

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/341050831>

Temporal dynamics of *Drosophila suzukii* in vineyard landscapes

Article in *Entomologia Generalis* · May 2020

DOI: 10.1127/entomologia/2020/0858

CITATIONS

6

READS

275

3 authors:



Lionel Delbac

French National Institute for Agriculture, Food, and Environment (INRAE)

98 PUBLICATIONS 502 CITATIONS

[SEE PROFILE](#)



Adrien Rusch

French National Institute for Agriculture, Food, and Environment (INRAE)

122 PUBLICATIONS 3,467 CITATIONS

[SEE PROFILE](#)



Denis Thiery

French National Institute for Agriculture, Food, and Environment (INRAE)

428 PUBLICATIONS 4,920 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



New concept of plant protection based on: DSS and natural defense messengers [View project](#)



Biological control of grape pests and phytoplasma vectors based on natural ennemy or ecological regulation [View project](#)



Temporal dynamics of *Drosophila suzukii* in vineyard landscapes

Lionel Delbac*, Adrien Rusch, and Denis Thiéry

SAVE, INRAE (French National Research Institute For Agriculture, Food And Environment), Bordeaux Science Agro, ISVV, Villenave d'Ornon, France

* Corresponding author: lionel.delbac@inrae.fr

With 1 figure and 2 tables

Abstract: *Drosophila suzukii* is an invasive pest which became a serious threat to stone and berry fruit production in Europe. Knowledge about the host range of this pest and the effect of the succession of available hosts over time is however lacking in vineyard landscapes. Our study aimed to evaluate the host range of *D. suzukii* throughout the year in a vineyard-dominated area. We assessed egg deposition and emergence on nine wild and cultivated plant species sampled in twenty vineyard landscapes during two years. The temporal dynamics of *D. suzukii* presence was observed on five fruit species (*Viscum album* L., *Prunus avium* L., *Sambucus nigra* L., *Rubus fruticosus* L. aggr. and *Vitis vinifera* L. cv. Merlot) with different phenologies. Infestations on host plants depended on the season and the proportion of other fruits species in the landscape around the vineyard plots. The data collected enabled us to provide estimates of the population dynamics among different hosts and generations of the pest and to propose a pattern of temporal succession of host plant species adapted to our regional and agroecological context.

Keywords: Spotted Wing Drosophila, Drosophilidae, grapevine, population dynamics, host range

1 Introduction

Biological invasions currently cause major ecological and economical impacts at the global scale (Arim et al. 2006; Ziska et al. 2011) and are particularly threatening the agricultural production sector (Biondi et al. 2018; Drechsler et al. 2016; Lurgi et al. 2016; Seebens et al. 2017). One of the major challenges in the management of invasive species is to understand the spatiotemporal dynamics of the colonization to be able to predict potential future area of establishment and to provide operational guidelines for the management of invasive species.

Since 2008 in Europe, the Spotted Wing Drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), has invaded most western countries, originating from South-East Asia, and now threatening the production of several crops (Asplen et al. 2015). This species is a highly polyphagous pest attacking healthy fruit before ripening, unlike other drosophila which exploit ripe or post ripening fruits (Rota-Stabelli et al. 2013). Apart from other fruit flies, the female is able to pierce the hard skin of soft and stone fruit thanks to its ovipositor making fruits unmarketable (Hamby et al. 2016). The recent invasion of *D. suzukii* resulted in yield losses that

can reach 80% of the production for stone fruits and red berries (Baker et al. 2010; Lee et al. 2011b). On grape, *D. suzukii* affects the harvest in quantity and quality since 2011 in several European vineyards (Delbac et al. 2014, 2017; Kehrli et al. 2014; Linder et al. 2015; Marchand 2015; Marchesini et al. 2014; Mori et al. 2014). The direct harmfulness of this insect is linked to its unique ability within its taxonomic group to pierce the thick skin of the grape berry (Atallah et al. 2014). Moreover, field and lab experiments confirm the ability of *D. suzukii* to develop sour rot epidemics on its own or as a pioneering species to other *Drosophila* species associated with sour rot epidemics (Ioriatti et al. 2018; Rombaut et al. 2017; Entling & Hoffmann 2020). Sour rot impacts the chemical composition and quality of berries, must and wine (Barata et al. 2011a, b, 2012) going as far as the rejection by consumers of such wines (Campo et al. 2012). *Drosophila suzukii* can thus be considered as a serious pest to grapes, and rigorous sorting of the bunches are therefore necessary to eliminate those affected by the disease and avoid these qualitative alterations (Marchand 2015) leading to increased production costs (Linder et al. 2015).

The invasive and establishment success of *D. suzukii* is expected to be the result of new ecological active colonization,

very high polyphagy and the absence of selective pressure on it (Gibert 2012). Because, *D. suzukii* is a highly polyphagous species with a multitude of hosts in both cultivated and wild environments, it can therefore be assumed that this drosophilid has a capacity to exploit successive plant resources along the year, allowing continuous population growth in agricultural landscapes (Wang et al. 2016; Tait et al. 2020). In France, the role of host plants has recently been studied in northern part of the country (Poyet et al. 2015). In this lab study, the authors tested 67 fruit species, half of them allowing complete reproduction cycle of *D. suzukii*, and about a quarter of them a partial development. Two other studies, in different climatic regions, showed the important role of wild *Rubus*, *Prunus*, *Sambucus* and *Phytolacca* genera in the life cycle of *D. suzukii* (Kenis et al. 2016; Lee et al. 2015). Producing scientific knowledge about the role of both wild and cultivated species availability in space and time is crucial in order to understand population dynamics of this pest species and to be able to predict suppressive or enhancing context. Indeed, this insect has a seasonal activity timing where any delay in the phenology of the host plant could cause a discontinuity of the population's abundance along environmental gradients (Santoemma et al. 2019). To compensate failures in resources constancy for egg-laying, dispersion of reproducers is needed and the search for alternative host plants partially drives the dispersal phases of *D. suzukii* adults over short and long distances (Tait et al. 2018; 2020). The role of these wild plant species as a source of *D. suzukii* is probably crucial in real agricultural landscapes and has recently been studied (Briem et al. 2018; Wang et al. 2019; Weißinger et al. 2019). However, it remains poorly explored in oceanic region of Europe. Moreover, the roles of the spatial distribution as well as the phenology of different wild plant species that affect population dynamics of this pest in the landscape remains largely unknown in vineyard landscapes.

Vineyard dominated areas, like other areas dominated by perennial crops, are relatively more stable in time compared to annual landscapes. This relative temporal stability (Bruggisser et al. 2010) and the fact that vineyards are grown as monoculture (Shields et al. 2016; Svercel et al. 2009), suggest a major role played by wild plant species in the surrounding habitats (i.e., woodland, grasslands, hedges) for *D. suzukii*. The diversity of host plant species in the landscapes might be a key driver of population dynamics as suggested by studies on other insect species but remains largely unknown for *D. suzukii* (Letourneau et al. 2012; Ortega & Pascual 2014; Rusch et al. 2013; Thomson & Hoffmann 2009).

In this study, we examined the phenology of *D. suzukii* in vineyard landscapes. We aimed to (i) analyze the phenology throughout the year on successive host plant species, (ii) provide data about the host range of *D. suzukii* in the south western of France, and to (iii) estimate the potential of each plant species as a host.

2 Materials and methods

2.1 Study sites and sampling design

Twenty vineyard plots were selected in the Saint-Emilion Appellation area, (South East of the Bordeaux vineyard, France; 44°53'39.7"N, 0°09'20.5"W). The climate of this region is oceanic with a mild temperature and several days of rain throughout the year (Fermaud et al. 2016). The study area covers an area of 12,000 ha in the Appellation area where vine cultivation is dominant in the landscape (Verpy et al. 2014). This landscape is fragmented by alternation of vineyard plots, residential areas but also a landscape habitat composed of fallows, natural meadows, hedges, groves and more or less cultivated forests. The plots were chosen to provide a variability of landscape situation and presence of host plant resources, hence allowing to determine the susceptibility of various cultivated and wild fruit species to the egg-laying and development of *D. suzukii* in natural conditions throughout the year. The selection was done in order to minimize intra-plot variability. We selected plots using the Merlot variety, dominant cultivar in the Bordeaux vineyard (Delbac et al. 2017), and under conventional production method. This wine-growing area is, like the rest of the Bordeaux vineyard, a mandatory zone for the control of Flavescence dorée (Chuche & Thiéry 2014). Based on regulatory decisions (GDON du Libournais 2020), this was reduced to one to two insecticides instead of classically three in June on the vine plots involved in our study plots. Those applications were followed in July and/or August by a treatment against *Lobesia botrana* (Denis & Schiffermüller).

The network of plots is located along a landscape complexity gradient composed of different plant cover like trees (*Quercus robur* L., *Pinus pinaster* Aiton, *Robinia pseudo-acacia* L.), shrubs (*Prunus spinosa* L., *Sambucus nigra* L.) or bushes (*Rubus fruticosus* L. aggr., wild *Vitis* sp). We calculated landscape metrics using ArcGis software (Version 10.4, ESRI) in a 100 m radius around each sampled vineyard plot. The plots are spread over a maximum distance of 16.1 km and are 7 ± 3.5 km apart on average. We calculated the proportion of Semi-Natural Habitat (SNH) as the percentage of land consisting of woodland, grasslands, hedgerows, shrubs and bushes. SNH ranged from 0 to 31.7% in our experimental design. The borders of the plots consisted of roads, hedges, forests or vineyard plots. The grapevine ranged from 29.8 to 93.4% in our experimental design. This metric was correlated with other landscape metrics, as other studies have pointed out (Roschewitz et al. 2005; Woltz et al. 2012).

2.2 *Drosophila suzukii* population assessment

We collected the potential wild host plants of *D. suzukii* in the surrounding environment around each plot (in a 100 m radius) from July 2016 to December 2017. The minimum distance between the plot edges and the sampling area was

4.7 meters. To determine the host plants to be collected, we relied on the study carried out in northern France on potential host plants of *D. suzukii* (Poyet et al. 2015). We supplemented it with information from other studies in Europe and North America. Based on the presence of these host plants in our region (Tela Botanica 2019), we built a list of potential wild host plant species that we searched and collected in the study area around the plots during the whole survey. We took different samples depending on the type of fruit produced by the plants: 30 fruits when plant species produced berries, drupes or rose hips, five when plant species produced corymbs (*S. nigra*) and spadix (*Arum maculatum* L.) or ten when plant species produces bunches (*V. vinifera* cv Merlot). To assess the infestation on grapes, bunches were sampled randomly every two weeks, along a transect of thirty meters from the edge of the row towards the inside of the vineyard plot during ripening until harvest or maturity. In the lab, we assessed presence of eggs and adults on all samples. For eggs, the assessment was performed on 30 fruits by sample for all plant species (for this we sub-sampled 30 fruits from the corymbs, the spadix or the bunches) using dissecting microscope at 20 times magnification. We then checked the emergence of adults during 21 days, of each initial fruit batches collected in the field, maintained under laboratory conditions under an LD 16: 8 h photoperiod at 22°C and HR 70%. Adults were identified to the species criteria published for *D. suzukii* (Withers & Allemand 2012) using dissecting microscope at 20 to 50 times magnification. Following the control of egg-laying infestations and the monitoring of adult emergence of *D. suzukii*, we determined the categories of fruit types according to their sensitivity to the insect: (i) no egg-laying, (ii) oviposition but no development to adulthood, (iii) egg-laying and complete development (Poyet et al. 2015). The data from batches of plant species whose too small sample size (i.e. < 5) were not included in this study.

2.3 Statistical analysis

In order to determine the host status of each plant species collected (non host, partial development, complete development), we calculated the rate of occurrence for both the number of eggs laid and the number of emerging adults. All data were collected at the same sampling scale, namely the fruit (berry, drupe, rose hip, corymb, spadix or bunch).

We then examined the temporal dynamics of *D. suzukii* through time considering emergence from the different plant species (only taking into account plant species that allow for the emergence of the insect). To assess the temporal dynamics of emergence from different host plants through time, we used a one-way analysis of variance using the host plant species as the explanatory variable and sampling date that resulted in adult emergence, as the response variable. Sampling date was expressed as Julian dates. A data transformation was performed to stabilize variance and make the data more normal distribution-like. For that we applied a Box-Cox transformation technique to data of the “Julian

days” variable to determine the type of transformation required (Sakia 1992). Average Julian date among host plant species were then compared using a Tukey test to classify temporal switch in host plant species based on adult emergence. The analysis was performed with the RStudio software (version 1.1).

3 Results

Throughout the experiment, 237 fruit samples were collected from 27 July 2016 to 12 December 2017, all belonging to nine plant species: seven wild/non cultivated species (*A. maculatum*, *P. spinosa*, *Rosa canina* L., *R. fruticosus* aggr., *S. nigra*, *Solanum nigrum* L., *Viscum album* L.), one cultivated species for production (*V. vinifera* cv Merlot) and one cultivated in allotment gardens or on the edge of plots (*Prunus avium*) (Tab. 1 & 2). The plant species corresponding to the three *D. suzukii* behavior and development traits were recorded as follow:

- i) no egg-laying found: three plant species were classified in this category: *P. spinosa*, *R. canina* and *S. nigrum*;
- ii) oviposition detected but no adult development: only *A. maculatum* was classified in this category, with only one sample on which we observed the eggs.
- iii) egg-laying and complete development: five plant species, i.e. *V. album*, *P. avium*, *S. nigra*, *R. fruticosus* aggr. and *V. vinifera* cv Merlot, were classified under this category. On average, we observed egg-laying in only 54.1% of the samples collected. The highest occurrences, around 75%, are observed for *P. avium*, *R. fruticosus* and *S. nigra*. The lowest, 10.9%, are rated for *V. vinifera* cv Merlot. The occurrences are quite similar for emergence.

During the emergences, we obtained only adults from *D. suzukii* except for grape where other drosophilid species accounted for 6.1 and 62.4% of emergences, respectively in 2016 and 2017. Among other species, we observed four adults of *D. simulans* in 2016 that emerged almost a week after those of *D. suzukii*. In 2017, the 846 adults of *D. simulans* and the 328 adults of *D. melanogaster* emerged at the same time. The level of infestation of *D. suzukii* was much higher in 2017 with associated rot damage than in 2016 (1.2 vs 0.1 adult per bunch respectively). Although grape harvest was later in 2016 than in 2017 (October 6th vs September 26th respectively), the infestations were always observed no earlier than 3 weeks before these dates and mainly just before the harvest. Most of the grapes collected and monitored in the laboratory showed emergences after the harvest time. The individuals of *D. suzukii* and other species were therefore mainly present as larvae or pupae at harvest; and *D. suzukii* could therefore be found in the winepress at the winery, since the average temperature usually recorded

Table 1. Occurrence of eggs laid and emerging adults of *D. suzukii* per plant species in field assessments conducted in Bordeaux vineyard, during 2016 and 2017, and experimental details.

Scientific name	Number of samples	% samples with eggs	% samples with adults	Date
No egg laid				
<i>Prunus spinosa</i> L.	2	0	0	20 Sep. 2016
	4	0	0	5 Jul. to 30 Aug. 2017
<i>Rosa canina</i> L.	7	0	0	29 Aug. to 16 Nov. 2016
	3	0	0	16 to 30 Aug. 2017
<i>Solanum nigrum</i> L.	4	0	0	21 Sep. to 14 Dec. 2016
	1	0	0	30 Aug. 2017
Eggs laid, no development				
<i>Arum maculatum</i> L.	4	0	0	3 Aug. to 20 Sep. 2016
	6	16.7	0	5 Jul. to 30 Aug. 2017
Development				
<i>Prunus avium</i> L.	7	85.7	85.7	10 May to 14 Jun. 2017
<i>Rubus fruticosus</i> L. aggr.	24	79.2	62.3	27 Jul. to 7 Dec. 2016
	37	86.5	73.0	5 Jul. to 15 Nov. 2017
<i>Sambucus nigra</i> L.	11	Na ^a	63.63	27 Jul. to 29 Aug. 2016
	9	77.8	77.8	5 Jul. to 16 Aug. 2017
<i>Viscum album</i> L.	2	0	0	7 to 14 Dec. 2016
	12	41.7	41.7	8 Feb. to 12 Dec. 2017
<i>Vitis vinifera</i> L. cv Merlot	54	Na ^a	27.8	9 Sep. to 6 Oct. 2016
	59	11.9	28.8	23 Aug. to 4 Oct. 2017

^a Not acquired

during harvest allows a development in more than 2-3 weeks (Sánchez-Ramos et al. 2019).

In 2016, only 37 plant individuals were analyzed from three plant species (*S. nigra*, *R. fruticosus* aggr. and *V. vinifera* cv Merlot) with seven, 15 and 15 individuals respectively. In 2017, 62 plant individuals were analyzed from five plant species (*P. avium*, *R. fruticosus* aggr., *S. nigra*, *V. album* and *V. vinifera* cv Merlot) with six, 27, seven, five and 17 individuals respectively. Because there was no statistical difference in the interaction year x species ($F_{2, 82} = 0.31$; $P = 0.738$), all the data were pooled together to analysis concerning *R. fruticosus*, *S. nigra* and *V. vinifera*.

The analysis of variance gives us significant differences between temporality in the species ($F_{4, 94} = 111.19$; $P < 0.001$). Plant species were thus categorized into groups that are statistically different based on the probability of mean differences and the alpha level (0.05): *V. album*, *P. avium*, *S. nigra*, *R. fruticosus* aggr. and *V. vinifera* cv Merlot, ranked in chronological order of fructification respectively.

4 Discussion

Our study aimed to analyze the phenology of *D. suzukii* on successive resources throughout the year, to better character-

ize its host range in vineyard landscapes of the southwestern part of France. Our results demonstrate that several plant species, at least five, can serve as host plant and possibly population reservoirs in vineyard landscapes of western France. Our longitudinal analyses of plant phenology and imago emergence makes it possible to build a scenario of resource continuity over the life cycle of *D. suzukii* in these landscapes (Fig. 1). Throughout the year, *V. album* can be considered a favorable host in mid spring, followed by *P. avium* in late spring. Two species were identified as resource in early summer: *S. nigra* and *R. fruticosus* aggr.; the latter having the longest attractiveness until mid-fall. Finally, in late summer until early autumn, *V. vinifera* (Merlot variety) was the most colonized host.

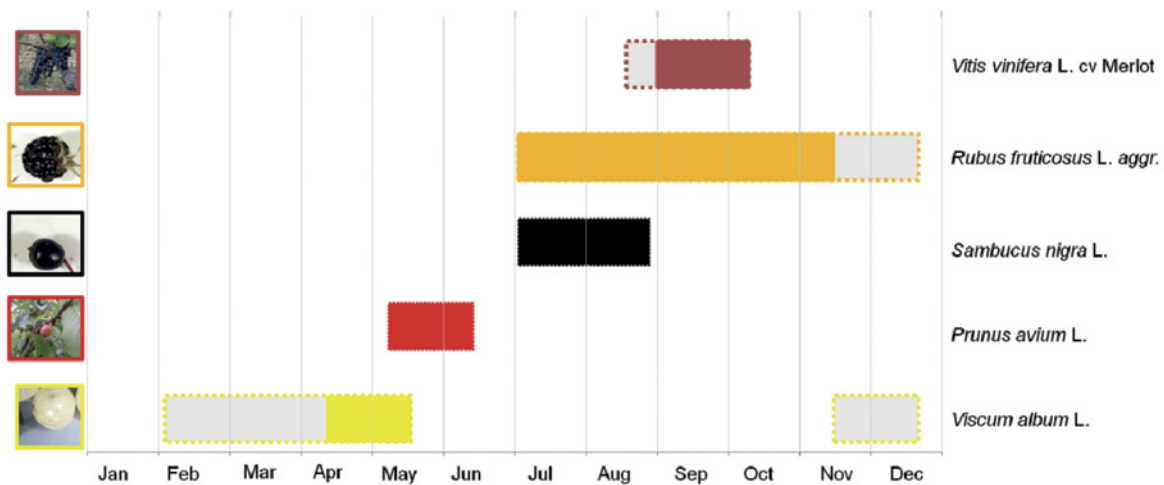
This survey confirmed results from previous laboratory and field studies about the potential of several plant species to serve as a host for *D. suzukii* (Tab. 2). We confirmed that four out of the seven plants species (i.e., *P. avium*, *R. fruticosus* aggr., *S. nigra* and *V. vinifera* cv Merlot) found in the largest field study conducted so far on *D. suzukii* host range (Kenis et al. 2016) were host plant allowing the complete cycle (strict definition of a host plant); i.e. development of eggs to adults. In our study, *V. album* was also identified as host plant for *D. suzukii* which confirmed Briem et al. (2016), but was not the case in Kenis et al. (2016). Several

Table 2. Classification of the different host plants tested according to their development capacity for *Drosophila suzukii*: comparison between the bibliographic data and those obtained during the experiment in the Bordeaux region between 2016 and 2017.

Scientific name	Laboratory infestations						Field infestations						This study
	(a)	(b)	(c)	(d)	(e)	(f)	(a)	(b)	(c)	(d)	(f)	(g)	
<i>Prunus spinosa</i> L.					dvt							dvt	Ø
<i>Rosa canina</i> L.	Ø				Ø		dvt					dvt	Ø
<i>Solanum nigrum</i> L.	Ø				dvt		dvt			Ø		dvt	Ø
<i>Arum maculatum</i> L.					dvt								w
<i>Prunus avium</i> L.				dvt	dvt	dvt				dvt	dvt	dvt	dvt
<i>Rubus fruticosus</i> L. <i>aggr.</i>					dvt					dvt		dvt	dvt
<i>Sambucus nigra</i> L.	dvt			dvt	dvt		dvt			dvt		dvt	dvt
<i>Viscum album</i> L.		dvt			dvt		dvt					Ø	dvt
<i>Vitis vinifera</i> L.													
cv NA												dvt	
cv Cabernet Sauvignon						dvt							
cv Crimson Seedless						dvt							
cv Dornfelder			dvt						dvt				
cv Merlot													dvt
cv Pinot Noir													Ø
cv Thomson Seedless						dvt					Ø		

Ø: no eggs laid; w: eggs laid, no development; dvt: eggs and development to adults

(a): Arnó et al. (2016); (b): Briem et al. (2016); (c): Entling and Hoffmann (2019); (d): Lee et al. (2015); (e): Poyet et al. (2015); (f): Wang et al. (2019); (g): Kenis et al. (2016); (h): Weißinger et al. (2019)

**Fig. 1.** Pattern of the seasonal activity of *Drosophila suzukii* in the Bordeaux vineyard with the chronological susceptibility of the different host plants collected in 2016 and 2017 allowing the development. For each species, the sampling periods are represented by grey and dotted rectangles and emergences by rectangles with solid lines and color.

species such as *R. canina* were classified as a non-host species in our case (according to Poyet et al. (2015)), were classified as a host species allowing full development of *D. suzukii* in another field study (Kenis et al. 2016). Differences in host susceptibility between field and laboratory experiments are common (Arnó et al. 2016). In the specific case of *R. canina*, these authors clearly showed the difference in the classification for infestations of *D. suzukii* of the same fruit batch between *in natura* and laboratory. Differences between laboratory and in real field conditions were also noticed in several cases, e.g. *S. nigrum* (Arnó et al. 2016; Kenis et al. 2016; Lee et al. 2015). Nevertheless, the level of infestations calculated under laboratory conditions (Arnó et al. 2016; Briem et al. 2016; Lee et al. 2015; Poyet et al. 2015; Wang et al. 2019) should be viewed as the maximum development potential of *D. suzukii* for each resource plant.

Several phenomena can explain the differences in host selection by females of *D. suzukii* found in different studies. If conditions are different, a plant species can be classified as host or non-host depending on the diversity of potential hosts in the landscape and the results strongly depend on local conditions (Ioriatti et al. 2015; Kenis et al. 2016; Kim et al. 2015; Lee et al. 2015), frequency of host plant distribution (Elsensohn & Loeb 2018; Poyet et al. 2014), temporal availability of the host (Poyet et al. 2015), variability in the sample size (Kenis et al. 2016), fruit properties (Arnó et al. 2016; Burrack et al. 2013; Entling et al. 2019; Kinjo et al. 2013; Lee et al. 2011a), as well as climatic conditions (Kenis et al. 2016). That is why the results we have obtained give important information adapted to our climatic and geographical conditions, which was carried out only in mountain conditions (Tonina et al. 2016).

These resources are important for the population dynamics of *D. suzukii*. In our monitoring, we noted that the insect life cycle was conditioned by several factors that may interact. We observed a synchronization of the insect in relation to the presence of fruit of its host plant, egg-laying being carried out during the process of maturation. However, egg-laying and development of *D. suzukii* can also be observed on overripe fruits or fruit composts (Bal et al. 2017). The phenological stage of the host is among the most relevant host trait for the development of phytophagous species (Kennedy & Storer 2000; Straw 1991; van Asch & Visser 2007). Indeed, *D. suzukii* is a frugivorous species that attacks in general fresh and healthy, maturing fruits (Keesey et al. 2015; Lee et al. 2011a; Poyet et al. 2014; Rota-Stabelli et al. 2013). Beyond this stage, other fruit fly species can develop (Poyet et al. 2015) and *D. suzukii* is replaced by more competitive species (Iacovone et al. 2015). This is particularly the case on grape (Delbac et al. 2014, 2017).

We can assume that the distribution of host plant species in vineyard landscapes (i.e., blackberry represents 95% of wild resources as in other wine-growing landscapes in Europe (Weißinger et al. 2019)) must have influenced the number of eggs laid by *D. suzukii* either through concen-

tration - dilution processes or simply due to modified probability of host location depending on host plant frequency. Concentration of host plants is known to lead to concentration of phytophagous insects that feed on them (Root 1973; Sholes 2008), especially through increased distance of attraction due to resource concentration and mediated by visual or olfactory stimuli (Stanton 1983). *Drosophila suzukii*, such as most fruit flies, can adapt its foraging behavior to actively move towards nutritive resources (Becher et al. 2012; Bell 1990; Legal et al. 1992; Thiéry et al. 2013). Among the different host plant species, blackberry is one of the most interesting host plant for *D. suzukii* as it has one of the best host potentials during a long time period (Bellamy et al. 2013), it creates a very suitable environment for *D. suzukii* development (Diepenbrock & Burrack 2017) that reduced the development time period (Poyet et al. 2015). This reduced development time is a major driver of insect fitness since it limits time of exposure to natural enemies (Benrey & Denno 1997; Häggström & Larsson 1995). Considering the fitness gain provided by grape, the attraction to this resource may appear surprising as compared to the host range quoted above (Bellamy et al. 2013). Fruit flies are attracted by organic acids produced by many fruits (Ai et al. 2010) and *D. suzukii* is attracted by the odors of plants such as Beta-cyclocitral (Keesey et al. 2015). This volatile molecule is characteristic of young grapes at the beginning of berry formation in summer (Rambla et al. 2016). This is during this period that a sharp increase in the abundance of *D. suzukii* adults in traps is observed in vineyard plots suggesting that flies are particularly attracted to grape (Delbac et al. 2017; Ioriatti et al. 2015). At this time period, the quantity of host plants in semi-natural habitats are very limited, (e.g., *R. fruticosus*, Briem et al. 2018), and the flies are therefore searching for new food resources. The spillover of *D. suzukii* populations from uncultivated habitats to fruit crops has been confirmed by trapping experiment (Wang et al. 2016). Although grape has the least host potential among different cultivated fruit species for *D. suzukii* (Bellamy et al. 2013), this highly abundant resource in vineyard-dominated areas is available for females that can lay eggs when the berry skin is less resistant such as after ripening (Entling et al. 2019; Ioriatti et al. 2015; Shrader et al. 2019).

We have observed that the succession of resources over time, i.e., the presence of fruits of several plant species, is essential for *D. suzukii* to complete its complete life cycle throughout the year in our wine-growing landscapes. As this insect is polyphagous, with host plants in both wild and cultivated environments (Kenis et al. 2016), it requires temporal continuity of its host plants (Poyet et al. 2015). An interruption in the temporal continuity of these will then disrupt the population dynamics of *D. suzukii*, which is common in phytophagous insects (Schellhorn et al. 2015). For *D. suzukii*, these breaks in resource continuity can occur at several periods during the year (i.e. the grape harvest represents a break in the temporal continuity of host fruits). One of the key phases

of this population dynamics and the resulting crop infestations is the end of the insect diapause (Panel et al. 2018). At this time, the ovaries of *D. suzukii* are functional and females can thus lay eggs (Arnó et al. 2016; Briem et al. 2016). The choice of receptive host fruits present is then limited and only mistletoe was suitable and available for this function in our study. In our monitoring network, the vineyard plots near the areas where mistletoe infested trees are located will then be the ones where we find the most adult individuals trapped in spring (data not shown). As the vine is a relatively late host crop compared to other host crops, several periods of interruption of resource continuity may still occur. We have shown in our data that *R. fruticosus* aggr. receptivity period may be very significant for the life cycle of *D. suzukii* since it extends over 4.5 months. The genus *Rubus* is known to be crucial for the seasonal activity of the insect (Klick et al. 2016). Blackberry represents, around our vineyard plots, the largest proportion of wild host plants and it could play a major relay host candidate before colonizing grapes. In fall, the final level of grape infestation by *D. suzukii* will therefore be determined by the development of the insect through the presence or absence of receptive and successive host plants in the perimeter of the plots. This can be confirmed in 2017 where one of our twenty plots, with one of the highest rates of resource host plants around, was not harvested due to high level of damages with more than 10 *D. suzukii* per cluster and the presence of rot (acid and grey mold). Several studies have recently shown that landscape context and particularly the proportion of semi-natural habitats significantly influenced population dynamics of *D. suzukii* in blueberry (Haro-Barchin et al. 2018), cherry (Hennig & Mazzi 2018; Santoiemma et al. 2018) or raspberry crops (Klick et al. 2016; Pelton et al. 2016). Our results provide an explanation about the positive effect of semi-natural habitats and the key role of wild host plant species in the vineyard landscape for *D. suzukii* population dynamics. *Drosophila suzukii* population must develop through various nearby receptive hosts to promote grape infestation, and the landscape is an important component to be taken into account when assessing the epidemic risk of this pest on vine. It is therefore necessary to consider a spatiotemporal study of the presence of the resource host plants around the vineyard plots.

Semi-natural habitats that host wild plants for *D. suzukii* are also known to have positive effects on the level of biological pest control provided by natural enemies, i.e., conservation biological control (Tscharntke et al. 2007). Moreover, such habitats could affect the level of pest control provided by augmentative (e.g., *Trichopria drosophilae* (Perkins)) (Rossi Stacconi et al. 2018), classical biological control (e.g., *Ganaspis brasiliensis* (Ihering)) (Daane et al. 2016), or by conserving fortuitous parasitoids (Mazzetto et al. 2016). It is therefore of major importance to study the balance of positive and negative effects of wild host plants and their habitats on top-down control in vineyard landscapes as this remains largely unexplored.

In conclusion, our study demonstrates that several plant species (five in our southwestern of France ecological conditions) are host plants for *D. suzukii* throughout the year and we established a pattern of plant species succession allowing the continuous presence of the insect in our geographical area. This knowledge allows us to understand potential resource continuity in time and how this will affect population dynamics of a major invasive pest species in agricultural landscapes. We here confirm the presence of a sequence of fruit availability and the important role played by the vineyard surrounding vegetation as reservoir or eventually hotspots of infestation. The next step will be to quantify the impact of the spatial and temporal distribution of these resource host plants on the insect's population dynamics to analyze the predictive ability of such landscape indicators. Our results allow us to better understand how to improve the pest monitoring by specifically targeting the host plants to be sampled according to the period. This pest monitoring is necessary to assess the risk in a given plot of land. Improved monitoring will favor the adaptation of the management procedures to the specific characteristics of the plot. Further studies would interestingly focus on the different resources around the vineyards and their potential function as hotspots for *D. suzukii*.

Acknowledgments: We thank Delphine Binet for technical assistance during the fieldwork, and are thankful to the farmers for authorizing us to access to their fields and for their interest in the project. Authors are grateful to the associate editor Antonio Biondi and the anonymous reviewers for valuable comments improving the manuscript. This research was performed within the cluster of excellence COTE. The research presented in this paper was partially funded by the InvaProtect project (European Union's INTERREG V Upper Rhine program 2016-2018).

References

- Ai, M., Min, S., Grosjean, Y., Leblanc, C., Bell, R., Benton, R., & Suh, G. S. B. (2010). Acid sensing by the *Drosophila* olfactory system. *Nature*, 468(7324), 691–695. <https://doi.org/10.1038/nature09537>
- Arim, M., Abades, S. R., Neill, P. E., Lima, M., & Marquet, P. A. (2006). Spread dynamics of invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 103(2), 374–378. <https://doi.org/10.1073/pnas.0504272102>
- Arnó, J., Solà, M., Riudavets, J., & Gabarra, R. (2016). Population dynamics, non-crop hosts, and fruit susceptibility of *Drosophila suzukii* in northeast Spain. *Journal of Pest Science*, 89(3), 713–723. <https://doi.org/10.1007/s10340-016-0774-3>
- Asplen, M. K., Anfora, G., Biondi, A., Choi, D.-S., Chu, D., Daane, K. M., ... Desneux, N. (2015). Invasion biology of Spotted Wing *Drosophila* (*Drosophila suzukii*): A global perspective and future priorities. *Journal of Pest Science*, 88(3), 469–494. <https://doi.org/10.1007/s10340-015-0681-z>

- Atallah, J., Teixeira, L., Salazar, R., Zaragoza, G., & Kopp, A. (2014). The making of a pest: The evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 281(1781), 20132840. <https://doi.org/10.1098/rspb.2013.2840>
- Baker, R., Baufeld, P., Grassi, A., Guitian Castrillon, J. M., Hauser, M., Hueppelsheuser, T., ... OEPP/EPPO (2010). Pest risk analysis for: *Drosophila suzukii*. *European and Mediterranean Plant Protection Organization* 11-17189.
- Bal, H. K., Adams, C., & Grieshop, M. (2017). Evaluation of off-season potential breeding sources for Spotted Wing *Drosophila* (*Drosophila suzukii* Matsumura) in Michigan. *Journal of Economic Entomology*, 110(6), 2466–2470. <https://doi.org/10.1093/jeet/tox252>
- Barata, A., Campo, E., Malfeito-Ferreira, M., Loureiro, V., Cacho, J., & Ferreira, V. (2011a). Analytical and sensorial characterization of the aroma of wines produced with sour rotten grapes using GC-O and GC-MS: Identification of key aroma compounds. *Journal of Agricultural and Food Chemistry*, 59(6), 2543–2553. <https://doi.org/10.1021/jf104141f>
- Barata, A., Pais, A., Malfeito-Ferreira, M., & Loureiro, V. (2011b). Influence of sour rotten grapes on the chemical composition and quality of grape must and wine. *European Food Research and Technology*, 233(2), 183–194. <https://doi.org/10.1007/s00217-011-1505-x>
- Barata, A., Malfeito-Ferreira, M., & Loureiro, V. (2012). Changes in sour rotten grape berry microbiota during ripening and wine fermentation. *International Journal of Food Microbiology*, 154(3), 152–161. <https://doi.org/10.1016/j.ijfoodmicro.2011.12.029>
- Becher, P. G., Flick, G., Rozpędowska, E., Schmidt, A., Hagman, A., Lebreton, S., ... Bengtsson, M. (2012). Yeast, not fruit volatiles mediate *Drosophila melanogaster* attraction, oviposition and development. *Functional Ecology*, 26(4), 822–828. <https://doi.org/10.1111/j.1365-2435.2012.02006.x>
- Bell, W. J. (1990). Searching behavior patterns in insects. *Annual Review of Entomology*, 35(1), 447–467. <https://doi.org/10.1146/annurev.en.35.010190.002311>
- Bellamy, D. E., Sisterson, M. S., & Walse, S. S. (2013). Quantifying host potentials: Indexing postharvest fresh fruits for spotted wing drosophila, *Drosophila suzukii*. *PLoS One*, 8(4), e61227. <https://doi.org/10.1371/journal.pone.0061227>
- Benrey, B., & Denno, R. F. (1997). The slow-growth-high-mortality hypothesis: A test using the Cabbage Butterfly. *Ecology*, 78, 987–999.
- Biondi, A., Guedes, R. N. C., Wan, F.-H., & Desneux, N. (2018). Ecology, worldwide spread, and management of the invasive South American Tomato Pinworm, *Tuta absoluta*: Past, present, and future. *Annual Review of Entomology*, 63(1), 239–258. <https://doi.org/10.1146/annurev-ento-031616-034933>
- Briem, F., Dominic, A. R., Golla, B., Hoffmann, C., Englert, C., Herz, A., & Vogt, H. (2018). Explorative data analysis of *Drosophila suzukii* trap catches from a seven-year monitoring program in southwest Germany. *Insects*, 9(4), 125. <https://doi.org/10.3390/insects9040125>
- Briem, F., Eben, A., Gross, J., & Vogt, H. (2016). An invader supported by a parasite: Mistletoe berries as a host for food and reproduction of Spotted Wing *Drosophila* in early spring. *Journal of Pest Science*, 89(3), 749–759. <https://doi.org/10.1007/s10340-016-0739-6>
- Bruggisser, O. T., Schmidt-Entling, M. H., & Bacher, S. (2010). Effects of vineyard management on biodiversity at three trophic levels. *Biological Conservation*, 143(6), 1521–1528. <https://doi.org/10.1016/j.biocon.2010.03.034>
- Burrack, H. J., Fernandez, G. E., Spivey, T., & Kraus, D. A. (2013). Variation in selection and utilization of host crops in the field and laboratory by *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), an invasive frugivore. *Pest Management Science*, 69(10), 1173–1180. <https://doi.org/10.1002/ps.3489>
- Campo, E., Saenz-Navajas, M. P., Cacho, J., & Ferreira, V. (2012). Consumer rejection threshold of ethyl phenylacetate and phenylacetic acid, compounds responsible for the sweet-like off odour in wines made from sour rotten grapes. *Australian Journal of Grape and Wine Research*, 18(3), 280–286. <https://doi.org/10.1111/j.1755-0238.2012.00198.x>
- Chuche, J., & Thiéry, D. (2014). Biology and ecology of the Flavescence dorée vector *Scaphoideus titanus*: A review. *Agronomy for Sustainable Development*, 34(2), 381–403. <https://doi.org/10.1007/s13593-014-0208-7>
- Daane, K. M., Wang, X.-G., Biondi, A., Miller, B., Miller, J. C., Riedl, H., ... Walton, V. M. (2016). First exploration of parasitoids of *Drosophila suzukii* in South Korea as potential classical biological agents. *Journal of Pest Science*, 89(3), 823–835. <https://doi.org/10.1007/s10340-016-0740-0>
- Delbac, L., Rouzes, R., Rusch, A., & Thiéry, D. (2017). Geographical area extension of *Drosophila suzukii* (Diptera: Drosophilidae) in Bordeaux vineyards. *IOBC/WRPS Bulletin*, 128, 28–36.
- Delbac, L., Rusch, A., Rouzes, R., Ravidat, M. L., Launes, S., & Thiéry, D. (2014). *Drosophila suzukii* est-elle une menace pour la vigne? *Phytoma*, 679, 16–21.
- Diepenbrock, L. M., & Burrack, H. J. (2017). Variation of within-crop microhabitat use by *Drosophila suzukii* (Diptera: Drosophilidae) in blackberry. *Journal of Applied Entomology*, 141(1-2), 1–7. <https://doi.org/10.1111/jen.12335>
- Drechsler, M., Touza, J., White, P. C. L., & Jones, G. (2016). Agricultural landscape structure and invasive species: The cost-effective level of crop field clustering. *Food Security*, 8(1), 111–121. <https://doi.org/10.1007/s12571-015-0539-5>
- Elsensohn, J. E., & Loeb, G. M. (2018). Non-crop host sampling yields insights into small-scale population dynamics of *Drosophila suzukii* (Matsumura). *Insects*, 9(1), 5. <https://doi.org/10.3390/insects9010005>
- Entling, W., Anslinger, S., Jarausch, B., Michl, G., & Hoffmann, C. (2019). Berry skin resistance explains oviposition preferences of *Drosophila suzukii* at the level of grape cultivars and single berries. *Journal of Pest Science*, 92(2), 477–484. <https://doi.org/10.1007/s10340-018-1040-7>
- Entling, W., & Hoffmann, C. (2020). (in press). Single and combined effects of *Drosophila suzukii* and *Drosophila melanogaster* on sour rot development in viticulture. *Journal of Applied Entomology*. <https://doi.org/10.1111/jen.12721>
- Fermaud, M., Smits, N., Merot, A., Roudet, J., Thiéry, D., Wery, J., & Delbac, L. (2016). New multipest damage indicator to assess protection strategies in grapevine cropping systems. *Australian Journal of Grape and Wine Research*, 22(3), 450–461. <https://doi.org/10.1111/ajgw.12238>
- GDON du Libournais (2020). Lutte contre la Flavescence Dorée. http://www.gdon-libournais.fr/download_docs_FD.php. Accessed on 16 January 2020.
- Gibert, P. (2012). Plasticité phénotypique et réponses adaptatives aux changements environnementaux chez les insectes.

- Habilitation à Diriger des Recherches. Université Claude Bernard Lyon1 (France).
- Hägström, H., & Larsson, S. (1995). Slow larval growth on a sub-optimal willow results in high predation mortality in the leaf beetle *Galerucella lineola*. *Oecologia*, 104(3), 308–315. <https://doi.org/10.1007/BF00328366>
- Hamby, K. A., Bellamy, D. E., Chiu, J. C., Lee, J. C., Walton, V. M., Wiman, N. G., ... Biondi, A. (2016). Biotic and abiotic factors impacting development, behavior, phenology, and reproductive biology of *Drosophila suzukii*. *Journal of Pest Science*, 89, 605–619. <https://doi.org/10.1007/s10340-016-0756-5>
- Haro-Barchin, E., Scheper, J., Ganuza, C., De Groot, G. A., Colombari, F., van Kats, R., & Kleijn, D. (2018). Landscape-scale forest cover increases the abundance of *Drosophila suzukii* and parasitoid wasps. *Basic and Applied Ecology*, 31, 33–43. <https://doi.org/10.1016/j.baec.2018.07.003>
- Hennig, E. I., & Mazzi, D. (2018). Spotted Wing *Drosophila* in sweet cherry orchards in relation to forest characteristics, bycatch, and resource availability. *Insects*, 9(3), 118. <https://doi.org/10.3390/insects9030118>
- Iacovone, A., Girod, P., Ris, N., (2015). Worldwide invasion by *Drosophila suzukii*: Does being the “cousin” of a model organism really help setting up biological control? Hopes, disenchantments and new perspectives. *Revue d'Ecologie (La Terre et la Vie)*, 70, 207–214.
- Ioriatti, C., Guzzon, R., Anfora, G., Ghidoni, F., Mazzoni, V., Villegas, T. R., ... Walton, V. M. (2018). *Drosophila suzukii* (Diptera: Drosophilidae) contributes to the development of sour rot in grape. *Journal of Economic Entomology*, 111(1), 283–292. <https://doi.org/10.1093/jee/tox292>
- Ioriatti, C., Walton, V., Dalton, D., Anfora, G., Grassi, A., Maistri, S., & Mazzoni, V. (2015). *Drosophila suzukii* (Diptera: Drosophilidae) and its potential impact to wine grapes during harvest in two cool climate wine grape production regions. *Journal of Economic Entomology*, 108(3), 1148–1155. <https://doi.org/10.1093/jee/tov042>
- Keeseey, I. W., Knaden, M., & Hansson, B. S. (2015). Olfactory specialization in *Drosophila suzukii* supports an ecological shift in host preference from rotten to fresh fruit. *Journal of Chemical Ecology*, 41(2), 121–128. <https://doi.org/10.1007/s10886-015-0544-3>
- Kehrli, P., Richoz, P., Linder, C., & Baroffio, C. (2014). The importance of *Drosophila suzukii* for grapevine production. *IOBC/WPRS Bulletin*, 105, 211–218.
- Kenis, M., Tonina, L., Eschen, R., van der Sluis, B., Sancassani, M., Mori, N., ... Helsen, H. (2016). Non-crop plants used as hosts by *Drosophila suzukii* in Europe. *Journal of Pest Science*, 89(3), 735–748. <https://doi.org/10.1007/s10340-016-0755-6>
- Kennedy, G. G., & Storer, N. P. (2000). Life systems of polyphagous arthropod pests in temporally unstable cropping systems. *Annual Review of Entomology*, 45(1), 467–493. <https://doi.org/10.1146/annurev.ento.45.1.467>
- Kim, M. J., Kim, J. S., Park, J. S., Choi, D. S., Park, J., & Kim, I. (2015). Oviposition and development potential of the Spotted-Wing *Drosophila suzukii* (Diptera: Drosophilidae), on uninjured Campbell Early grape. *Entomological Research*, 45(6), 354–359. <https://doi.org/10.1111/1748-5967.12142>
- Kinjo, H., Kunimi, Y., Ban, T., & Nakai, M. (2013). Oviposition efficacy of *Drosophila suzukii* (Diptera: Drosophilidae) on different cultivars of blueberry. *Journal of Economic Entomology*, 106(4), 1767–1771. <https://doi.org/10.1603/EC12505>
- Klick, J., Yang, W. Q., Walton, V. M., Dalton, D. T., Hagler, J. R., Dreves, A. J., ... Bruck, D. J. (2016). Distribution and activity of *Drosophila suzukii* in cultivated raspberry and surrounding vegetation. *Journal of Applied Entomology*, 140(1-2), 37–46. <https://doi.org/10.1111/jen.12234>
- Lee, J. C., Bruck, D. J., Curry, H., Edwards, D., Haviland, D. R., Van Steenwyk, R. A., & Yorgey, B. M. (2011a). The susceptibility of small fruits and cherries to the Spotted-Wing *Drosophila suzukii*. *Pest Management Science*, 67(11), 1358–1367. <https://doi.org/10.1002/ps.2225>
- Lee, J. C., Bruck, D. J., Dreves, A. J., Ioriatti, C., Vogt, H., & Baufeld, P. (2011b). In Focus: Spotted Wing *Drosophila suzukii*, across perspectives. *Pest Management Science*, 67(11), 1349–1351. <https://doi.org/10.1002/ps.2271>
- Lee, J. C., Dreves, A. J., Cave, A. M., Kawai, S., Isaacs, R., Miller, J. C., ... Bruck, D. J. (2015). Infestation of wild and ornamental noncrop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). *Annals of the Entomological Society of America*, 108(2), 117–129. <https://doi.org/10.1093/aesa/sau014>
- Legal, L., David, J. R., & Jallon, J. M. (1992). Toxicity and attraction effects produced by *Morinda citrifolia* fruits on the *Drosophila melanogaster* complex of species. *Chemoecology*, 3(3-4), 125–129. <https://doi.org/10.1007/BF01370140>
- Letourneau, D. K., Bothwell Allen, S. G., & Stireman, J. O. (2012). Perennial habitat fragments, parasitoid diversity and parasitism in ephemeral crops. *Journal of Applied Ecology*, 49(6), 1405–1416. <https://doi.org/10.1111/1365-2664.12001>
- Linder, C., Kehrli, P., & Kuske, S. (2015). Guide viti d'Agroscope – *Drosophila* du cerisier. *Revue Suisse de Viticulture, d'Arboriculture et d'Horticulture*, 48, 50.
- Lurgi, M., Wells, K., Kennedy, M., Campbell, S., & Fordham, D. A. (2016). A landscape approach to invasive species management. *PLoS One*, 11(7), e0160417. <https://doi.org/10.1371/journal.pone.0160417>
- Marchand, D. (2015). Résultats de l'enquête vaudoise *Drosophila suzukii* et pourriture acide en 2014. *Revue Suisse de Viticulture, d'Arboriculture et d'Horticulture*, 47, 260–263.
- Marchesini, E., Mori, N., & Aldrichetti, F. (2014). *Drosophila suzukii* (Matsumura) a new pest of grape in Veneto Region (North-East Italy). *IOBC/WPRS Bulletin*, 105, 229–232.
- Mazzetto, F., Marchetti, E., Amiresmaeli, N., Sacco, D., Francati, S., Jucker, C., ... Tavella, L. (2016). *Drosophila* parasitoids in northern Italy and their potential to attack the exotic pest *Drosophila suzukii*. *Journal of Pest Science*, 89(3), 837–850. <https://doi.org/10.1007/s10340-016-0746-7>
- Mori, N., Vincenzi, S., Marchesini, E., Curioni, A., & Duso, C. (2014). The effect of *Drosophila suzukii* attack during grape drying process in Veneto Region (north-eastern Italy). *IOBC/WPRS Bulletin*, 105, 225–228.
- Ortega, M., & Pascual, S. (2014). Spatio-temporal analysis of the relationship between landscape structure and the olive fruit fly *Bactrocera oleae* (Diptera: Tephritidae). *Agricultural and Forest Entomology*, 16(1), 14–23. <https://doi.org/10.1111/afe.12030>
- Panel, A. D. C., Zeeman, L., Van der Sluis, B. J., van Elk, P., Pannebakker, B., Wertheim, B., & Helsen, H. (2018). Overwintered *Drosophila suzukii* are the main source for infestations of the first fruit crops of the season. *Insects*, 9(4), 145. <https://doi.org/10.3390/insects9040145>
- Pelton, E., Gratton, C., Isaacs, R., Van Timmeren, S., Blanton, A., & Guédot, C. (2016). Earlier activity of *Drosophila suzukii* in

- high woodland landscapes but relative abundance is unaffected. *Journal of Pest Science*, 89(3), 725–733. <https://doi.org/10.1007/s10340-016-0733-z>
- Poyet, M., Eslin, P., Heraude, M., Le Roux, V., Prévost, G., Gibert, P., & Chabrierie, O. (2014). Invasive host for invasive pest: When the Asiatic cherry fly (*Drosophila suzukii*) meets the American black cherry (*Prunus serotina*) in Europe. *Agricultural and Forest Entomology*, 16(3), 251–259. <https://doi.org/10.1111/afe.12052>
- Poyet, M., Le Roux, V., Gibert, P., Meirland, A., Prévost, G., Eslin, P., & Chabrierie, O. (2015). The wide potential trophic niche of the asiatic fruit fly *Drosophila suzukii*: The key of its invasion success in temperate europe? *PLoS One*, 10(11), e0142785. <https://doi.org/10.1371/journal.pone.0142785>
- Rambla, J. L., Traperro-Mozos, A., Direccion, G., Rubio-Moraga, A., Granell, A., Gómez-Gómez, L., & Ahrazem, O. (2016). Gene-metabolite networks of volatile metabolism in Airen and Tempranillo grape cultivars revealed a distinct mechanism of aroma Bouquet production. *Frontiers in Plant Science*, 7, 1619. <https://doi.org/10.3389/fpls.2016.01619>
- Rombaut, A., Guilhot, R., Xuereb, A., Benoit, L., Chapuis, M. P., Gibert, P., & Fellous, S. (2017). Invasive *Drosophila suzukii* facilitates *Drosophila melanogaster* infestation and sour rot outbreaks in the vineyards. *Royal Society Open Science*, 4(3), 170117. <https://doi.org/10.1098/rsos.170117>
- Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (Brassica Oleracea). *Ecological Monographs*, 43(1), 95–124. <https://doi.org/10.2307/1942161>
- Roschewitz, I., Thies, C., & Tschardt, T. (2005). Are landscape complexity and farm specialisation related to land-use intensity of annual crop fields? *Agriculture, Ecosystems & Environment*, 105(1-2), 87–99. <https://doi.org/10.1016/j.agee.2004.05.010>
- Rossi Stacconi, M. V. R., Amiresmaeli, N., Biondi, A., Carli, C., Caruso, S., Dindo, M. L., ... Ioriatti, C. (2018). Host location and dispersal ability of the cosmopolitan parasitoid *Trichopria drosophilae* released to control the invasive spotted wing *Drosophila*. *Biological Control*, 117, 188–196. <https://doi.org/10.1016/j.biocontrol.2017.11.013>
- Rota-Stabelli, O., Blaxter, M., & Anfora, G. (2013). *Drosophila suzukii*. *Current Biology*, 23(1), R8–R9. <https://doi.org/10.1016/j.cub.2012.11.021>
- Rusch, A., Valantin-Morison, M., Sarthou, J. P., & Roger-Estrade, J. (2013). Effect of crop management and landscape context on insect pest populations and crop damage. *Agriculture, Ecosystems & Environment*, 166, 118–125. <https://doi.org/10.1016/j.agee.2011.05.004>
- Sakia, R. M. (1992). The Box-Cox transformation technique: A review. *The Statistician*, 41(2), 169–178. <https://doi.org/10.2307/2348250>
- Sánchez-Ramos, I., Gómez-Casado, E., Fernández, C. E., & González-Núñez, M. (2019). Reproductive potential and population increase of *Drosophila suzukii* at constant temperatures. *Entomologia Generalis*, 39(2), 103–115. <https://doi.org/10.1127/entomologia/2019/0794>
- Santoemma, G., Fioretto, D., Corcos, D., Mori, N., & Marini, L. (2019). Spatial synchrony in *Drosophila suzukii* population dynamics along elevational gradients. *Ecological Entomology*, 44(2), 182–189. <https://doi.org/10.1111/een.12688>
- Santoemma, G., Mori, N., Tonina, L., & Marini, L. (2018). Semi-natural habitats boost *Drosophila suzukii* populations and crop damage in sweet cherry. *Agriculture, Ecosystems & Environment*, 257, 152–158. <https://doi.org/10.1016/j.agee.2018.02.013>
- Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, 30(9), 524–530. <https://doi.org/10.1016/j.tree.2015.06.007>
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., ... Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8(1), 14435. <https://doi.org/10.1038/ncomms14435>
- Shields, M. W., Tompkins, J. M., Saville, D. J., Meurk, C. D., & Wratten, S. (2016). Potential ecosystem service delivery by endemic plants in New Zealand vineyards: Successes and prospects. *PeerJ*, 4, e2042. <https://doi.org/10.7717/peerj.2042>
- Sholes, O. D. V. (2008). Effects of associational resistance and host density on woodland insect herbivores. *Journal of Animal Ecology*, 77(1), 16–23. <https://doi.org/10.1111/j.1365-2656.2007.01317.x>
- Shrader, M. E., Burrack, H. J., & Pfeiffer, D. G. (2019). *Drosophila suzukii* (Diptera: Drosophilidae) oviposition and adult emergence in six wine grape varieties grown in Virginia. *Journal of Economic Entomology*, 112(1), 139–148. <https://doi.org/10.1093/jee/toy305>
- Stanton, M. L. (1983). Spatial pattern in the plant community and their effects upon insect serach. In: Ahmad, S. (ed) *Herbivorous insects: host-seeking behavior and mechanisms*. Elsevier, New-York, pp 125–156.
- Straw, N. A. (1991). Resource limitation of tephritid flies on lesser burdock, *Arctium minus* (Hill) Bernh. (Compositae). *Oecologia*, 86(4), 492–502. <https://doi.org/10.1007/BF00318315>
- Svercel, M., Christen, D., Moëgne-Loccoz, Y., Duffy, B., & Défago, G. (2009). Effect of long-term vineyard monoculture on rhizosphere populations of pseudomonads carrying the antimicrobial biosynthetic genes phlD and/or hcnAB. *FEMS Microbiology Ecology*, 68, 25–36. <https://doi.org/10.1111/j.1574-6941.2009.00649.x>
- Tait, G., Cabianca, A., Grassi, A., Pfaf, F., Oppedisano, T., Puppato, S., ... Walton, V. M. (2020). *Drosophila suzukii* daily dispersal between distinctly different habitats. *Entomologia Generalis*, 40(1), 25–37. <https://doi.org/10.1127/entomologia/2019/0876>
- Tait, G., Grassi, A., Pfaf, F., Crava, C. M., Dalton, D. T., Magarey, R., ... Anfora, G. (2018). Large-scale spatial dynamics of *Drosophila suzukii* in Trentino, Italy. *Journal of Pest Science*, 91(4), 1213–1224. <https://doi.org/10.1007/s10340-018-0985-x>
- Tela Botanica (2019): Tela Botanica. Le réseau des botanistes francophones. <https://www.tela-botanica.org/>. Accessed on 8 January 2019.
- Thiéry, D., Brévault, T., Quilici, S., Dormont, L., & Schatz, B. (2013). Recherche de la plante hôte à distance. In N. Sauvion, P. A. Calatayud, D. Thiéry, & F. Marion-Poll (Eds.), *Interactions insectes-plantes* (pp. 319–346). Versailles, France: Quae. <https://doi.org/10.4000/books.irdeditions.22497>
- Thomson, L. J., & Hoffmann, A. A. (2009). Vegetation increases the abundance of natural enemies in vineyards. *Biological Control*, 49(3), 259–269. <https://doi.org/10.1016/j.biocontrol.2009.01.009>
- Tonina, L., Mori, N., Giomi, F., & Battisti, A. (2016). Development of *Drosophila suzukii* at low temperatures in mountain areas. *Journal of Pest Science*, 89(3), 667–678. <https://doi.org/10.1007/s10340-016-0730-2>
- Tschardt, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., ... Vidal, S. (2007). Conservation biological control

- and enemy diversity on a landscape scale. *Biological Control*, 43(3), 294–309. <https://doi.org/10.1016/j.biocontrol.2007.08.006>
- van Asch, M., & Visser, M. E. (2007). Phenology of forest caterpillars and their host trees: The importance of synchrony. *Annual Review of Entomology*, 52(1), 37–55. <https://doi.org/10.1146/annurev.ento.52.110405.091418>
- Verpy, A., Gil, F., Mary, S., Delbac, L., & Thiéry, D. (2014). Temporal differences in *Lobesia botrana*'s life cycle at local scale, the example of the Saint-Emilion vineyard. *IOBC-WPRS Bulletin*, 105, 197–204.
- Wang, X., Kaçar, G., & Daane, K. N. (2019). Temporal dynamics of host use by *Drosophila suzukii* in California's San Joaquin valley: Implications for area-wide pest management. *Insects*, 10(7), 206. <https://doi.org/10.3390/insects10070206>
- Wang, X.-G., Stewart, T. J., Biondi, A., Chavez, B. A., Ingels, C., Caprile, J., ... Daane, K. M. (2016). population dynamics and ecology of *Drosophila suzukii* in Central California. *Journal of Pest Science*, 89(3), 701–712. <https://doi.org/10.1007/s10340-016-0747-6>
- Weißinger, L., Schrieber, K., Breuer, M., & Müller, C. (2019). Influences of blackberry margins on population dynamics of *Drosophila suzukii* and grape infestation in adjacent vineyards. *Journal of Applied Entomology*, 143(8), 802–812. <https://doi.org/10.1111/jen.12669>
- Withers, P., & Allemand, R. (2012). Les Drosophiles de la région Rhone-Alpes (Diptera, Drosophilidae). *Bulletin de la Société Entomologique de France*, 117, 473–482.
- Woltz, J. M., Isaacs, R., & Landis, D. A. (2012). Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. *Agriculture, Ecosystems & Environment*, 152, 40–49. <https://doi.org/10.1016/j.agee.2012.02.008>
- Ziska, L. H., Blumenthal, D. M., Runion, G. B., Hunt, E. R., Jr., & Diaz-Soltero, H. (2011). Invasive species and climate change: An agronomic perspective. *Climatic Change*, 105(1-2), 13–42. <https://doi.org/10.1007/s10584-010-9879-5>

Manuscript received: 3 April 2019

Revisions requested: 8 January 2020

Modified version received: 18 February 2020

Accepted: 6 March 2020