



Streams and rural abandonment are related to the summer activity of the invasive pest *Drosophila suzukii* in protected European forests

Alberto Maceda-Veiga^{a,b,c,*}, Sergio Albacete^d, Miguel Carles-Tolrá^e, Juli Pujade-Villar^a, Jan Máca^f, Ralph Mac Nally^g

^a Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona (UB), 08028 Barcelona, Spain

^b IRBio-UB, Institute of Research in Biodiversity, 08028 Barcelona, Spain

^c EBD-CSIC, Department of Integrative Ecology, 41092 Sevilla, Spain

^d CREA, 08193 Cerdanyola del Vallès, Spain

^e Avda. Príncipe de Asturias, 30, Barcelona, Spain

^f Na Potoce 276, 39181 Veselí nad Lužnicí, Czech Republic

^g School of BioSciences, The University of Melbourne, Parkville, VIC, Australia

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ABSTRACT

Protected native-forested areas may be occupied by fruit pests, and so, studies exploring the biotic and abiotic determinants of fruit-pest abundance in forested areas may reduce damages in crops and wild forest frugivores. The Spotted Wing *Drosophila* (SWD) *Drosophila suzukii* is an economically important fruit pest in many temperate regions around the world. During the dry summer in northwestern Spain, we assessed 24 native riparian and 32 non-riparian chestnut forest patches as non-crop habitats for the SWD. We surveyed chestnut forests in 2017 and found a positive association between spatial proximity of forest patches to streams and SWD captures, which led us to study in 2019 the stream-SWD associations in greater detail. We explored whether native-insect communities and changes in vegetation structure related to rural abandonment were associated with variation in SWD captures, while accounting for the effects of covariates, including stream distance. There were no significant associations in the riparian and non-riparian-habitat surveys between the captures of SWDs and those of native insects, including 22 families of flies and 10 families of parasitic wasps. However, captures of SWDs and of other drosophilid flies were positively related to each other and the direction of the association was reversed by stream distance, which suggests the potential role of streams in regulating interactions among non-riparian insects, including SWD. We also found correlative evidence that degraded riparian forests and the abandonment of traditional forest practices in chestnut forests may be contributing to the spread of SWD. Given the numbers of SWDs in our forest samples were similar to values in August in crop areas, it is advisable that future studies address the impacts of SWD invasion on native forest frugivores, which have been overlooked in studies of this widely distributed invasive species.

1. Introduction

The spread of exotic species is among the most pernicious consequences of global change (Ricciardi et al., 2013; Kumschick et al., 2015). Millions of organisms are transported annually, either deliberately or accidentally, into areas beyond their native ranges (Seebens et al., 2017). While many introduced species fail to establish self-sustaining populations and spread, some exotic species become invasive, often causing pronounced environmental and economic impacts on recipient regions (Kumschick et al., 2015). Eradication is unfeasible for invasive

pests with already wide distributional ranges (Genovesi, 2005), but their adverse impacts might be mitigated through ecosystem interventions; i. e. the ‘ecosystem-based management’ (EBM) of invasive species (Zavala et al., 2001; Hulme, 2006).

Many factors can explain invasive pest damages although species’ abundance can be particularly important (Kumschick et al., 2015). Community-ecology theory posits that the disproportionate abundance of a species is due to altered top-down and bottom-up controls (Hairston et al., 1960; Pace et al., 1999). Invasive pests may occupy ‘unexploited’ ecological niches in recipient ecosystems or compete more efficiently

* Corresponding author at: Faculty of Biology, Avda. Diagonal, 643, 08028 Barcelona, Spain.

E-mail address: albertomaceda@gmail.com (A. Maceda-Veiga).

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than native species for resources (Fridley and Sax, 2014). Invasive pests also may not have effective parasites or predators in invaded habitats, or if they do, they are more likely to escape from predation than native species due to the lack of co-evolution (Prior et al., 2015). The abundance and diversity of potential competitors with, or consumers of, invasive pests are expected to be greater in relatively intact, native-species rich assemblages (i.e. the biotic-resistance hypothesis, Elton, 1958; Jeschke et al., 2012). However, intact assemblages now are scarce due to land-use alterations and climate change (Gallagher and Carpenter, 1997). Therefore, exploring how the abundance of invasive pests depends on local environmental characteristics and the composition of biological assemblages in relatively unmanaged habitats may assist managers to develop a systemic approach for the EBM of invasive pests.

The Spotted Wing Drosophila *Drosophila suzukii* Matsumura (SWD) is a vinegar fly (Diptera: Drosophilidae) native to eastern and South-east Asia that has invaded temperate regions of Europe, America, Africa, Australia, and other parts of Asia through the fruit trade (Calabria et al., 2012; Asplen et al., 2015; Boughdad et al., 2020). SWD damage arises from oviposition wounds, internal larval feeding and associated microbial infections to high-value fleshy fruits (e.g. cherries, strawberries) (Goodhue et al., 2011; Mazzi et al., 2017). With economic losses of 3–4 million € p.a. in Trentino, Italy, alone (Ioriatti et al., 2012), the biology of SWD has been studied in detail, including the potential use of parasites for biocontrol (Gabarra et al., 2015; Lee et al., 2019; Stacconi et al., 2018). On average, SWD takes 10 days at 25 °C to complete its life-cycle, with greater fecundity and longevity at lower temperatures and high humidity (e.g. >75%, Tochen et al., 2016). Forest habitats, which can provide these conditions and suitable food, have been reported as non-crop habitats for SWD (e.g. Arnó et al., 2016; Hennig and Mazzi, 2018; Santoiemma et al., 2019). The adequacy of forests for SWD depends on plant species composition (Kenis et al., 2016; Santoiemma et al., 2018; Tonina et al., 2018), but how changing forest landscapes due to rural abandonment might affect SWD has not been specifically studied. Rural abandonment has led to plantations and forest regeneration in what had

been open landscapes and to greater structural understory complexity and canopy density in woodlands (Gondard et al., 2006; Spitzer et al., 2008; Malavasi et al., 2018). Low light and greater moisture in forests may help SWD to survive during the dry season if the presence of host plants, such as wild blackberries (Kenis et al., 2016), increases in unmanaged forests (Albacete et al., 2020). No study has yet linked the abundance of SWD to forest management and to potential SWD predators or competitors, which is a logical first stage for exploring the potential of an EBM approach for SWD (Fig. 1). Any resulting inferences are likely to be important for potentially reducing the spread of SWD through forest regions to crop-dominated areas and for potentially reducing SWD damages to the forest fleshy fruits (e.g. *Sambucus nigra*, blackberries), upon which many wild frugivores feed (e.g. birds, mammals, e.g. Guitián and Munilla, 2008).

Here, we explored how riparian and non-riparian forest patches differing in structural properties may affect the abundance of SWD during the summer in an increasingly forested Spanish region within the European Habitats Directive (92/43/EEC). In 2017, we surveyed insect communities in chestnut forests at differing distances from streams with two goals: (1) to explore the role of streams in providing suitable forest conditions for SWD given the effects that proximity of chestnut-forest patches to streams appears to have on various groups of insects in chestnut forests (Albacete et al., 2020); and (2) to determine the relative importance of alterations in the forest environment and biological assemblages for explaining variation in SWD abundance. In 2019, we used the same insect traps in riparian forests to study the stream–SWD association in greater detail, and establish whether changes in forest conditions arising from rural abandonment might influence SWD activity. We expected SWD captures, which are a measure of abundance activity (e.g. Basoalto et al., 2013; Santoiemma et al., 2018), to increase in bait traps close to rivers because SWD numbers are greater in more humid crops (Tochen et al., 2016). Fewer captures of SWD were expected in forests with diverse understories because greater plant diversity often has been associated with more natural enemies for agricultural pests

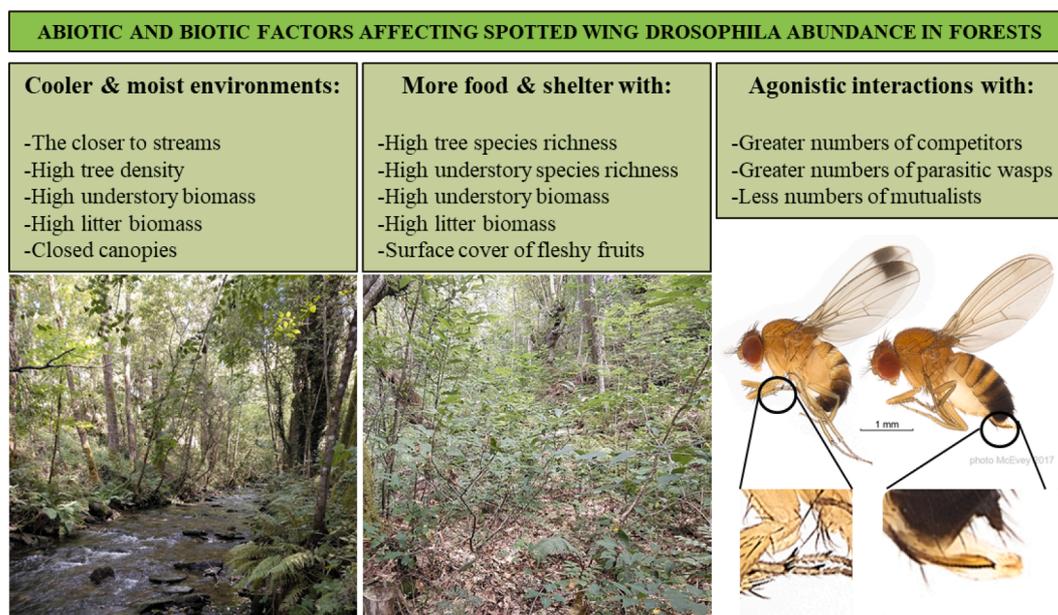


Fig. 1. Abundances of *Drosophila suzukii* are expected to be regulated by microclimatic conditions, resource availability and the effects of these two factors on the abundance of other species with which *D. suzukii* might interact. Forest-vegetation structure and proximity to streams alter forest microclimate (Moore et al. 2005), affecting directly the life cycle of *D. suzukii* and determining indirectly the quantity and quality of food. Plant species diversity and litter biomass affect the amount and diversity of shelter and food resources (sap, fungi, yeasts) that *D. suzukii* might exploit (Starmar 1981; Asplen et al. 2015). The abundances of other fermented-liquid feeders (e.g. sap beetles, native drosophilids) are expected to reduce the abundance *D. suzukii* through trophic competition, as might natural populations of parasitoid wasps through predation (Asplen et al. 2015; Gabarra et al. 2015). The pictures show (from left to right): the Cabe stream with a well-developed riparian cover, an unmanaged chestnut woodland, and two individuals of *D. suzukii* with the characteristic sex combs and spotted wings of males and the serrated ovipositor of females.

(Russell, 1989; Hatt et al., 2020) and with fewer host plants for SWD (e.g. *Rubus ulmifolius*; Albacete et al., 2020). Last, high abundances and diversities of other insects feeding on similar substrates might be expected to be negatively associated with SWD captures because local communities can provide biotic resistance to exotic species invasions (Nunez-Mir et al., 2017). Therefore, we expected conservation actions for native forests in the region to have the potential additional value of managing SWD if there are positive associations between SWD captures and the characteristics typical of damaged riparian forests or of the abandonment of traditional chestnut forest management.

2. Materials and methods

2.1. Study area

The study area is located between the Sites of Community Importance in the European Union ‘SCI ES1120016 Río Cabe’ and ‘ES1120001 Ancares-Courel’ (Habitats Directive 92/43/EEC) in northwestern Spain (Fig. 2). The Cabe stream drains the valley on the slopes of which grow the focal chestnut forests. Chestnut forests were almost all *Castanea sativa* and riparian tree species were *Alnus glutinosa*, *Fraxinus excelsior* and *Corylus avellana*. Chestnut and riparian forests are protected forest habitats within the EU’s Habitats Directive (92/43/EEC). The climate is temperate oceanic sub-mediterranean (Rivas-Martínez et al., 2011); fog is frequent, there is abundant rain (800–1800 mm annually), and the average annual temperature is 16 °C, although summers can be dry and warm (<60 mm, >27 °C).

The region has domestic agricultural activities that have declined greatly in the last 30 years due to young people moving away from the region to urban areas, which led to land-use abandonment and chronosequences of forests varying in vegetation structure depending on the degree of ‘abandonment’. Fruits vulnerable to the SWD pest (e.g. figs,

cherries) were never grown here commercially but are seldom present in the study area, particularly close to villages. However, wild blackberries (*R. ulmifolius*) border the streams at reaches with altered riparian vegetation, outgrowth in forest edges and cover the forest ground in unmanaged forests. Traditional forest management prevent climbing plants such as *R. ulmifolius* from colonizing the ground and the trees. Epiphytic lichen communities on chestnuts and water quality analysis in the Cabe stream indicate that air and water quality are good (Maceda-Veiga and Gómez-Bolea, 2017; Albacete et al., 2020).

2.2. Insect surveys

We surveyed 32 small private properties of chestnut forests and 24 patches of riparian forests. Surveys in chestnut forests were conducted from the 2nd to the 19th August 2017 in 19 km² of the municipality of O Incio. Surveys in riparian forests were carried out from the 9th to 28th August 2019 along 3.7 km each of the Cabe and Louzara streams in the municipalities of O Incio and Samos, respectively. Surveys were conducted in August because this is the warmest and driest month in the region (Meteogal), and so, is likely to be when the activity of SWD might be more influenced by dry weather. Moreover, August is within the fruiting period of *R. ulmifolius* (Jordan, 1984), which is a widespread host plant for SWD in the study area (Albacete et al., 2020), of the 84 plant species known to be hosts for SWD (Kenis et al., 2016). Last, August is the month before the annual clearance of understorey plants in chestnut forests for harvesting chestnuts, which is when chestnut forest patches are more structurally complex, and so, the associations between insects and the structural development of vegetation, which we assumed to be proxy for the abandonment of forest practices, can be studied in detail (Albacete et al., 2020; Matas et al., 2020).

SWDs were captured incidentally as part of a monitoring program that we are conducting in the region for exploring stream-terrestrial

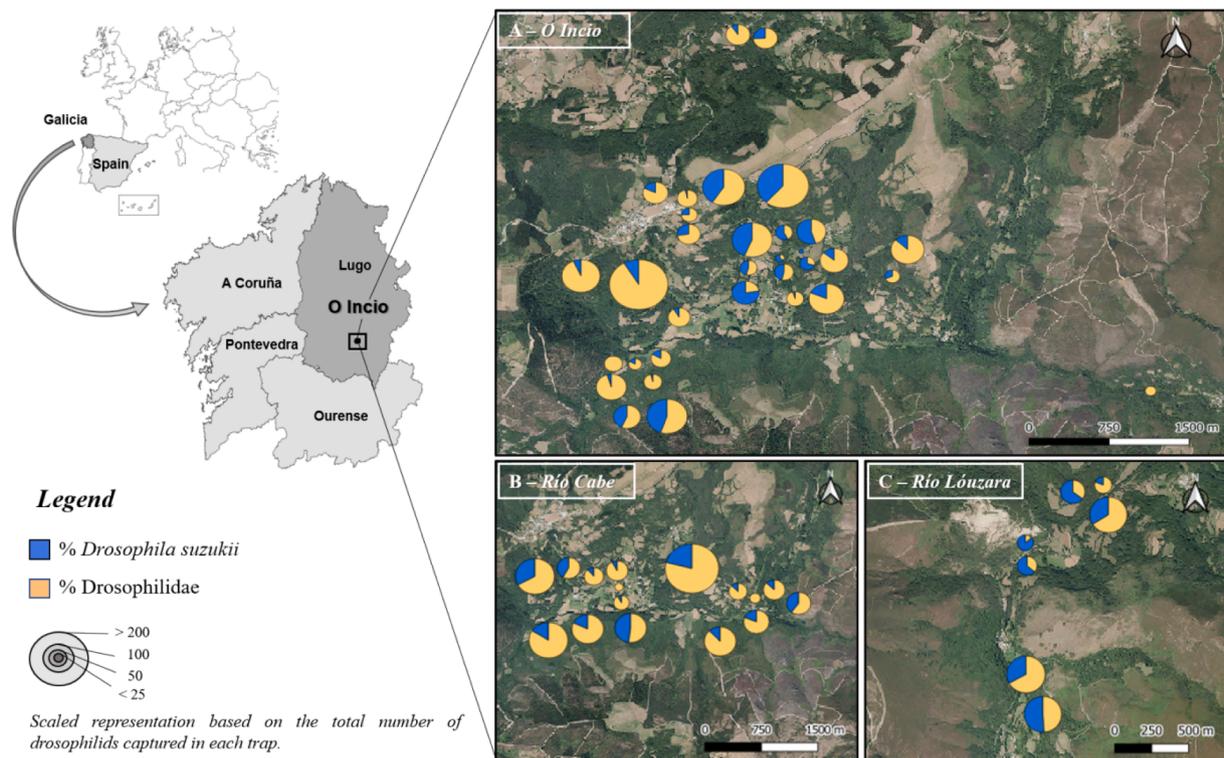


Fig. 2. Aerial photograph of the study area in north-western Spain (Galicia) with locations of the 32 chestnut-forest private properties surveyed in 2017 to explore relationships between the abundance of the invasive *Drosophila suzukii* with stream distance and other forest-patch characteristics (A), and locations of the 24 riparian forest patches surveyed in 2019 to study the stream-*D. suzukii* invasion relationships in greater detail (B and C). The colors in pie charts indicate captures of *D. suzukii* (blue) and those of other Drosophilidae (orange), whereas the area of pie charts is proportional to the total abundance of Drosophilidae, including *D. suzukii*. Original image from Google Earth®. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

arthropod associations in changing forest landscapes. We used fermented liquid traps to emulate the presence of ephemeral and patchy resources for insects as do dung and carrion traps for insects (Braack, 1987; Gibbs and Stanton, 2001). Our traps are a modified version of the widely used beer trap (Dvorák et al., 2010; Manko et al., 2019); we placed a 200-ml polyethylene container (5 cm diameter) with a funnel, filled with Estrella Galicia® beer, vinegar, and sugar as a bait (Carles-Tolrá et al., 2017; Matas et al., 2020). The container had a lid with an inverted U-shape to prevent rain from entering the trap. We hung the traps on a tree branch at c. 1.5 m from the ground and c. 40 cm from the trunk on the north side of the canopy (e.g. Santoemma et al., 2018). Traps set in 2017 attracted many insects (3824 individuals, 5 orders, 40 families), including SWDs and other drosophilids (Albacete et al., 2020), and thus, the same design was used for the riparian-forests surveys in 2019. Captures included other fermented liquid-feeders (e.g. Nitidulidae, Staphylinidae, Heleomyzidae, Muscidae, Sarcophagidae) and predatory wasps, so that variation in insect captures was appropriate to explore how these guilds and the forest habitat conditions might influence SWD captures. Fermented-liquid feeders feed on rotting fruit, including fleshy fruits damaged by SWD oviposition (Hennig and Mazzi, 2018), and so, may compete with SWD for yeast-rich substrates used by adult SWD and by adults and larvae of other flies as a source of food (Basoalto et al., 2013). Parasitoid and other predatory wasps prey on different species of fermented-liquid feeders, including drosophilids (Harris, 1991; Knoll et al., 2017; Lee et al., 2019), and so, we expected changes in wasp numbers to have the potential to directly or indirectly affect SWD captures.

Landowners allowed us to set only one trap for flying insects in the chestnut-forest patches and we placed the trap at the centre of each forest patch (Albacete et al., 2020; Matas et al., 2020), as we did for the riparian-forest patches. In the pilot study, we set three traps in four of the studied sites and mean \pm SD of SWD captures were 27 ± 11 , respectively. Forest habitats were relatively homogeneous at the patch scale, and we measured forest-patch features for each exact trap location and included patch size as covariate (see below). This design fulfilled our goal because we aimed to explore how insect associations in traps were influenced by changes in the local forest vegetation and the forest microclimatic conditions. Both vegetation structure and stream distance may affect the forest microclimate (Zellweger et al., 2019), which, by means of altering the microbial-driven process of fermentation, might affect the release of volatile compounds from the traps that attract insects (Basoalto et al., 2013). Insects from each trap were preserved in 70% ethanol and were identified in the laboratory to the lowest possible taxonomic level (Appendix S1).

2.3. Forest-patch characteristics

Insect traps were placed in the centre of each forest patch, at which we measured the habitat predictors for the chestnut and riparian forests, all described in Appendix S2 in detail and outlined briefly below. Our measurements were taken at forest-patch in the four cardinal points around each trap using 10×10 m plots (Albacete et al., 2020; Matas et al., 2020). In 2019, in the riparian forest patches, we used the most informative predictors from the 2017 chestnut dataset alongside other descriptors widely used in riparian studies.

The chestnut-forest potential predictors were related to indicators of rural abandonment, namely tree density, lighting, understory plant richness and height, deadwood accumulation and litter biomass (Albacete et al., 2020), and various covariates, including stream distance (Appendix S2). Unmanaged woodlands become closer (i.e. denser canopies) and have greater dead biomass accumulation (leaf litter, deadwood) than the managed ones (Gondard et al., 2006; Spitzer et al., 2008; Albacete et al., 2020). Moreover, a few vigorous plants monopolize the understory plant community, including *Pteridium aquilinum* and *R. ulmifolius*. Given the latter has fleshy fruits for SWD, we added to the list of candidate predictors for chestnut forests the individual surface

cover of *R. ulmifolius*.

The shared potential predictors and covariates between chestnut and riparian datasets were plant richness, forest-patch size, understory plant height, temperature, the distance to the nearest village and the spatial distribution of traps (Appendix S2). The riparian dataset had more-detailed descriptors of *R. ulmifolius* (distance to the nearest *R. ulmifolius* patch and surface area of this patch) because this species is common in riparian areas (e.g. Maceda-Veiga et al., 2016). We also included the cover and width of riparian canopy following the QBR (Munné et al., 2003) and RBA (Barbour et al., 1999) official protocols for riparian areas. Riparian-forest patches mostly were close to meadows, which had an edge of *R. ulmifolius*, and so, the study of associations between riparian forest, *R. ulmifolius* and SWD was pertinent. Given chestnut forest patches had more variable habitats around, we added to the list of potential covariates for the chestnut-forest dataset the percentage of chestnut forests, secondary roads, and open habitats (grasslands/shrublands) (Appendix S2). We used a buffer of 500-m radius from the trap because this was the appropriate distance for studying variation in captures of fermented-liquid feeders and parasitoid wasps in our study area (Albacete et al., 2020).

2.4. Statistical analysis

All analyses were conducted in R (R Core Team, 2018) using the functions referred to below. The number of captured SWD specimens was the response variable (i.e. activity abundance) and the individual captures of other specimens of Drosophilidae, parasitoid wasps or other fermented-liquid feeders were the potential predictors used as proxies for the biotic resistance that native insect assemblages might exert on the SWD invasion. Another predictor for the insect biotic-resistance hypothesis was the Chao-estimated richness of trap captures (Walther and Moore, 2005). River was a categorical factor for the riparian-forest model and the forest-patch features were the habitat potential predictors. Continuous and discrete variables were log-transformed to reduce data skew and all potential predictors were transformed to units of standard deviation using the R function *scale*. The respective sets of candidate predictors for the chestnut and riparian forests were individually elided until all predictors had VIFs ≤ 3 to deal with collinearity, as recommended by Zuur et al. (2010).

We used general linear models coupled to the R function *dredge* in the package *MuMin* (Barton, 2018) to explore the most relevant combination of predictors to explain variation in SWD log-transformed captures. We built one initial model for the chestnut dataset and one for the riparian dataset, including all potential predictors individually in each model, and the following interactions. For the *chestnut-forest models*, the interactions were between stream distance and the vegetation features related to microclimate (understory height and tree density), and between stream distance and the biotic resistance insect predictors. For the *riparian-forest models*, the interactions were between all potential predictors and the categorical factor 'River'. Other interactions for the two model sets were initially found to be statistically uninformative using exploratory random forest models (see Appendices S3 and S4). For each dataset, we used to the function *model.avg* in the package *MuMin* to calculate the averaged regression coefficients of potential predictors among the set of 'best' models (Akaike Information Criterion corrected for small sample sizes, $AICc \leq 2$). The most parsimonious models included all predictors and covariates whose 95% CI do not include 0 s and that were statistically significant at $P \leq 0.05$ using *F*-tests. The overall adequacy of these best models was assessed by means of adjusted- R^2 (the R function *rsq*).

If the biotic-resistance predictors were not included in the final models, we used *F*-tests at $P \leq 0.05$ and changes in Adjusted- R^2 to assess whether these predictors were statistically uninformative to explain variation in SWD captures.

3. Results

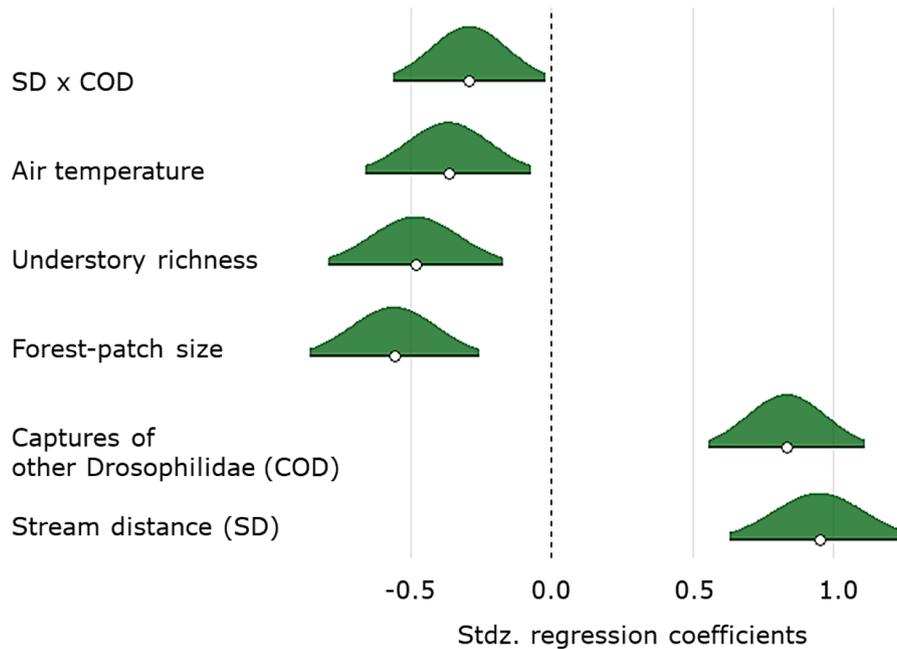
3.1. Chestnut-forest patches

SWDs were captured in 31 of the 32 surveyed chestnut-forest patches, and the total number of individuals captured was 498 (mean/patch \pm SD = 12 ± 11) (Fig. 2). Of the other 3415 captured insects, 1322 (39%) were other drosophilid flies, 1845 (54%) were flies of 21 other

families, and 33 (0.9%) were parasitoid wasps of 10 families (Appendix S1).

Two of the 18 predictors (total plant richness and deadwood cover) showed collinearity issues with the four insect potential predictors related to the biotic resistance hypothesis at $VIF \leq 3$ (Appendix S5 and S6). We removed total plant richness because its values were strongly associated with understory richness in chestnut forests, which was retained as a predictor in the list (Appendix S6). Deadwood cover was

A. Chestnut-forest model (Adj. $R^2 = 0.63$)



B. Riparian-forest model (Adj. $R^2 = 0.88$)

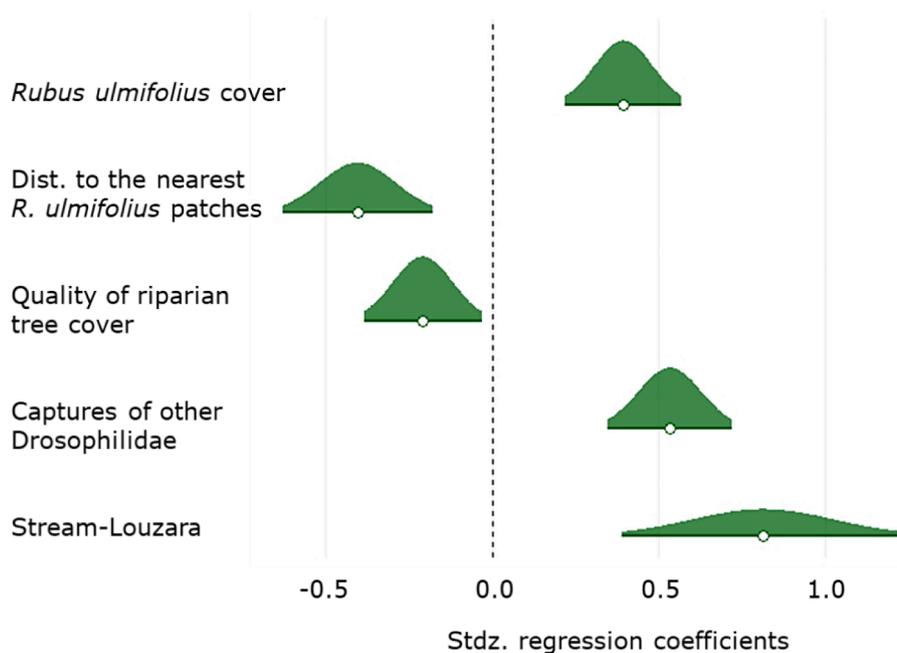


Fig. 3. Probability distributions for standardized regression coefficients (effect sizes) of the most informative and parsimonious general linear models (the ‘best’ models in Tables 1B and 2B) identified to explain variation in captures of the invasive pest *Drosophila suzukii* in chestnut forests (A) and riparian forests (B) in north-western Spain.

deleted because the other variable with VIF > 3 was understory richness, which had a higher individual explained variance in Random Forest models (2.2 vs 1.2, Appendix S3).

The best model for explaining variation of SWD captures ($R^2 = 0.63$, $N = 34$) included positive associations with stream distance and captures of other drosophilid flies and, to a lesser extent, inverse associations with forest-patch size, understory plant richness and air temperature (Fig. 3, Table 1). The association between stream distance and SWD captures was less pronounced when there were greater captures of other drosophilid flies (Fig. 4). The other insect predictors related to the biotic resistance hypothesis did not much affect SWD captures (Table 1).

3.2. Riparian-forest patches

SWDs were captured in 21 of the 24 surveyed riparian-forest patches in 2019, and the total number of individuals captured was 283 (mean/patch \pm SD = 14 ± 18) (Fig. 2). Of the other 1032 insects captured, 659 were other drosophilid flies (64%), 273 were flies of other families (26%) and 50 were parasitoid wasps (5%) (Appendix S1).

The sites associated with the Louzara stream had significantly higher SWD captures than those of the Cabe stream (Fig. 3). There were collinearity issues with the insect predictors and air temperature and understory plant richness at $VIF \leq 3$ (Appendix S7), so that the two habitat predictors were excluded in the modelling. These predictors correlated with the width of the riparian forest and the latter was selected for simplicity (Appendix S8). The best model for riparian SWD captures had a good fit ($R^2 = 0.88$, $N = 24$) and showed a strong positive association with the captures of other drosophilid flies (Fig. 5A, Table 2). There was an inverse association between SWD captures and the distance to the nearest *R. ulmifolius* patch (Fig. 5C). The associations between SWD captures and the quality of the riparian tree cover, and the

Table 1

Results from model averaging exploring the most informative non-riparian forest-patch predictors to explain variation in *D. suzukii* captures, including: (A) the top list of candidate models that were statistically indistinguishable from one another (models deviating ≤ 2 units of AICc), (B) the analysis-of-variance table for the best model (in bold) after excluding unimportant predictors (litter biomass and UTM-Y) using the R function *Anova* in the package *car*, and (C) the statistical comparison of this final model with and without the other native insect predictors related to the biotic resistance hypothesis.

(A)							
ID	Combination of predictors	df	logLik	AICc	delta	weight	Adjusted R^2
M1	134,568	8	-31.8	85.6	0	0.56	0.63
M2	13,456	7	-34.4	87.3	1.69	0.24	0.58
M3	123,457	8	-32.8	87.6	1.99	0.21	0.60
(B)							
Adjusted $R^2 = 0.63$		Sum of squares	df	F	P value		
Stream distance		17.4	1	34.1	<0.001		
Captures of other Drosophilidae		17.8	1	34.8	<0.001		
Forest-patch size		6.7	1	13.1	<0.001		
Understory richness		4.7	1	9.3	<0.001		
Air temperature		3	1	5.9	0.02		
Stream distance * Other Drosophilidae		2.3	1	4.4	0.04		
Residuals		13.3	26				
(C)							
Statistical comparisons with model B		Adjusted- R^2	Test	P value			
Model B + Native insect richness		0.63	$F_{1,25} = 1.24$	0.28			
Model B + Non-drosophilid fly captures		0.63	$F_{1,25} = 1.00$	0.33			
Model B + Parasitic wasp captures		0.62	$F_{1,25} = 0.40$	0.53			
Model B + Non-parasitic wasp captures		0.62	$F_{1,25} = 0.31$	0.58			

1, Stream distance; 2 Litter biomass; 3, Other Drosophilidae; 4, Forest-patch size; 5, Understory richness; 6, Air temperature; 7, UTM-Y; 8, Stream distance * Other Drosophilidae.

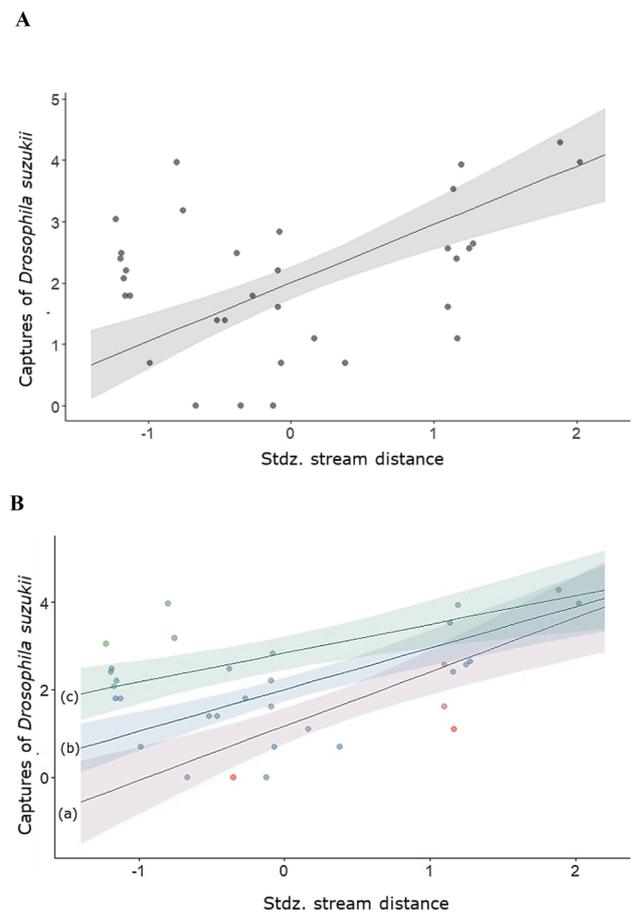


Fig. 4. Fitted regression lines ($\pm 95\%$ CI) of (A) captures of the invasive pest *Drosophila suzukii* in chestnut forests in relation to stream distance (4–620 m) and (B) of these stream distances as a fraction if drosophilid captures were at [a] minimum (0), [b] medium and [c] maximum numbers (1322) while accounting for other predictors and covariates (Full model in Table 1B, Adj. $R^2 = 0.63$; $N = 32$).

surface area of *R. ulmifolius* patches, were less clear probably due to narrow ranges for these potential predictors (Fig. 5BD). Insect predictors, other than captures of other drosophilid flies, did not have clear associations with SWD captures (Table 2).

4. Discussion

Our study provides some support for the idea that spatial proximity of forest patches to streams and the forest conditions arising from the abandonment of traditional forest practices (e.g. low understory plant richness) might affect the activity of the invasive pest Spotted Wing *Drosophila suzukii* (SWD) in chestnut forests, at least in summer. Moreover, we found that SWD captures were positively associated with the presence of narrow tree forest patches close to elongated *R. ulmifolius* patches, which is related to a poor riparian conservation status (Munné et al., 2003; Maceda-Veiga et al., 2016). Last, our summer captures of SWD were not significantly associated with captures of native insects from 40 families and five orders, including parasitoids, suggesting no support for the biotic-resistance invasion hypothesis (Nunez-Mir et al., 2017). Besides exploring the potential of an ecosystem-based management approach for this fruit pest, our findings may be useful for predicting the spread of SWD in many parts of Europe in which there is increasing forest cover arising from land-use changes in rural areas (Malavasi et al., 2018).

Before discussing the more general ramifications of our study, it must be noted the assumptions and limitations upon which our findings rest.

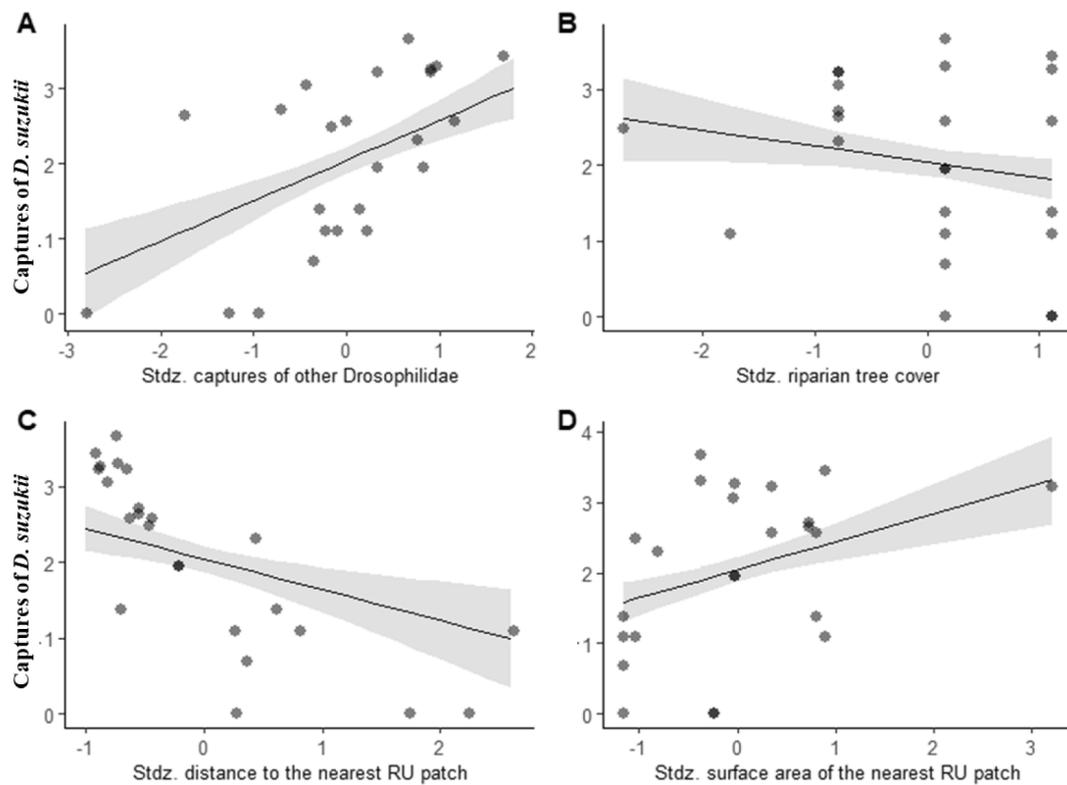


Fig. 5. Fitted regression lines ($\pm 95\%$ CI) of invasive pest *Drosophila suzukii* captures in riparian forests in relation to (A) the captures of other Drosophilidae in the riparian forests ranging from 0 to 659, (B) the quality of the riparian tree cover scoring from 5 to 25, (C) the distance to the nearest *R. ulmifolius* (RU) patch to the focal riparian forest ranging from 4 to 44 m and (D) the surface area of the *R. ulmifolius* patch in a range from 100 to 678 m², while accounting for other predictors and covariates (Full model in Table 2B, Adj. $R^2 = 0.88$; $N = 24$).

Table 2

Results from model averaging exploring the most informative riparian forest-patch predictors to explain variation in *D. suzukii* captures, including: (A) the top list of candidate models that were statistically indistinguishable from one another (models deviating ≤ 2 units of AICc), (B) the analysis-of-variance table for the best model (in bold) using the R function *Anova* in the package *car*, and (C) the statistical comparison of the final model with and without the other native insect predictors related to the biotic resistance hypothesis.

(A)							
Model ID	Combination	df	logLik	AICc	delta	weight	Adjusted R^2
M1	12,345	7	-4.53	34.25	0	0.57	0.88
M2	123,456	8	-1.4	34.8	0.54	0.43	0.92
(B)							
Adjusted $R^2 = 0.88$		Sum of squares	df	F	P value		
River		2.3	1	14.1	<0.01		
Captures of other Drosophilidae		5.1	1	31.5	<0.01		
Quality of the riparian tree cover		0.8	1	5.3	0.03		
Distance to the nearest <i>Rubus ulmifolius</i> patch		1.9	1	12.3	<0.01		
Surface area of <i>R. ulmifolius</i>		3.2	1	19.7	<0.01		
Residuals		2.9	18				
(C)							
Statistical comparisons with model B		Adjusted- R^2	Test		P value		
Model B + Native insect richness		0.88	$F_{1,17} = 0.02$		0.87		
Model B + Non-drosophilid fly captures		0.87	$F_{1,17} = 0.001$		0.98		
Model B + Parasitic wasp captures		0.87	$F_{1,17} = 0.02$		0.88		
Model B + Non-parasitic wasp captures		0.88	$F_{1,17} = 2.11$		0.16		

1, River; 2, Other Drosophilidae; 3, Quality of the riparian tree cover; 4, Distance to *Rubus ulmifolius* patches; 5, Surface area of *R. ulmifolius*; 6, River \times Surface area of *R. ulmifolius*.

First, our non-manipulative study cannot provide definite causal relationships between predictors and SWDs but has instead the ecological realism of having explored natural spatial gradients of biological and environmental conditions (Mac Nally and Quinn, 1998). Second, we had the sampling limitations of studying small private properties, but the

study area provided us the opportunity to study >100 year old native forests, which nowadays are rare in many forest landscapes in Europe and elsewhere (Spiecker, 2003). Although our surveys were only in summer, the numbers of SWD captured in the traps were within the mean capture rates in August in invaded regions with vulnerable crops

(e.g. <40 SWDs in California, Wang et al., 2016). Moreover, the greater captures of SWD near *R. ulmifolius* mats in the riparian forests suggest that our fermented liquid traps were sufficiently attractive to SWD despite the presence of blackberry, which is a host plant for SWD (Arnó et al., 2016; Kenis et al., 2016), and our surveys not having been designed specifically for capturing mostly SWDs but rather for many other groups of insects (see methods). Last, our inferences are based on bait traps, like most field studies on SWD (e.g. Haro-Barchin et al., 2018; Tonina et al., 2018; Urbaneja-Bernat et al., 2020). Therefore, our captures should be regarded as a measure of ‘abundance activity’ that may be affected, alongside the abundance of SWD *per se*, by any factor altering the emission of volatile compounds from the traps and their perception by the insects. One of the most important factors is the accumulation of insects in the traps (Basoalto et al., 2013). However, we did not find significant associations between the captures of SWD and those of other insects, suggesting that captures of other insects, ranging from 8 to 329 per trap, on SWD captures probably had very limited effects (Appendix S1).

4.1. Stream distance as an important predictor for SWD captures

We expected that the captures of SWD, which is regarded as a hygrophilous species (Tochen et al., 2016), would increase in the chestnut-forest patches nearer to streams, especially given that the summer of our 2017 surveys was relatively dry (33% less rain than the regional annual mean of 1408.3 l/m²). However, there were more SWD captures further from streams, which might mean that, among other factors, the chestnut-forest microclimatic conditions even distant from streams were suitable for SWD. Overnight fogs and mists, which all of our forest patches experience almost daily, might provide flies with sufficient humidity, which is consistent with the presence of hygrophilous lichens on the focal chestnut trees farther from streams (Maceda-Veiga and Gómez-Bolea, 2017). However, greater captures of SWD further from streams may indicate that our traps were not so important for water provision for SWD close to rivers as they were further away. Mean measured afternoon air temperature (\pm SD) in chestnut forests was 23.6 (\pm 2.2) °C, which is within the range of preferred temperatures for SWD (20–25 °C; Kanzawa, 1939). We also caught SWDs in 21 of the 24 riparian-forest patches at 18.3 (\pm 0.8) °C, so that the positive association between stream distance and SWD captures might indicate that the flies preferred the warmer chestnut forest patches. Wang et al., (2016) reported SWD in riparian forests, although they did not study in detail the association with the forest vegetation and environmental conditions. Pair-wise correlations between stream distance and air temperature or litter moisture in our focal forests were small (Spearman’s $\rho < |0.25|$), so that the forest vegetation in most chestnut forest patches probably was sufficiently developed to moderate the warm summer conditions, as has been reported for oak woodlands in the drier Mediterranean-climate region (Aragón et al., 2010).

4.2. The importance of native-insect associations to predict SWD captures

Although exploring outcomes of biotic interactions without time-series data and measures of fitness changes in organisms is challenging (see Levine, 1976; Case, 1990; Parker et al., 1999), the capture of various groups of native insects (40 families and 5 orders) allowed us to explore some relevant associations with SWD that will need further testing.

The positive association between SWD captures and spatial proximity of the focal chestnut forest patches to streams was less evident when there were greater captures of other drosophilid flies, suggesting that food competition among drosophilid species might have been greater further from streams. Drosophilid flies feed on substrates other than rotting fruits (e.g. soft rots, leaf yeasts, e.g. Starmer, 1981), so that there may have been enough diverse food types and water for drosophilid flies in the focal forests. Food competition also probably was weak

between SWD and other fermented-liquid feeders that we captured (e.g. Muscidae, Heleomyzidae, Nitidulidae) because there were no significant associations with SWD captures, which may be due to our traps having plenty of available food. Nonetheless, it is possible that different families of insects might have been attracted at different stages of the fermentation process in our traps. For example, although we did not study all drosophilid species in detail, we captured yeast feeders (e.g. *Drosophila obscura* group) and mushroom-breeding drosophilids (e.g. *Drosophila phalerata*) (Courtney et al., 1990), so that there is likely to have been at least some temporal resource differentiation among drosophilids.

The lack of a significant association between the captures of various families of parasitoids of dipterans and SWD suggests limited influence of native insects on SWD invasion, at least during the times of our summer surveys. However, the fewer captures of SWD in forest patches with greater understory plant richness may mean that the effects of parasitoids on SWD cannot be ruled out. Strips of diverse plant species often have insect predators of forest and agricultural pests (e.g. Caballero-López et al., 2012; Hatt et al., 2020), a feature that also holds for the focal chestnut forests (Albacete et al., 2020). Therefore, measures of vegetation structure might reflect time-integrated predator–prey dynamics of insects better than our snapshot captures. Our inferences might be improved if one had had greater captures of parasitoids because then we would have been able to examine species-by-species associations between SWD and parasitoids. We captured one or two individuals of families of parasitoids with species that attack SWD and that have been reported in Spain, including *Leptopilina bouvardi* (Figitidae), *Pachycrepoideus vindemmiae* (Pteromalidae) and *Trichopria drosophilae* (Diapriidae) (Wang et al., 2020). However, the presence of a parasitoid taxon does not allow us to infer the extent of its potential role in the control of SWD. Nonetheless, with the growing popularity of biological control methods for the management of SWD in crop areas (e.g. Haro-Barchin et al., 2018; Stacconi et al., 2018; Lee et al., 2019), we advocate the precautionary principle to prevent the introduction of exotic parasitoids. The ecological consequences of the release of exotic species into nature are not fully predictable (Parker et al., 1999; Ricciardi et al., 2013), so that the biological control of SWD based a natural enemy already in place should be the first option (e.g. Stacconi et al., 2018).

4.3. The lack of traditional forest management may promote SWD abundance and spread

Without human intervention, the understory of traditionally managed forests becomes dominated by a few fast-growing plants, some of them with fleshy fruits, such as *Hedera helix* and *R. ulmifolius* (Conedera et al., 2016). Moreover, the outgrowth of forest-edge creates a dense veil of these climber plants ‘up’ the edge-side trees, thereby reducing the diversity of plants and animals at the forest-patch scale (Hansson, 2001; Guitián et al., 2012). The strong positive association between SWD captures and the length of *R. ulmifolius* mats, which is the most common plant species in forest edges (Wang et al., 2016; Maceda-Veiga et al., 2016; Santoemma et al., 2018), suggests that the effectiveness of local forest interventions to manage SWD is likely to be limited. Moreover, SWD might be wind-dispersed from other habitats (Tait et al., 2018) or might move through habitats that, although unsuitable for SWD larvae, provide food for dispersing or itinerant adults (e.g. rotten fruit or decaying mushrooms), all of which are common in forests in many seasons.

Despite these limitations, our results suggest that maintaining species-diverse plant understories in chestnut woodlands and mature riparian tree cover might reduce the likelihood of these forests becoming colonization pathways for SWD. We found an inverse association between the riparian tree canopy cover and SWD captures, possibly because the fruiting of *R. ulmifolius* is limited under tree shade. Although *R. ulmifolius* was present in many forest understories during the surveys, there were none or few small fruits in the forest grounds compared to the

R. ulmifolius mats in forest edges (Mean \pm SD = 0.7 \pm 0.2 g vs 1.7 \pm 0.5 g, AMV unpublished data) from chestnut forests. This may explain the negative association between the forest-patch perimeter-radius ratio and SWD captures because the traps were nearer to the forest edge in smaller chestnut-forest patches.

5. Conclusions

Maintaining moderate human intervention in traditionally human managed forests by ground-layer management is recognized as being useful to maintain multiple components of native biodiversity, including in chestnut woodlands (Gutián et al., 2012; Nocentini et al., 2017; Roces-Díaz et al., 2018). Our study suggests that another benefit may be to reduce SWD spread because there would be lower biomasses of host plants for SWD and more diverse forest understories often promote natural enemies of dipterans (Sobek et al., 2009). Although frugivores might be regarded as being the 'losers' in this situation, forest edges are not completely eliminated in traditional management and the availability of fleshy fruits in the forest edge might benefit from lower SWD abundance. However, the likely complex interactions between SWD invasion and native wild frugivores need further investigation. Studies on SWD invasion would benefit from more forest-oriented perspectives complementing the traditional focus of SWD studies on human interests (i.e. forests as a source of SWDs to crop habitats).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Declaration of contributions

Conceived the research: AMV; Conducted the field work: AMV; Counted and identified (ID) taxa: AMV, SA, JPV (ID wasps) and MCT (ID dipterans); Analyzed data: AMV; Writing was led by AMV but all authors edited (particularly RM) and approved the final version.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.118942>.

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