



# Identifying candidate host plants for trap cropping against *Drosophila suzukii* in vineyards

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Received: 5 November 2023 / Revised: 22 December 2023 / Accepted: 11 January 2024 / Published online: 21 February 2024  
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## Abstract

The spotted wing drosophila (SWD), *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), is a serious pest in vineyards where it is difficult to control. Trap cropping, which involves manipulating the host plant composition in the crop vicinity to lure the pest away from grapes and towards more attractive host plant fruits, might be an interesting but so far neglected control approach to limit SWD egg-laying in grapes. An ideal trap crop should be more attractive to the pest than the actual crop and should ideally restrict pest development. We determined the attractiveness of fruits of 60 plant species for SWD egg-laying and their suitability for larval development in laboratory assays. Compared to grapes, 16 of the 60 fruits were strongly preferred by SWD females for egg-laying and additionally inhibited the development of SWD larvae into adults. Host preference was strongly influenced by the hardness of the fruit skin, and larval development was marginally affected by the acidity of fruits. However, none of the measured fruit traits had a significant effect on the emergence success of SWD. All 16 candidate trap crop plants should be further tested for their potential to reduce SWD infestation of grapes. We provide practical advice on the next steps to be taken for implementing a successful trap cropping strategy against SWD in commercial vineyards.

**Keywords** Sustainable pest control · Companion plants · Bottom up · Ecological engineering · Host quality · IPM

## Key message

- Trap crops might be an interesting control approach against *Drosophila suzukii* (SWD) in vineyards.
- We tested fruits of 60 plant species for their attractivity for egg-laying and larval development.
- We identified 16 host plants that restricted SWD development and were more attractive than grapes.
- We provide guidance for implementing trap cropping against SWD in commercial vineyards.

## Introduction

Soft-skinned crops, such as cherries, strawberries, raspberries or grapes, are strongly affected by the invasive spotted wing drosophila (SWD) *Drosophila suzukii* Matsumura (Diptera: Drosophilidae). Larval development occurs within the berries causing premature fruit rotting and reducing the marketable crop yield (Farnsworth et al. 2017; Goodhue et al. 2011). In grape production, oviposition punctures during grape maturation provide an entrance point for yeasts and bacteria associated with sour rot disease that impacts wine quality (Ioriatti et al. 2018; Rombaut et al. 2017) and can lead to significant economic loss (Knapp et al. 2021).

SWD is ubiquitous in agricultural landscapes in Europe and North America, subsisting throughout the year in semi-natural habitats and thus making it difficult to control (Cahenzli et al. 2018; Tonina et al. 2018). Effective pest management should therefore be considered beyond the field scale (Kenis et al. 2016) and integrating multiple control approaches (Fan et al. 2020; Haye et al. 2016). In viticulture, pest management strategies prioritise the use of preventive measures in order to avoid favouring the presence of SWD

Communicated by Antonio Biondi.

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within the crop (Knapp et al. 2019). For example, cultural techniques, such as leaf removal, mowing and/or nets, are often used to reduce SWD populations in vineyards (Linder et al. 2020, 2017). However, when pest densities are too high and preventive methods fail, farmers primarily rely on the application of insecticides (Knapp et al. 2019; Walsh et al. 2011). Although commercially viable biological control agents are available against SWD, their efficacy is usually low in open fields (Lee et al. 2019). Alternative control methods are therefore still needed to enhance Integrated Pest Management (IPM) strategies against SWD (Tait et al. 2021; Vreysen et al. 2007; Zhou et al. 2011).

Non-crop plant species can be exploited to modify crop-pest interactions within the agricultural system (González-Chang et al. 2019). Many polyphagous insect species, including agricultural pests such as SWD, show oviposition preference patterns among their host plants (Bellamy et al. 2013; Sarwar et al. 2013; West and Cunningham 2002). Understanding such preference patterns for SWD could help to develop a trap cropping strategy and consequently provide a sustainable and low-maintenance management option, which is currently lacking.

Trap cropping consists of planting preferred host plants in the proximity of the primary crop to lure the pest away from the harvested crop and thus mitigating pest damage (Hokkanen 1991; Shelton and Badenes-Perez 2006). To be efficient, trap crops should, however, retain the pest within the trap crop to minimise pest spill-over back to the harvested crop (Blaauw et al. 2017; Boucher et al. 2003; Holden et al. 2012; Ludwig and Kok 1998; Shelton and Badenes-Perez 2006). To achieve this, trap crops are frequently sprayed with insecticides, thus reducing both spill-over and the total amount of insecticide used on the crop (Cavanagh et al. 2009; Ellsworth et al. 1992; Lin et al. 2015; Mitchell et al. 2000; Tomaseto et al. 2019). Other measures that can be taken to limit pest spill-over include the release or conservation of natural predators (Gordon et al. 2017; Rhino et al. 2016; Rust 1977; Swezey et al. 2007; Virk et al. 2004), the mechanical removal of the pest and/or the mechanical destruction of the trap crop, thereby eliminating subsequent pest generations (Cotes et al. 2018; Rust 1977; Swezey et al. 2007). Moreover, trap cropping can also be combined with applying pest repellents in the harvested crop (e.g. push and pull) in order to divert the pest and reduce yield loss (Krause Pham and Ray 2015). Repulsive plant species or plant extracts as well as cultivation techniques that create unfavourable conditions for the pest can be implemented within the harvested crop to push the pest towards the trap crop (Cook et al. 2007; Khan et al. 2007; Lamy et al. 2018).

The implementation of so-called dead-end trap crops is a valuable alternative to traditional trap cropping. Dead-end trap crops are also preferred as oviposition sites compared to the harvested crop, but they do not allow the pest to develop

and multiply, and therefore function as an “ecological trap” (Battin 2004). Many herbivorous insect species make such suboptimal host choices as their nutritional or reproductive preferences are not always linked with their physiological performance (Gripenberg et al. 2010; Mayhew 2001). Dead-end trap cropping has been successfully implemented to control the sugarcane stem borer, *Chilo sacchariphagus* (Bojer, 1856) (Lepidoptera: Crambidae), in sugarcane crops on Reunion Island (Jacob et al. 2021; Nibouche et al. 2012, 2019) and has gained interest for controlling a range of other pest species (Badenes-Perez et al. 2014; Grundy et al. 2004; Mhatre et al. 2021; Rhino et al. 2014; Sacchi et al. 2021). Dead-end trap cropping to control SWD has recently received increased attention due to the discovery of disparities between SWD preference and SWD developmental performance in host plants (Diepenbrock et al. 2016; Poyet et al. 2015). For example, the presence of fruits of firethorn (*Pyracantha coccinea*) was able to reduce SWD infestation on strawberries in small-scale glasshouse experiments by 40 percent (Ulmer et al. 2020).

Oviposition preferences and larval performances of SWD are affected by fruit traits, and their effect has been studied in order to better understand difference in SWD susceptibility between crop varieties (Cloonan et al. 2018; Lee et al. 2015). It has been shown that colour and fruit skin hardness of different grape varieties are correlated with SWD’s host preference for egg-laying (Entling and Hoffmann 2020; Ioriatti et al. 2015; Kehrlri et al. 2017; Mazzetto et al. 2020; Shrader et al. 2019; Tonina et al. 2018). Moreover, traits related to fruit composition (e.g. acidity and sugar content) can affect multiple physiological processes in insects (Frago and Bauce 2014; Harrison 2001) and are most likely helpful indicators to differentiate variations in host suitability for the development of SWD (Kamiyama and Guédot 2019; Young and Long 2020). To evaluate the potential susceptibility of a crop or the potential value of a plant species for trap cropping or even dead-end trap cropping, it might therefore be useful to gain further insights in how fruit traits affect preference and performance of SWD across a broad range of host plant species.

In this study, we compared the relative fruit preferences of SWD for egg-laying and larval development in a large range of late-fruiting host plant species to identify candidate trap crops with a high potential to protect grapes. With the aim to identify fruits that are preferred for oviposition but unsuitable for SWD development, we evaluated 60 host plants with a fruiting period that at least partially overlaps with grape maturation, the period when grapes are most vulnerable to SWD damage. Under laboratory conditions, we studied 1) differences in egg-laying preferences of SWD between the fruits of 60 plant species in no-choice and multiple-choice experiments as well as 2) the developmental performance of SWD (emergence success, development time

and offspring body size) in the fruits of these plant species. Furthermore, we 3) investigated the impact of fruit traits on host preference and larval performance. We expected that skin hardness and fruit colour affect SWD preference for egg-laying while fruit acidity and sugar content would affect SWD developmental performance.

## Materials and methods

To select potential trap crop candidates, we first screened the literature to identify SWD plant host species and narrowed down host plants that have a fruiting period matching the grape maturation period in western Switzerland (Table S1) (Baroffio et al. 2014; Kenis et al. 2016; Lee et al. 2015; Mitsui et al. 2010; Poyet et al. 2015). Over 10 weeks between the 31st of July and the 1st of October 2018, we conducted weekly fruit sampling in botanical gardens, parks, natural hedges and garden centres enabling us to gather fruits of 60 plant species. Every Monday, we collected ripe fruits of approximately ten plant species and included ripening grapes from the grapevine cv. Mara (grown at the research station Agroscope, Nyon) and blueberries bought in a supermarket. The grape cultivar Mara was selected as a reference as it is one of most attractive grape cultivars for SWD in Switzerland and egg-infested berries are regularly reported from commercial vineyards (Kehrli et al. 2017). As most fruits were collected in nature and public places, the majority of species remained unsprayed and were free of any pesticides. Fruits were considered ripe when they presented a uniform and characteristic mature fruit colour specific to the plant species (turning from green to another colour) and detached easily from the fruit stalk. Fruits were collected very carefully and all fruits were collected intact and with their stalks to avoid fruit lesion. They were then stored in a cooler for transportation and kept at 4 °C until the begin of the experiment, which was always launched within the same week and latest 5 days after collection. Before experimentation, fruits were rinsed with tap water and individually checked for the presence of injuries or eggs under a stereo microscope. Only undamaged berries with intact stalks and without SWD eggs were used in preference tests.

### No-choice preference test

A no-choice preference test was performed for each plant species (Table S2) in order to assess a fruit's actual acceptability for egg-laying by SWD females. According to the quantity of ripe fruits available and the number of weeks a species was collected, the number of replicates varied among species between 4 and 21. Since fruits of the 60 plant species were of different size and weight, we aimed to expose approximately 1.5 g of intact fruit per species in

experimental jars. To avoid any experimental biases, fruits were precisely weighed directly before their placement into cylindrical plastic jars (3 cm diameter × 6 cm height) in order to know the exact quantity of exposed fruit mass in a jar. Then, three SWD females and one male were added to each jar, which was subsequently covered and closed with a fine mesh lid. All SWD adults used in the experiments were at least five days old and had been reared on a homemade growing medium consisting of mashed banana peel, agar, brewer's yeast, wheat flour, sugar, methylparaben, alcohol and water in a common rearing in contact with circa 50 to 200 conspecifics. It was therefore assumed that the large majority of SWD females had already mated at the beginning of the experiment. After the insertion of fruits and SWD, jars were stored in a growing chamber (22 °C, 75% RH, 16/8 day/night). After 24 h, flies were removed and the relative number of eggs laid in each jar was recorded under the stereo microscope. This number was divided by the actual weight of exposed fruit mass (= 'egg number per gram of fruit').

### Multiple-choice preference test

To assess SWD preference among host fruits for egg-laying, we set up a multiple-choice preference test with all collected species during that specific week (Table S2). We placed an equivalent quantity of different fruit species each on a petri dish lid of 3.5 cm diameter in a rectangular box (25 × 15 × 8 cm). As the number of fruit species and thus the quantity of fruit per box were not constant over the weeks, we adjusted the number of flies within the boxes, ensuring about 0.8 SWD female flies per gram of fruit. We always added half as many males than females to enable mating. After introducing the flies, we closed the boxes with a mesh lid to prevent condensation. The position of petri dish lids within the box and the place of a box within the growing chamber (22 °C, 75% RH, 16/8 day/night) were arbitrarily varied. After 24 h of exposure, we counted the number of eggs on each fruit species in a box under the stereo microscope and calculated the 'proportion of eggs laid' on each fruit species in a box. At each of the 10 sampling dates, six rectangular boxes were set up.

### Developmental assays

To determine the suitability of plant species for SWD development, we collected fruits in which eggs were laid in the no-choice preference test. All infested fruits of a replicate were put in individual jars (3 cm diameter × 6 cm height) and kept for three weeks in a growing chamber (22 °C, 75% RH, 16/8 day/night). This corresponds to about twice the average time estimated for SWD eggs to develop into adult flies at 22 °C (Tochen et al. 2014). From the previous experiments,

fruit weight (before SWD exposure) and the number of eggs were known for each replicate. We daily monitored the jars recording ‘development time’ as well as the number and the sex of emerging flies. We calculated the ‘emergence success’ as the number of emerged flies divided by the number of laid eggs for each replicate. Emerged flies were preserved in 70% ethanol in order to determine their body size. As the size of the body parts is allometrically correlated (Carreira et al. 2009), we quantified as a proxy for body size the ‘wing length’ of each individual by measuring on the right front wing the distance from the anterior crossvein to the end of the second longitudinal in  $\pm 1/10$  mm with the help of a stereo microscope.

### Fruit traits

To examine fruit traits that may be linked to host preferences in SWD, we measured for five fruits of each species ‘skin hardness’ and ‘skin elasticity’ using a texture analyser (TAxT2i Texture Analyzer, Stable Micro Systems, Needle probe P/2N 2 mm, United Kingdom). To explore determinants of fruit suitability, we measured weekly acidity (pH) and sugar content of each collected species. To extract the juice of each species, we crushed the surplus collected and intact fruits of each species and filtered the extracted juice. The sugar content of the juice was then determined in Brix units with a numerical refractometer (Altago Pocket Refractometer Pal-1, Japan), and juice’s acidity was measured using a pH meter (Mettler-Toledo T90 equipped with a D6i115-CS pH-electrode, Switzerland).

The impact of colour on the preference of SWD females for egg-laying was assessed for technical reasons only on a subset of 10 of the 60 plant species (i.e. *Ampelopsis glandulosa* var. *brevipedunculata* (= *Ampelopsis brevipedunculata*), *Cestrum fasciculatum*, *Cornus amomum*, *Phytolacca americana*, *Lycium barbarum*, *Lonicera xylostium*, *Prunus lusitanica*, *Rhamnus cathartica*, *Rubus fruticosus* var. *lockness*, *Sambucus ebulus*, *Sambucus nigra*) in 2019 and 2020. Potted plants of this ten plant species were maintained outdoors until the end of their flowering periods. Afterwards, they were transferred into insect-proof greenhouses to protect their fruits from natural SWD infestation. In the laboratory two-choice preference test running from August to September 2019 and 2020, we placed an equivalent quantity of a fruit of the species mentioned above and a Mara grape berry ( $n=22\text{--}68$  for each fruit species) on opposite ends inside a rectangular plastic box ( $5\times 7\times 2$  cm) covered with a mesh lid in a growing chamber (22 °C, 75% RH, 16/8 day/night). Before SWD exposure, each box was photographed (FinePix ISpro, Fujifilm ©, UV-Nikkor 105 mm lens, focal 6) under a constant light source (Polilight PL500, Rofin ©). Thereafter, we placed the equivalent of one SWD female per gram of fruit inside the box and kept them for a day in a growing

chamber (22 °C, 75% RH, 16/8 day/night). After 24 h, the number of eggs laid on each fruit species was recorded. We also determined the luminance and the hue of fruit colour on the picture of each box using the CIE 1976  $L^*a^*b$  colour space, a method commonly utilised in quantitative, comparative colour studies (Weatherall and Coombs 1992; Weller 2021). The colour space is based on the colour opponent theory, which describes the colour vision in humans and many insects, including *Drosophila melanogaster* (Schnaitmann et al. 2020; Song and Lee 2018). Three parameters describe the colour space, namely the parameters  $L$ ,  $a$  and  $b$ . The parameter  $L$  expresses the colour luminance and varies from 0 to 100 (black to white). The parameter  $a$  defines the colour hue on an axis from green to red ( $a < 0$  towards green,  $a > 0$  towards red), whereas  $b$  describes the colour hue from blue to yellow ( $b < 0$  towards blue,  $b > 0$  towards yellow). The  $L^*a^*b$  parameter values from each picture were extracted using Adobe Photoshop® (2020, version 21). As the colour of individual fruits was not always consistent over the whole fruit surface, we extracted  $L^*a^*b$  parameter values from an averaged surface area of the fruit. We used a white standard for each picture in order to correct for slight light differences between photographs.

### Statistical analyses

All statistical analyses were conducted in R (version 4.1.2; R Core Team 2021). To assess differences in SWD preference and performance among plant species in the no-choice test, we used linear mixed-effects models (LMMs) (library *lmerTest* version 3.1.3; Kuznetsova et al. 2017). We fitted three different models, each with either the ‘number of eggs per gram of fruit’ (preference), the ‘number of emerged adults per gram of fruit’ or the ‘emergence success’ (number of emerged adults/number of eggs laid) as response variables (Box-Cox transformed), and included ‘plant species’ as a fixed and the ‘experimental date’ as a random factor. We fitted two other models with the ‘development time’ and the ‘wing length’ as response variables thereby only applying the Box-Cox transformation to ‘wing length’. For these two models, ‘plant species’ and ‘sex’ were included as fixed factors, and the ‘experimental date’ and the ‘jar’ from which flies emerged as random factors. When informative, we performed multiple comparisons with a Bonferroni adjustment method (library *emmeans* version 1.7.2; Russel 2022). When assessing preference differences between host plants, we ran separate linear models with grapes and the other cultivated crops present in our preference tests (e.g. *Aronia melanocarpa*, *Vaccinium myrtillus*, *Lycium barbarum*, *Prunus domestica*, *Rubus fruticosus*, *Rubus idaeus* and *Sambucus nigra*) as reference levels in order to determine the number of host species more or less preferred than this particular cultivated crop species. This allowed us to evaluate if trap

cropping might also be applicable to these other tested crop species. All LMMs were assessed with a visual inspection of their residuals for normality and homoscedasticity as suggested by Zuur et al. (2009). As the set of collected plant species in our study changed each week, we scored fruit species according to the relative proportion of eggs laid on a single fruit species within each replicate and averaged it per week. We averaged the weekly scores per species for all plant species we repeatedly tested over the study period. This allowed us to compare if the preference ranking of species in no-choice experiment was coherent with the ranking of species in multiple-choice situations.

To evaluate the impact of fruit traits on pest preference and performance, we fitted LMMs with all possible combinations of predictor variables and followed a multi-model inference approach in order to select the most meaningful set of explanatory variables (Burnham and Anderson 2002; Grueber et al. 2011; Harrison et al. 2018). All models falling within six units of the Akaike information criterion (corrected for finite sample size; AICc) of the best model were used for model averaging except for more complex versions of models with fewer variables and a lower AICc (library MuMIn version 1.43.17; Barton 2022; Burnham and Anderson 2002; Richards 2005; Symonds and Moussalli 2011). We analysed the effect of ‘skin hardness’ and ‘skin elasticity’ as predictors on SWD preference for egg-laying, i.e. the ‘average egg number per gram of fruit per plant species’ (response variable). We included the ‘sampling date’ as a random factor. To analyse the effect of colour on the preference of SWD for egg-laying (i.e. the log-transformed ‘egg number per gram of fruit’), we built models with all combinations of L, a and b parameter values as predictors and used the ‘plant species’ and the ‘date of the experiment’ as random factors. Similarly, we separately analysed how the ‘emergence success’ (log-transformed), ‘wing length’ and ‘development time’ of SWD per plant species were associated with the ‘pH’ and ‘sugar content’ of fruits.

## Results

### Preference

Nearly no SWD adults died during the 24 h of exposure and the preference for egg-laying varied among host plants in our different choice tests. Overall, SWD laid eggs in the fruits of 56 out of the 60 tested host plants (Fig. 1, Table 1). In the no-choice test, the average number of eggs laid per gram of fruit varied from 0 in four host plants to  $17 \pm 5$  (mean  $\pm$  CI) in *Cornus amomum* (Anova type II:  $\chi^2 = 1121.8$ , df = 60,  $p$ -value < 0.001; Table 1, Table S3). In the multiple-choice test, the preference level expressed as the average proportion of eggs laid varied between 0 and 1 (Table 1). No eggs

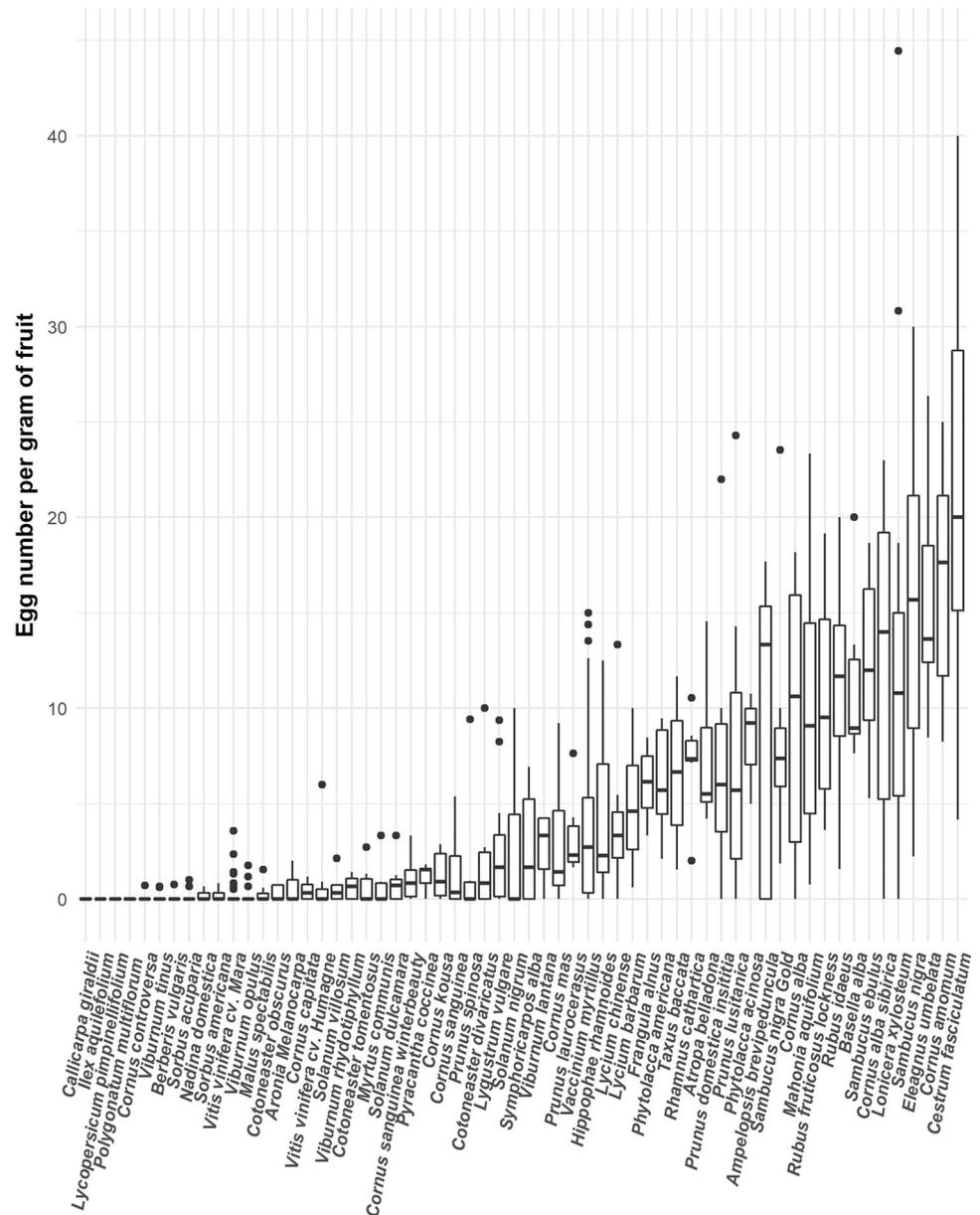
were laid on 12 of the 60 tested host plants, whereas 100% of laid eggs were deposited on *Cestrum fasciculatum* and *Prunus lusitanica* in these weeks’ multiple-choice setting. The ranks of average SWD preferences for plant species strongly correlated between no-choice and multiple-choice tests ( $r_{\text{Spearman}} = 0.78$ ,  $p$ -value < 0.001), suggesting robust and consistent preference choices amongst these two laboratory settings.

Emphasising the obtained results for the eight commercially grown crop species, about two-thirds of the tested host plant species were significantly more attractive for egg-laying than grapes (*Vitis vinifera* cv. Mara and Humagne) and the black chokeberry (*Aronia melanocarpa*) (Table 1, Table S3-5). Overall, around 4 to 90 times fewer eggs were laid on grapes than on the plant species preferred in the no-choice preference test and 7 to 62 times fewer eggs on plants preferred in the multiple-choice preference test. Only a third of host plants was more attractive than blueberries (*Vaccinium myrtillus*), with 1.5 to 5 times fewer eggs laid on blueberries than on the species preferred in the no-choice preference test, and 1.3 to 2.2 fewer eggs on plants preferred in the multiple-choice preference test (Table 1, Table S6). Only a few or no host plant species were preferred to crop species such as goji berries (*Lycium barbarum*), the European plum (*Prunus domestica* subsp. insititia), blackberries (*Rubus fruticosus* var. lockness), raspberries (*Rubus idaeus*) and the European elderberry (*Sambucus nigra*) (Fig. 1, Table S7-11).

### Developmental performance

Our developmental assays highlighted high variation in SWD developmental performance among tested host plants. No eggs developed into adults in the fruits of 24 of the 56 host plants suitable for oviposition (Fig. 2, Table 1). In the other 32 host plants, SWD was able to complete its life cycle with nine plant species having an emergence success lower than 10%, 11 plant species with an emergence success between 10 and 30%, 5 species between 31 and 60% and 7 plant species above 60% (Table 1). Hence, the average emergence success and the number of emerged flies per gram of fruit differed significantly between host plants, with *Rubus idaeus* showing the highest emergence success ( $86\% \pm 19\%$ ) (Table 1, emergence success:  $\chi^2_{\text{Anova type II}} = 634.9$ , d.f. = 56,  $p$ -value < 0.001, Table S12; emerged flies per gram of fruit:  $\chi^2_{\text{Anova type II}} = 917.4$ , d.f. = 56,  $p$ -value < 0.001, Table S13). The development time of SWD was unaffected by the sex but differed significantly among plant species ( $\chi^2_{\text{sex}} = 1.71$ , d.f. = 1,  $p$ -value = 0.19; Anova type II:  $\chi^2_{\text{plant species}} = 307.7$ , d.f. = 32,  $p$ -value < 0.001; Table S14). Development time varied more than a week among plant species, from 8 days in *Viburnum lantana* to 17.4 days in *Mahonia aquifolium* and *Prunus laurocerasus* (Table S15). Wing length was

**Fig. 1** Box plots of the number of eggs per gram of fruit laid by SWD females on different host species in the no-choice preference test



significantly smaller in males than females but did not vary among host plants ( $\chi^2_{\text{sex}} = 83.11$ , d.f. = 1,  $p$ -value < 0.001; Anova type II:  $\chi^2_{\text{plant species}} = 38.89$ , d.f. = 30,  $p$ -value = 0.13; Table S15). The wing length of females ranged from  $1.82 \pm 0.21$  mm in *Lonicera xylosteum* to  $3.35 \pm 0.12$  mm in *Solanum villosum*, whereas the wings of males were between  $1.78 \pm 0.1$  mm for *Rubus idaeus* and  $2.9 \pm 0.13$  mm in *Mahonia aquifolium*.

### Relationship between preference and developmental performance

For the 56 host plants suitable for oviposition, there was a significant correlation between oviposition preference

and emergence success ( $\tau_{\text{Kendall}} = 0.52$ ;  $p$ -value < 0.001; Fig. 3, Table 1). Attractive host plants that did not allow more than 10% of laid SWD eggs to develop into adults were *Ampelopsis brevipedunculata*, *Cestrum fasciculatum*, *Cornus amomum*, *Eleagnus umbellata*, *Phytolacca acinosa*, *Phytolacca americana*, *Prunus domestica* subsp. *insititia* and *Prunus lusitanica*. These species seem therefore to be particularly suited as attractive dead-end trap crops. On the other hand, plant species such as *Atropa belladonna*, *Cornus kousa*, *Frangula alnus*, *Sambucus ebulus*, *Rubus fruticosus*, *Rubus idaeus* and *Lycium barbarum* allowed more than 60% of eggs to develop into adults (Fig. 3, Table 1) and they might therefore be considered as potential sources for SWD spill-over.

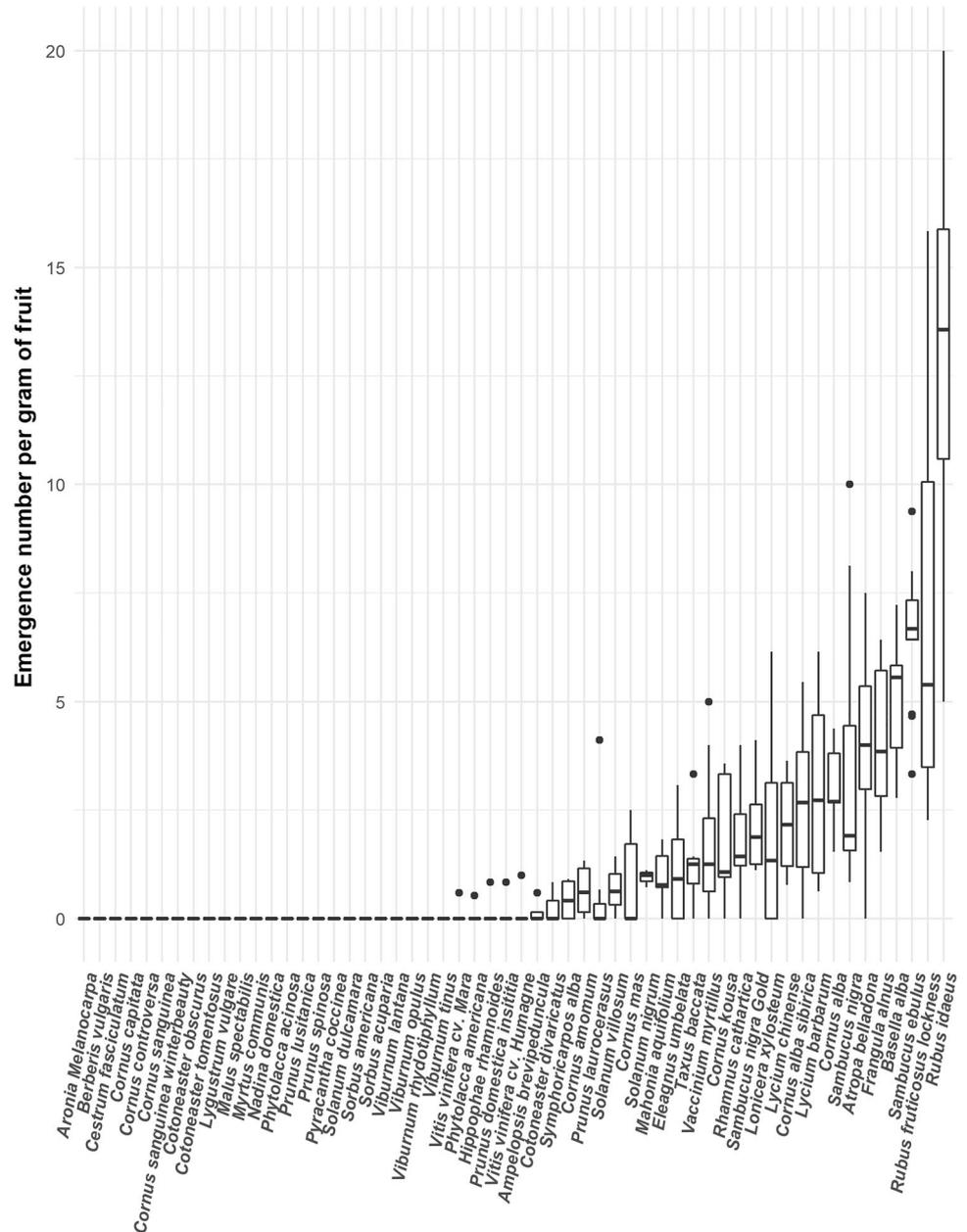
**Table 1** Mean ± the 95% confidence interval (CI = 1.96 \* SE) of the 4 response variables. Plant species are ordered according to the emergence success

Plant species	SWD preference compared to grapes	Emergence success category	Mean ± CI egg number per gram of fruit (no-choice)	Mean ± CI egg proportion (multiple choice)	Mean ± CI emergence per gram of fruit	Mean ± CI emergence success [percent]
<i>Cornus controversa variegata</i>	=	< 10%	0.1 ± 0.2	0	0	0
<i>Viburnum tinus</i>	=	< 10%	0.11 ± 0.14	0	0	0
<i>Berberis vulgaris</i>	=	< 10%	0.11 ± 0.22	0	0	0
<i>Sorbus aucuparia</i>	=	< 10%	0.12 ± 0.16	0	0	0
<i>Nandina domestica</i>	=	< 10%	0.18 ± 0.23	0.02 ± 0.03	0	0
<i>Sorbus americana Belmonte</i>	=	< 10%	0.21 ± 0.27	0	0	0
<i>Viburnum opulus</i>	=	< 10%	0.26 ± 0.29	0.01 ± 0.01	0	0
<i>Malus spectabilis</i>	=	< 10%	0.3 ± 0.43	0	0	0
<i>Cotoneaster obscurus</i>	=	< 10%	0.32 ± 0.3	0	0	0
<b><i>Aronia melanocarpa</i></b>	=	< 10%	0.36 ± 0.26	0.01 ±	0	0
<i>Cornus capitata</i>	=	< 10%	0.45 ± 0.56	0.14 ± 0.17	0	0
<i>Viburnum rhydotiphylum</i>	=	< 10%	0.61 ± 0.46	0.03 ± 0.03	0	0
<i>Cotoneaster tomentosus</i>	=	< 10%	0.69 ± 0.77	0	0	0
<i>Myrtus communis</i>	=	< 10%	0.72 ± 0.9	0.05 ± 0.07	0	0
<i>Solanum dulcamara</i>	=	< 10%	0.88 ± 0.88	0.03 ± 0	0	0
<i>Cornus sanguinea</i> ‘Winter Beauty’	=	< 10%	1.11 ± 1.01	0.07 ± 0.06	0	0
<i>Pyracantha coccinea</i>	>	< 10%	1.18 ± 0.48	0.23 ± 0.07	0	0
<i>Cornus sanguinea</i>	>	< 10%	1.35 ± 0.96	0.03 ± 0.03	0	0
<i>Prunus spinosa</i>	>	< 10%	1.6 ± 2.57	0	0	0
<i>Ligustrum vulgare</i>	>	< 10%	2.5 ± 1.59	0.23 ± 0.16	0	0
<i>Viburnum lantana</i>	>	< 10%	2.74 ± 1.3	0.04 ± 0.07	0	0
<i>Prunus lusitanica</i>	>	< 10%	7.97 ± 6.38	1 ± 0	0	0
<i>Phytolacca acinosa</i>	>	< 10%	8.44 ± 1.62	0.1 ± 0.08	0	0
<i>Cestrum fasciculatum</i>	>	< 10%	21.7 ± 8.76	1 ± 0	0	0
<i>Hippophae rhamnoides</i>	>	< 10%	4.29 ± 2.29	0.07 ± 0.05	0.08 ± 0.15	1 ± 1
<i>Ampelopsis brevipedunculata</i>	>	< 10%	8.81 ± 6.18	0.59 ± 0.23	0.15 ± 0.29	1 ± 2
<b><i>Vitis vinifera cv. Humagne</i></b>	=	< 10%	0.47 ± 0.56	0.02 ± 0.02	0.14 ± 0.28	2 ± 5
<i>Cotoneaster divaricatus</i>	>	< 10%	2.4 ± 3.11	0.08 ± 0.07	0.28 ± 0.54	3 ± 5
<i>Cornus amonum</i>	>	< 10%	16.76 ± 5.27	0.44 ± 0.29	0.65 ± 0.48	3 ± 3
<i>Phytolacca americana</i>	>	< 10%	6.27 ± 2.09	0.56 ± 0.28	0.08 ± 0.15	4 ± 7
<b><i>Prunus domestica cv. instiita</i></b>	>	< 10%	7.63 ± 5.32	0.26 ± 0.12	0.14 ± 0.27	6 ± 11
<b><i>Vitis vinifera cv. Mara</i></b>	=	< 10%	0.24 ± 0.14	0.06 ± 0.04	0.07 ± 0.1	8 ± 12
<i>Eleagnus umbelata</i>	>	< 10%	15.76 ± 4.69	0.24 ± 0.05	1.09 ± 0.97	9 ± 10
<i>Prunus laurocerasus</i>	>	10-30%	3.3 ± 1.58	0.5 ± 0.12	0.68 ± 1.14	11 ± 15
<i>Cornus mas</i>	>	10-30%	2.88 ± 1.64	0.12 ± 0.06	0.8 ± 0.61	14 ± 12
<i>Cornus alba sibirica</i>	>	10-30%	12.27 ± 6.56	0.99 ± 0.03	2.62 ± 1.63	16 ± 7
<i>Symphoricarpos alba</i>	>	10-30%	2.72 ± 2.22	0.07 ± 0.08	0.44 ± 0.49	17 ± 23
<i>Solanum nigrum</i>	>	10-30%	2.69 ± 2.92	0.05 ± 0.04	0.94 ± 0.23	18 ± 8
<i>Taxus baccata</i>	>	10-30%	6.62 ± 2.83	0.17 ± 0.22	1.28 ± 0.76	21 ± 12
<i>Rhamnus cathartica</i>	>	10-30%	7.28 ± 1.93	0.16 ± 0.11	1.81 ± 0.95	23 ± 12
<i>Mahonia aquifolium</i>	>	10-30%	10.16 ± 5.94	0.5 ± 0.32	0.99 ± 0.46	27 ± 25
<i>Lonicera xylosteum</i>	>	10-30%	13.27 ± 6.24	0.3 ± 0.14	2.15 ± 1.29	29 ± 21
<b><i>Sambucus nigra</i></b>	>	10-30%	15.24 ± 4.14	0.34 ± 0.16	3.62 ± 1.56	29 ± 11
<i>Sambucus nigra fruitjaune</i>	>	10-30%	8.92 ± 5.12	0.53 ± 0.34	2.12 ± 0.84	30 ± 14
<b><i>Vaccinium myrtillus</i></b>	>	31-60%	4.19 ± 1.45	0.45 ± 0.11	1.6 ± 0.53	37 ± 13
<i>Cornus alba</i>	>	31-60%	9.52 ± 5.67	0.36 ± 0.2	3.02 ± 0.85	41 ± 26
<i>Lycium chinense</i>	>	31-60%	4.3 ± 3.2	0.76 ± 0.17	2.18 ± 0.95	50 ± 15
<i>Basella alba</i>	>	31-60%	11.29 ± 3.22	0.99 ± 0.02	5.01 ± 1.17	51 ± 18
<i>Solanum villosum</i>	=	31-60%	0.59 ± 0.67	0.03 ± 0.05	0.68 ± 0.81	56 ± 58
<i>Atropa belladonna</i>	>	> 60%	7.49 ± 2.71	0.58 ± 0.3	4.03 ± 1.81	60 ± 27
<i>Sambucus ebulus</i>	>	> 60%	11.93 ± 2.05	0.66 ± 0.21	6.58 ± 0.71	62 ± 13
<i>Cornus kousa</i>	>	> 60%	1.27 ± 0.92	0.29 ± 0.25	1.79 ± 1.38	67 ± 41
<b><i>Lycium barbarum</i></b>	>	> 60%	4.92 ± 2.5	0.98 ± 0.04	3 ± 1.66	67 ± 22
<i>Frangula alnus</i>	>	> 60%	6.07 ± 1.41	0.61 ± 0.24	4.13 ± 1.42	69 ± 23
<b><i>Rubus fruticosus var. lockness</i></b>	>	> 60%	10.46 ± 4.38	0.9 ± 0.2	7.22 ± 3.66	71 ± 24
<b><i>Rubus idaeus</i></b>	>	> 60%	11.28 ± 4.38	0.17 ± 0.04	13.07 ± 3.74	86 ± 19
<i>Callicarpa giraldii</i>	NA	NA	0	0	NA	NA
<i>Ilex aquifolium</i>	NA	NA	0	0	NA	NA
<i>Lycopersicum pimpinellifolium</i>	NA	NA	0	0	NA	NA
<i>Polygonatum multiflorum</i>	NA	NA	0	0.01 ± 0.02	NA	NA

**Table 1** (continued)

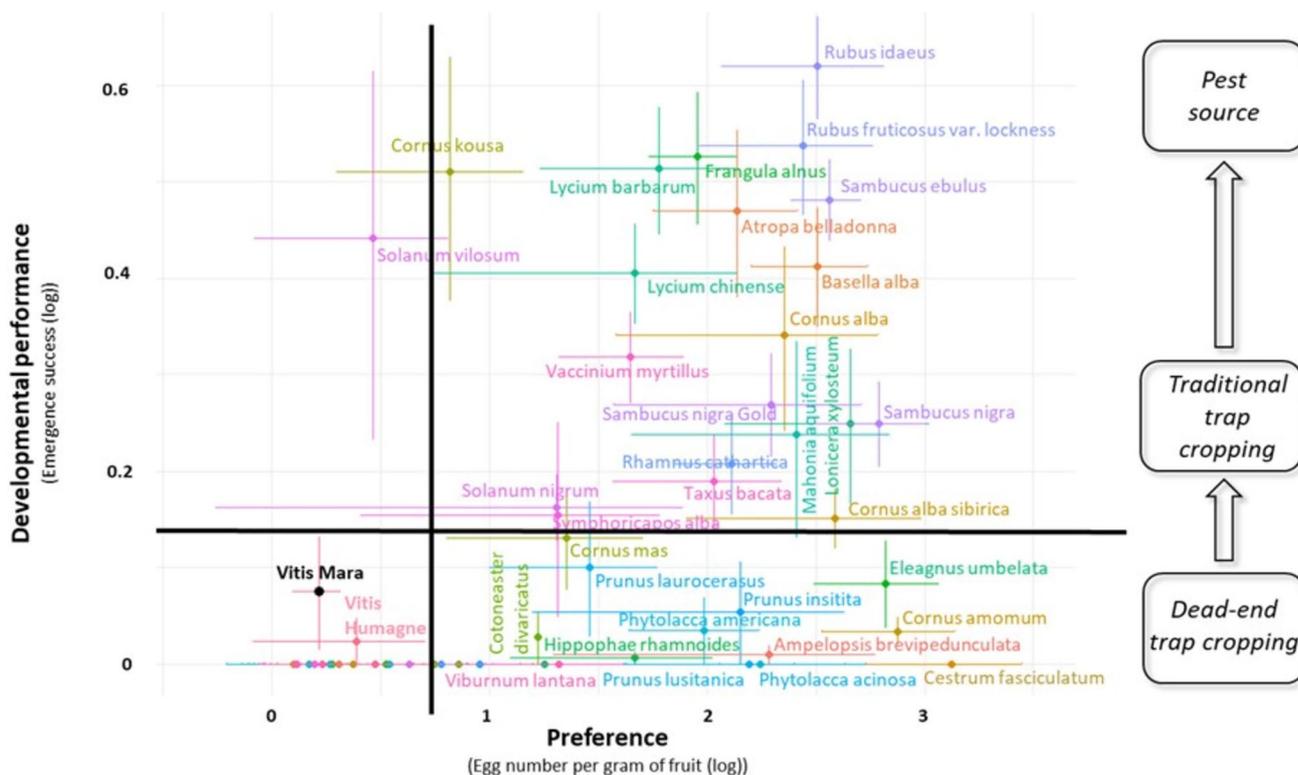
SWD preference compared to grapes: = : no significant difference of preference compared to grapes, > : significantly higher preference for egg-laying than grapes. Plant species in bold are also crop species. Plant species in which no eggs were laid are indicated with NA. Plant species highlighted in green correspond to plant species identified as potential dead-end trap crops (e.g. ‘emergence success’ < 10% and ‘egg number per gram of fruit’ in the no-choice test > 1), plant species highlighted in light green correspond to plant species identified as potential traditional trap crops (e.g. ‘emergence success’ between 10 and 30% and ‘egg number per gram of fruit’ in the no-choice test > 1), whereas plant species highlighted in light red correspond to plant species that might be potential pest contamination sources (e.g. ‘emergence success’ > 60% and ‘egg number per gram of fruit’ in the no-choice test > 1)

**Fig. 2** Box plots of the number of emerged SWD adults per gram of fruit from different host species in the two preference tests



Oviposition preference was not affected by development time ( $\tau_{\text{Kendall}} = -0.05$ ;  $p\text{-value} = 0.70$ ) or wing length ( $\tau_{\text{Kendall}} = -0.23$ ;  $p\text{-value} = 0.08$ ), and the latter two

were also uncorrelated with each other ( $\tau_{\text{Kendall}} = -0.01$ ;  $p\text{-value} = 0.93$ ). These pest performance criteria are therefore no helpful indicators to identify potential trap

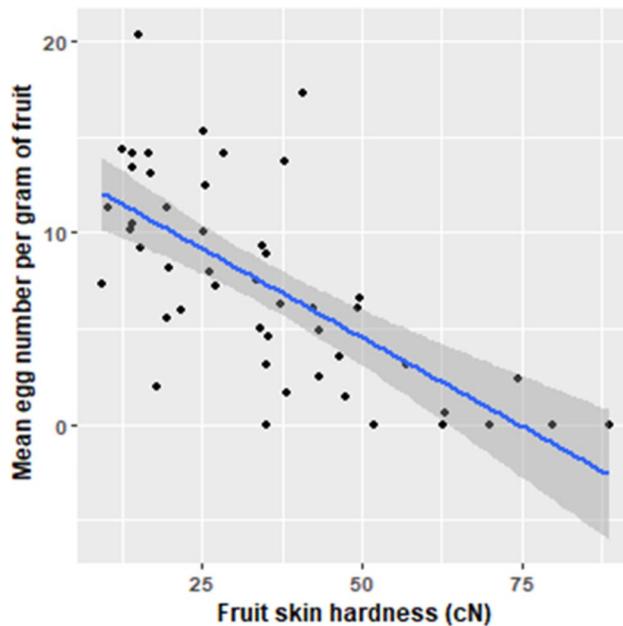


**Fig. 3** Relationship between the preference and the performance of SWD among host fruit species. Plant species are indicated with a dot. Horizontal bars are confidence intervals of SWD preference, and vertical bars are confidence intervals of the plant species’ emergence

success. On the right side of the scatter plot, the position of the labels (dead-end trap crops, traditional trap crops, pest sources) along the y-axis is arbitrary but described visually the discussion section

crop candidates. However, the oviposition preference of SWD was negatively correlated with fruit skin hardness ( $R^2 = 0.46$ ;  $F_{1, 46} = 39.09$ ,  $p\text{-value} < 0.001$ ; Fig. 4, Table S18). To prevent egg-laying, the model predicted a threshold value of 74.5 cN and the ripe fruits of seven host plants exceeded this skin hardness value (Table S15). Fruit elasticity had no effect on the oviposition preference of SWD (Table 2, Table S17). Similarly, the colour of fruits did also not explain oviposition preferences between grapes and the other 11 host plants tested (Anova II  $L$  parameter  $\chi^2 = 0.05$ , d.f. = 1,  $p\text{-value} < 0.83$ , Anova II  $a$  parameter  $\chi^2 = 0.01$ , d.f. = 1,  $p\text{-value} < 0.93$ , Anova II  $b$  parameter  $\chi^2 = 0.5$ , d.f. = 1,  $p\text{-value} < 0.48$ ; Table 3, Table S19).

The emergence success of SWD was not explained by the sugar content or the pH of fruits (Anova II  $\text{sugar content}$  SS=0.03, d.f. = 1,  $F\text{-value} = 0.89$ ,  $p\text{-value} = 0.35$ ; Anova II  $\text{pH}$  SS=0.03, d.f. = 1,  $F\text{-value} = 1.05$ ,  $p\text{-value} = 0.31$ ; Table S20). Development time from egg to adult was shortest in fruits with an acidity level between a pH of 4 to 5.5 with 23 host plants falling in this range (Fig. 5, Table S15). It was increased by up to three days for a pH decrease from 4 to 2 (Fig. 5). Moreover, sugar content had a significant effect on the wing size of



**Fig. 4** Linear regression plot between the mean egg number per gram of fruit of each plant species in the no-choice preference test and the skin hardness expressed in centinewton (cN)

SWD offspring (Anova II  $\chi^2=8.85$ , d.f. = 1,  $p$ -value < 0.01; Table S19-20) with an average increase in wing length of 0.3 mm with every 10° Brix (Fig. 6; Table S21).

**Table 2** Model selection based on AICc between the SWD preference for egg-laying and fruit skin hardness as well as fruit elasticity. ( $x^2$ ) indicates the test of a quadratic fit for the predictor

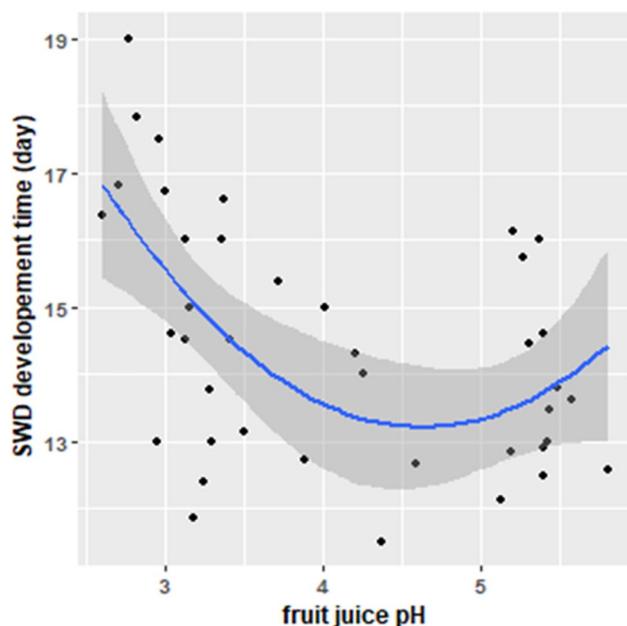
Model predictors	df	AICc	$\Delta$ AICc
Hardness	3	271.73	0.00
Hardness, hardness ( $x^2$ )	4	273.15	1.41
Hardness*elasticity	5	274.78	3.04
Null model (1)	2	299.26	27.52
Elasticity	3	300.27	28.54

\* indicate an interaction

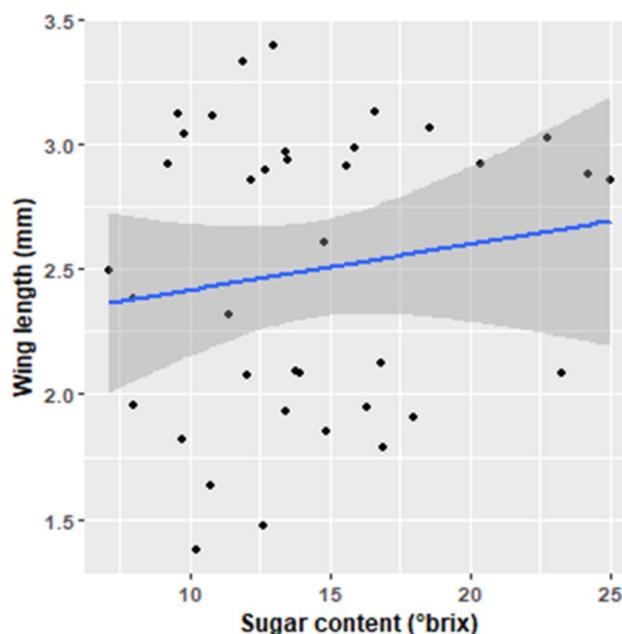
**Table 3** Model selection based on AICc between the SWD preference for egg-laying and fruit colour

Model predictors	df	AICc	$\Delta$ AICc
null model (1)	4	1565.73	0.00
$b$	5	1567.24	1.51
$L$	5	1567.68	1.95
$a$	5	1567.73	1.99
$a,b$	6	1568.46	2.73
$L,b$	6	1568.98	3.25
$L,a$	6	1569.68	3.95
$L,a,b$	7	1570.16	4.42

$L$ ,  $a$  and  $b$  correspond to the parameters used to characterise colour



**Fig. 5** Quadratic regression between the mean development time of SWD in a plant species and the pH of the juice of its fruits. It was shortest in fruits with an acidity level between a pH of 4 to 5.5, similar to the pH level range of for example mango, orange or pomelo (Laloknam et al. 2010)



**Fig. 6** Linear regression plot between the mean wing length of emerged SWD in a plant species and the sugar content of the juice of its fruits expressed in Brix degree (°Brix)

## Discussion

We identified 16 host plants, namely *Ampelopsis brevipedunculata*, *Cestrum fasciculatum*, *Cornus amomum*, *Cornus sanguinea*, *Cornus sanguinea* ‘Winter Beauty’, *Cotoneaster divaricatus*, *Eleagnus umbelata*, *Hippophae rhamnoides*, *Ligustrum vulgare*, *Phytolacca acinosa*, *Phytolacca americana*, *Prunus lusitanica*, *Prunus spinosa*, *Prunus domestica* cv. *institia*, *Pyracantha coccinea* and *Viburnum lantana*, for which SWD showed a strong preference to lay eggs compared to grapes but in which SWD developmental performance was weak (i.e. less than 10% of the eggs laid developed into adults; highlighted in green in Table 1). These plant species seem therefore to be ecological traps for SWD (Delibes et al. 2001) and might thus be interesting candidates to further investigate their potential as dead-end trap crops for SWD (Fig. 3). Ten other host plant species were preferred over grapes for egg-laying but allowed 10 to 30% of eggs to emerge, namely *Cornus alba sibirica*, *Cornus mas*, *Lonicera xylosteum*, *Mahonia aquifolium*, *Prunus laurocerasus*, *Rhamnus cathartica*, *Sambucus nigra*, *Solanum nigrum*, *Symphoricarpos alba* and *Taxus baccata* (Table 1, highlighted in light green). These plant species could be considered for traditional trap cropping (Fig. 3), but their use would probably have to be accompanied by additional control measures (e.g. mechanical destruction of infested fruits or vacuuming of emerged adults) to limit pest spill-over into vineyards. Finally, we identified seven plant species *Atropa belladonna*, *Cornus kousa*, *Frangula alnus*,

*Lycium barbarum*, *Rubus fruticosus* lockness, *Rubus idaeus* and *Sambucus ebulus* with both high preference and performance scores (Table 1, highlighted in red). As they allow over 60% of eggs to develop into adults, they might bear the risk of acting as SWD contamination sources in the vicinity of vulnerable crops (Fig. 3).

## Preference

SWD laid eggs in 56 of the 60 host plants tested, confirming its strong polyphagous behaviour (Kenis et al. 2016; Lee et al. 2015; Poyet et al. 2015). Although our SWD population has been reared over several generations on a homemade growing medium in the laboratory, our results are consistent with previous studies (Abraham et al. 2015; Aly 2018; Bellamy et al. 2013; Burrack et al. 2013; Lee et al. 2011; Olazcuaga et al. 2019) and confirm that grapes are much less attractive to SWD than other commercial crops such as blackberries, blueberries, elderberries, goji berries, plum or raspberries. Yet, we are not able to exclude that the preference choices and/or the performance of wild SWD individuals might deviate from our reared SWDs, as has been found in other *Drosophila* species (Mery and Kawecky 2002; Soto et al. 2015). However, since our findings are in accordance with the current literature (Abraham et al. 2015; Aly 2018; Bellamy et al. 2013; Burrack et al. 2013; Kamiyama and Guédot 2019; Lee et al. 2011; Olazcuaga et al. 2019), we believe that our results reflect by and large the behaviour of SWD in the agricultural and natural environment. Recently, Akutsu and Matsuo (2022) found that not only fruit colour, skin hardness or texture influences the oviposition choices of SWD females, but also fruit shape, surface area and volume. In our studies, the number of eggs per fruit surface area (assuming spherical shape) and the number of eggs per gram of fruit were highly correlated (Fragnière 2022) so that standardising oviposition by the weight of fruits is probably a sufficiently accurate method; fruits can easily be weighed, while estimating surface area or volume would need to assume a specific shape (most fruits are not perfect spheres), which likely differs among fruit species and thus might introduce plant-specific biases.

Interestingly, SWD preference ranking of host plants for egg-laying was similar under no choice versus multiple choice conditions in the laboratory. This suggests that innate SWD preferences were consistent across our different experimental settings and can thus guide the selection of plant candidates for trap cropping (Holden et al. 2012; Mathews et al. 2017). Yet, environmental conditions affecting SWD preference under field conditions are only partially understood and the realised host range does not comprise all potential hosts (Braga and Janz 2021). Beside previous experiences as juveniles or adults, the host choice of herbivores is determined by their innate preferences, the

actual availability of hosts, and environmental cues (Carasco et al. 2015; Schaffner 2001; Silva and Clarke 2020; Singer 1986). To incorporate this complexity, preference tests in more natural settings (e.g. potted plants exposed in the field) might offer a standardised way to study how innate host preferences change in the actual environment (Briese 2005; Wapshere 1974, 1989).

Our results confirm that SWD lays more eggs in fruit species with softer skin, in line with the results of Burrack et al. (2013). Egg-laying of SWD also decreases with increasing skin hardness within a single crop, as has been shown for different grape cultivars (Asplen et al. 2015; Entling and Hoffmann 2020; Ioriatti et al. 2015; Kehrlı et al. 2017; Mazzetto et al. 2020; Shrader et al. 2019; Tonina et al. 2018), varieties of cherries (Kamiyama and Guédot 2019) or blueberries (Kinjo et al. 2013). In our study, the regression line of the linear model indicates that SWD would avoid laying eggs in fruits with a skin hardness of 75 cN or more. Tested host species with a skin hardness close to this threshold of 75cN were currant tomato (*Lycopersicon pimpinellifolium*), Solomon's seal (*Polygonatum multiflorum*), the laurustinus (*Viburnum tinus*), the mountain-ash (*Sorbus aucuparia*), the American mountain-ash (*Sorbus americana* Belmonte), the Asiatic apple (*Malus spectabilis*) and the blackthorn (*Prunus spinosa*). Our data show that these species can be considered as irrelevant host plants for SWD as the number of eggs laid was close to zero and no adults were able to emerge (Table 1). In our dataset, the oviposition preferences of SWD females did not correlate with fruit elasticity or colour. Yet, it is generally assumed that colour plays an important role in the fruit choice behaviour of SWD (Lee et al. 2011; Little et al. 2019). Within a species, colour provides valuable information about fruit maturation and ripeness (Lee et al. 2011), but it does not necessarily indicate host suitability across plant species. Overall, the fruit skin hardness threshold of 75 cN can be used to rapidly estimate the approximate potential for oviposition of so far untested plant species and to develop mechanical control strategies such as the application of fruit coating products (Tait et al. 2022). However, it does on its own not allow to predict the actual attractiveness of species as other fruit traits and environmental factors influence SWD host preference.

## Performance

The three chosen performance criteria (namely development time, wing length and emergence success) to evaluate the suitability of host plants for SWD development were not correlated, suggesting that these three traits are regulated by different mechanisms that are independent of the host plant's identity. Still, SWD showed variation in two of the three criteria among plant species, indicating an overall variation in SWD performance among host species.

Although we studied the relation between fruit traits and SWD development performance across a large range of 60 host plant species, we did not manage to identify any trait fundamentally affecting emergence success. Moreover, such a relationship between SWD performance and fruit traits could also not be shown within a single species such as among grape cultivars (Pelton et al. 2017). Yet, we found that the development time was controlled by the acidity of fruits. Shortest development times were observed when fruit acidity was between a pH of 4 and 5.5, below and above this optimum the duration for the egg-to-adult development increased. A longer development time at lower fruit acidity has similarly been observed in the two vinegar fly species *D. melanogaster* and *D. hydei* (Hodge et al. 1996). In line with the results for tart cherries (*Prunus cerasus*) (Kamiyama and Guédot 2019), SWD development time increased in fruits with lower sugar content. Moreover, the amount of sugar also affected SWD wing length with fruits of higher sugar content leading to the emergence of flies with longer wings. As the size of different body parts is usually correlated (Carreira et al. 2009) and an increased body size is associated with higher fecundity, higher courtship success and longer survival in *D. melanogaster* (Partridge et al. 1987; Rodrigues et al. 2015), it can be assumed that these larger SWD also have a higher fitness. Overall, host plants with an optimal acidity level and high sugar content in ripe fruits might therefore be able to shorten development time and increase individual fitness thereby leading to potentially more SWD generations and higher pest populations.

### Trap cropping

Our data clearly indicate that not all crops are similarly suitable for implementing a trap cropping strategy against SWD. For example, grapes or black chokeberry (*Aronia melanocarpa*) is less attractive for SWD egg-laying compared to many other economic crops and wild host plant species. It was therefore straightforward to identify 16 plant species that do not support SWD development but that are significantly more attractive than grapes (see Table 1). These 16 species are potential candidates that might be used for developing a dead-end trap cropping strategy in order to protect vineyards against SWD and thus promoting bottom-up pest control (Simon et al. 2011). The black chokeberry would also be suitable for trap cropping as it scored similarly to grapes regarding SWD preference. The cultivation of black chokeberry is popular in its native area of North America (Shahin et al. 2019), and our dataset could be used to identify suitable candidates for trap cropping. However, highly attractive crop species such as blackberries (*Rubus fruticosus*), raspberries (*Rubus idaeus*) or black elderberries (*Sambucus nigra*) apparently lack alternative host plant species that are preferred over

them for egg-laying. The planting of a trap crop in their vicinity would therefore most likely have little effect on SWD pressure and crop damage. Moreover, these three crops are frequently grown over large areas and are locally abundant thereby potentially maintaining local SWD populations at high densities (Santoemma et al. 2019). Similarly, few host plants were preferred for oviposition over crop species such as blueberry (*Vaccinium myrtillus*), Goji berries (*Lycium barbarum*) or plums (*Prunus domestica subsp. insititia*). Consequently, it will also be challenging for these commercial species to discover a suitable trap crop that might protect them against SWD.

In order to select trap crop candidates for grapes, we ranked the emergence success of different plant species. Since the implications of developmental performance on population growth are yet unclear, we propose to first test candidate trap crops with the lowest emergence success. After conducting a small-scale field experiment, Nibouche et al. (2012) regarded a survival rate below 10% to be sufficient to consider the wild sweetcane *Erianthus arundinaceus* as a dead-end trap crop against larvae of the sugarcane stem borer *Chilo sacchariphagus*. In the following, they planted this trap crop at the border of commercial sugarcane fields and thereby reduced pest damage by a factor of 2.8 to 4.4 (Nibouche et al. 2019). Thus, the 16 host plant species highly preferred over grapes for egg-laying and with emergence success below 10% in our study (see Table 1) might be considered as promising candidates for dead-end trap cropping. In addition, we identified 10 plant species that have an intermediate emergence success of 10 and 30% that are significantly more attractive than grapes for SWD (Table 1). These species might be considered for traditional trap cropping, but their use would have to be combined with additional control measures that limit pest spill-over (Blitzer et al. 2012). As SWD eggs and larvae develop within fruits, the efficacy of most insecticides is low. The mechanical destruction of infested fruits or a regular vacuuming of emerged adults might therefore be more appropriate to limit spill-over (Haye et al. 2016; Schetelig et al. 2018; Tait et al. 2021). Overall, our assessments provide a list of totally 26 candidate host plants suitable for trap cropping.

To further develop a trap cropping strategy, the choice of the candidates should be adapted to the local environment and the ecological requirements (Asgarzadeh et al. 2014). For instance, several of the mentioned candidates are considered as invasive plant species in Europe, e.g. *Phytolacca americana* and *Prunus laurocerasus* (Info Flora 2014). Consequently, these species should only be considered for further experimental testing in central Europe, if appropriate control measures that prevent entirely their dispersal are available and can be implemented.

## Perspective

To develop trap cropping against SWD in vineyards, the phenology of candidates should be followed first of all under field conditions in order to estimate more accurately their fruiting period and their synchrony with grape maturation. To cover the long ripening period of grapes, a combination of different trap crop plant species might be best suited. For example, such multi-species trap cropping was most efficient in decreasing beetle damage in broccoli (Parker et al. 2016). Second, the actual protection effect of single candidates or combination of candidates should be evaluated under standardised semi-field conditions. For this, potted grapevines could be exposed next to potted candidate trap crops to a defined number of mated SWD females within insect enclosure cages. This will allow to assess grape infestation and the actual level of crop protection for each treatment. Based on these findings, the optimal ratio between selected trap crops and grapevines as well as their spatial arrangement (e.g. “perimeter trap cropping” versus “intercropping trap cropping”) could be tested in experimental vineyards. This will allow to get further insights into the efficiency and configuration of a successful trap cropping strategy. Such experiments would help to determine the practical feasibility of trap cropping in commercial vineyards and to conduct cost–benefit analyses in order to calculate the expected financial gain from protecting grapes by trap cropping against SWD infestation.

Our data might also be valuable to address applied ecological or environmental issues. For example, our findings stress that plant species such *Atropa belladonna*, *Cornus kousa*, *Frangula alnus*, *Lycium barbarum*, *Rubus fruticosus lockness*, *Rubus idaeus* and *Sambucus ebulus* might be contamination sources in agricultural landscapes. Due to the high SWD emergence success, their presence might be limited in the vicinity of vulnerable crops thereby minimising the risk of pest spill-over (Kristan III 2003). Moreover, bottom-up forces have been shown to directly affect the abundance of herbivores (Ylloja et al. 1999). It appears that both, the quality and the abundance of host plants, are crucial for explaining population dynamics in herbivores (Underwood 2009; West and Cunningham 2002). However, pest individuals’ performance does not necessarily lead to changes in their population dynamics (Karimzadeh et al. 2004; Zaugg et al. 2013). To better anticipate pest abundance and movements in the landscape and improve the pest control of mobile pest species such as SWD (Klick et al. 2016; Tait et al. 2018; Vacas et al. 2019), it might be critical to identify the role of each host plant for creating source or sink habitats and to discover possible “ecological traps” (Delibes et al. 2001). How SWD preference and performance on individual host plants contribute to SWD population dynamics is only partly understood, but our data might also be useful

to predict pest dynamics in agricultural landscapes including their movement patterns between semi-natural habitats and crops (Carriere et al. 2012; Choquenot and Parkes 2001).

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10340-024-01748-3>.

**Acknowledgements** We thank Françoise Klötzli-Estermann, Julie Laurent, Maëlle Corminboeuf, Sébastien Hévin and Eric Remolif for their technical support as well as two anonymous reviewers for their helpful comments. Financial support for carrying out this research was provided by the transnational funding bodies that are partners of the H2020 ERA-net project, CORE Organic Cofund and the cofund from the European Commission (PCI2018-093015/Project BIOVINE).

**Author contributions** PK, SB and AF designed the experiments. AF conducted the experiments with help from PK. AF analysed the data with input from SB and PK. AF wrote the first draft of the manuscript, which all authors then revised. All authors read and approved the final manuscript.

**Funding** Open access funding provided by Agroscope. The financial support was provided by the transnational funding bodies that are partners of the H2020 ERA-net project, CORE Organic Cofund and the cofund from the European Commission (PCI2018-093015/Project BIOVINE).

**Data availability** The data that support the findings of this study are openly available at: <https://doi.org/https://doi.org/10.5281/zenodo.10018931>.

## Declarations

**Conflict of interest** All authors declare not having financial interests to disclose.

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