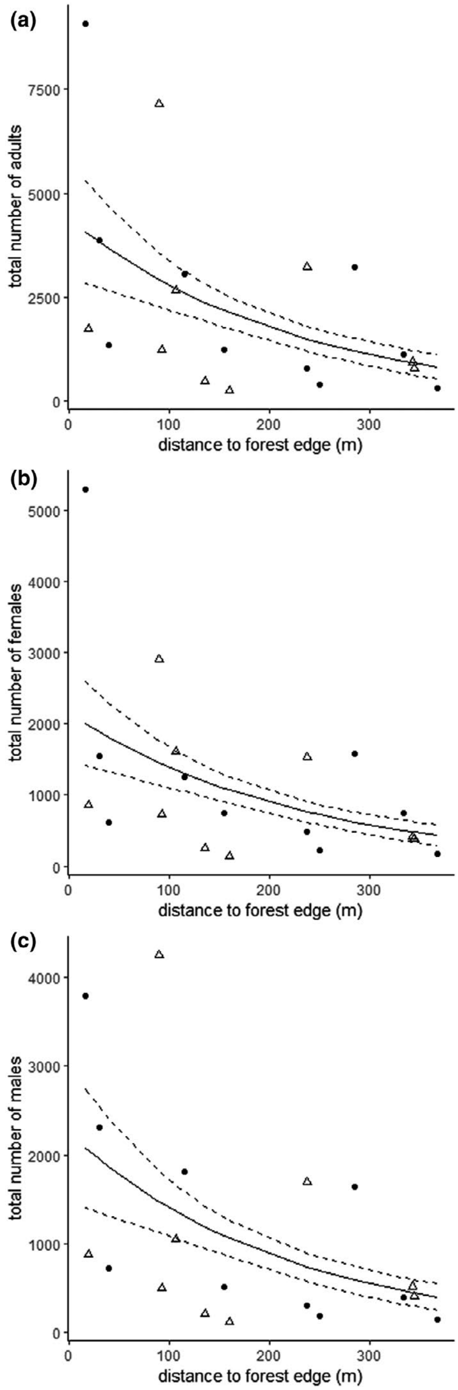

FIGURE 5 The number of caught SWD (a) adults, (b) females and (c) males in raspberry orchards (●) and surrounding agricultural land (Δ) with respect to distance to the forest edge. The black line indicates the regression line and the dotted lines the 95% confidence intervals

4.1 | Implications for management in raspberry orchards

The results of this study have several implications for the management of raspberry orchards. First, forests harbour large populations of SWD, and therefore there might be a spillover threat to raspberry orchards. However, this is only the case for raspberry orchards closer than 200 m from forest. The distance from the raspberry orchard to forest should be taken into account in the planning and management of orchards. In the first step of risk management, the farmer should locate the orchard farther away from forest, as this alone will reduce SWD damage. However, this is not always possible, and therefore, the owner must anticipate extra management costs. In this case, environmentally friendly methods for the control of SWD should be used (Schetelig et al., 2018), as forest also hosts beneficials (Haro-Barchin et al., 2018) that would otherwise be affected by insecticides (Croft & Brown, 1975; Roubos et al., 2014; Ruberson et al., 1998). An option could be the use of insect netting (1 mm mesh or finer; height of 2.5–4 m) applied only laterally around the orchard, thus allowing the passage of pollinators whilst concomitantly hampering the entry of SWD (Cini et al., 2012; Leach et al., 2016; Weber et al., 2016). The removal of forests near orchards would be a pointless management strategy because even a small forest remnant can create a spillover effect (Santoiemma et al., 2018). In addition, there would be a negative effect on the provision of ecosystem services as already mentioned (González et al., 2015; Haro-Barchin et al., 2018). Furthermore, forests have high biodiversity (Arroyo-Rodríguez et al., 2020; Lindenmayer et al., 2006), and their removal would also be in conflict with the forestry sector, which places importance on many other functions in addition to wood production (Etxano et al., 2018).

The surrounding agricultural land can be a habitat for SWD (Pelton et al., 2016); however, populations in grasslands are much smaller (Santoiemma, Trivellato, et al., 2019). The surrounding agricultural land is mostly a combination of agricultural land, annual weeds, hedgerows and bushes, which often contain host plants that could harbour large populations of SWD or could function as steppingstones from forests. However, in this study, we did not find larger SWD populations in agricultural land surrounding raspberry orchards; therefore, the former seems unlikely to be the causal agent for the spillover effect. Thus, we do not recommend removing these habitat structures from the agricultural landscape. Additionally, these habitat structures provide shelter for natural enemies (Garratt et al., 2017; Veres et al., 2013) and other species, which increases biodiversity in the agricultural landscape (Holland & Fahrig, 2000; Lecq et al., 2017; Montgomery et al., 2020).

Context-dependent integrated management which focusses on females or males is needed. Males are predominantly found near forest edges, and management should mainly focus on nearby forests later in the season. Females damage fruit (Cini et al., 2012) and are more likely to be found in all parts of the agricultural landscape. It is therefore key to find control methods focusing mostly on females (e.g. Jaffri et al., 2020), which seem to be the most problematic since they can disperse over longer distances.

Finally, the SWD population accumulated later in the season in all three habitats (Briem et al., 2018; Santoiemma, Trivellato, et al., 2019, this study). The use of early raspberry varieties is therefore recommended to avoid large-scale SWD damage (Pelton et al., 2016; Schöneberg et al., 2021).

TABLE 5 Model statistics for the analysis of the difference in the trapping of SWD depending on the distance between forests and orchards. The results are for all specimens and separately for females and males, presented as an estimate, standard error, z value, p value and significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$)

Model	Variable	Estimate	Std. Error	z value	Pr(>|z|)	
Adult	(Intercept)	8.388	0.324	25.92	< 0.001	***
	Distance	−0.004	0.002	−2.96	0.003	**
Female	(Intercept)	7.674	0.314	24.466	< 0.001	***
	Distance	−0.004	0.001	−2.953	0.003	**
Male	(Intercept)	7.717	0.343	22.471	< 0.001	***
	Distance	−0.005	0.002	−2.887	0.004	**

In conclusion, we showed that the habitat type, landscape, temporal and sex-specific context are important factors regulating the abundance of the highly invasive SWD. In our study, forest contained more adults than raspberry orchards and surrounding agricultural land. Raspberry orchards closer to the forest are more susceptible to attack because there is a stronger SWD adult spillover effect. Males are more abundant closer to forest, while females tend to occur also farther away. In general, adult abundance increased dramatically towards the end of the season. Using the knowledge that all activities depend on the context, it is possible to develop specific integrated pest management strategies to reduce SWD damage to raspberry crops.

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CONFLICTS OF INTEREST

There was no conflict of interest.

AUTHOR CONTRIBUTIONS

MG, MR and JR conceived the research. All authors conducted experiments. MG analysed data and conducted statistical analyses. MG and AK wrote the manuscript. JK secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.80gb5mkr6.

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