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REVIEW ARTICLE

Natural compounds for controlling *Drosophila suzukii*. A review

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Abstract

The drosophilid fly *Drosophila suzukii* is an invasive pest that has recently started threatening fruit production in Europe. In contrast to many other fruit flies, *D. suzuk*ii is able to lay eggs in ripening and mature fruits where larvae develop, rendering fruits unmarketable. This preference for ripening fruit requires pest control shortly before harvest, implying a high risk of residues on the fruit if synthetic insecticides are used. As the current management practices largely rely on chemical control, the need for alternative solutions has emerged. Here, we review the studies published up to now on the efficacy of natural compounds against *D. suzukii.* Several natural compounds were identified that act as repellents, contact or ingestion toxicants, fumigants, ovicides or oviposition deterrents. The most promising compounds of each group were (i) essential oils (EOs) such as the EO of thyme or its major ingredient thymol which repelled flies from fresh fruits for at least 24 h; (ii) *Leptospermum ericoides* and *L. scoparium* EOs, which expressed contact toxicity at a $LD_{50} < 1.2$ μg/fly; (iii) the combination of erythritol and sucrose, which was a potent ingestion toxicant against adults and (iv) a chitinase from *Euphorbia characias* against larvae (both of the latter two resulted in 100% mortality); (v) the EO ingredients perilla aldehyde, geranial and neral showed the highest insecticidal activities as fumigants ($LC_{50} < 1.52$ mg/l air for males and 2.6 mg/l air for females) and (vi) powdered sulphur was reported to be the most efficient oviposition deterrent, reducing the number of eggs deposited into the fruits by 76%. To enable a wider use of the natural compounds in sustainable agriculture, more information on (i) potential effects on non-target organisms, (ii) field performance and (iii) life cycle analyses results is currently needed.

Keywords Climate change · Crop protection · Insecticides · Reducing pesticides · Spotted wing drosophila

Abbreviations

AChE	Acetylcholinesterase
AST	Average survival time
BA	Butyl anthranilate
CT	Concentration tested
DEET	*N*,*N*-diethyl-meta-toluamide
DMB	Methyl 2,4-dimethoxy-6-methylbenzoate
EA	Ethyl anthranilate
EO	Essential oil
ESE	Ethanolic seed extract
GST	Glutathione-S-transferase
MDA	Methyl *N*,*N*-dimethylanthranilate

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1 Introduction

Drosophila suzukii (Matsumura), also called spotted wing drosophila, is a fruit fly with a clear sexual dimorphism: males have a dark spot on the wings while females have not (Fig. 1) (Cini et al. 2012). Native to Southeast Asia, *D. suzukii* was first observed in the USA as well as in Europe (Spain and Italy) in 2008. Since then, it has been spreading north- and eastwards (Asplen et al. 2015). In a climate change impact study, a temperature-driven population dynamics model using data derived from several Global Circulation Models (CMIP5) suggested that northern latitudes may experience increased *D. suzukii* populations due to milder winter conditions (Langille et al. 2017). In fact, *D. suzukii* reached Luxembourg in 2014, where it was first observed on red wine cultivars after a very mild winter (Schultz and Molitor 2016). *D. suzukii* is considered as a serious pest for soft-skinned fruits for several reasons. First, their serrated ovipositor allows the females to pierce the skin of ripening and ripe fruit to deposit eggs inside of the fruit. After a few days, the eggs hatch and the larvae develop while feeding on the fruit tissue, rendering the infested fruit useless for direct sale and processing. The oviposition wound in the fruit skin allows infection by fungi and bacteria and increases the risk of rapid fruit decay. After the larval stage, pupation occurs and a new generation of adults emerges. Second, *D. suzukii* can use a wide range of wild and cultivated host plants, such as sweet cherry, strawberry, raspberry, apricot, plum, fig or grape for oviposition (Cini et al. 2012). Third, *D. suzukii* has a high fecundity coupled with a short generation cycle. Females can lay more than 400 eggs in their lifetime and at optimum conditions of temperature, humidity and food resources, 8 days is sufficient for an egg to become an adult fly. Multiple generations and an exponential increase of the population can easily occur during the cropping season (Cini et al. 2012; Hamby et al. 2016). Current management practices are based mainly on the application of synthetic insecticides (belonging to the families of the pyrethroids or organophosphates or the active ingredient spinetoram) or bioinsecticides (spinosad and pyrethrin). Between one and 8 applications are necessary to insure an effective protection during fruit ripening depending on the crop and its susceptibility, the pest pressure and other environmental factors (Asplen et al. 2015; Shawer et al. 2018). The chemical protection is often complemented by cultural measures including sanitation (leaf removal in the cluster zone, selective removal of ripe and overripe fruit from the parcels, covering the crops with nets) and the reduction of the harvest intervals (Asplen et al. 2015; Haye et al. 2016; Schultz and Molitor 2016). The biological control of *D. suzukii* is still under investigation. Some efficient parasitoids have been identified with most of them being native to Asia, while the predators identified so far had an insufficient effect on the *D. suzukii* population (Asplen et al. 2015; Haye et al. 2016). Concerning entomopathogenic nematodes and fungi, laboratory tests indicated good efficacy, but optimization with regard to survival during transport and in natural matrices like soil is needed before high control efficacy can be expected in the field (Asplen et al. 2015; Haye et al. 2016). Since *D. suzukii* has a strong preference for ripe fruit, little time remains for pesticide degradation before harvest and consumption if synthetic insecticides are used. Therefore, there is a strong interest in controlling *D. suzukii* by methods other than synthetic pesticides.

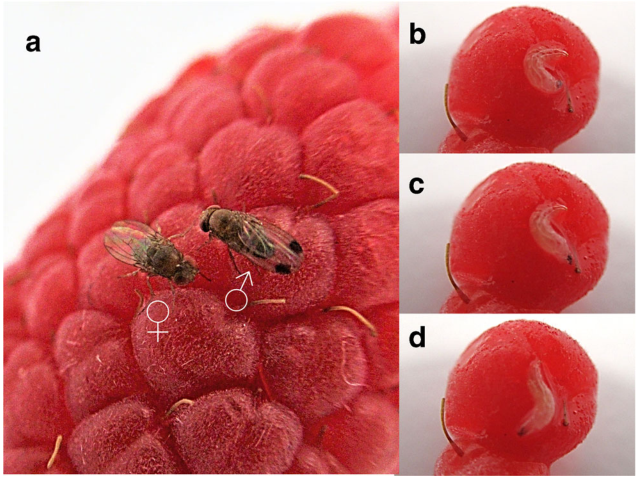

Fig. 1 **a** Female (left) and male (right, with spotted wings) adults of *Drosophila suzukii* on a raspberry fruit. **b**–**d** Time series (**b** 0 s, **c** 45 s, **d** 100 s) of a *D. suzukii* larvae feeding on a raspberry fruit

The purpose of this review was to identify the most effective natural extracts and compounds tested against *D. suzukii* up to now. We used the broad definition of natural compounds including biotic materials produced by organisms, and other natural materials, such as soil components or coal. Tested natural compounds that showed no effects against *D. suzukii* are also listed. Knowledge gaps that currently hinder a widespread use of natural compounds for controlling *D. suzukii* are summarized. This review was written following the recommendations outlined by Pautasso (2013).

1.1 Classification of tested compounds

The natural compounds tested for controlling *D. suzukii* can be classified according to their currently established general mode of action:

Compounds

- that have a repulsive effect on the flies are subsequently referred to as *repellents*,
- that require physical contact for expressing toxic effects are subsequently referred to as *contact toxicants*,
- that require oral uptake for expressing toxic effects are subsequently referred to as *feeding toxicants*,
- that have an activity via the gaseous phase are subsequently referred to as *fumigants*,
- that reduce the number of eggs laid are subsequently referred to as *oviposition repellents* and that fatally affect egg development as *ovicides*.

Some compounds may have multiple modes of action and therefore can belong to several groups. It is also possible that some compounds have effects that are not yet known. Therefore, the present classification represents the current state of knowledge and may be subject to change when new experimental studies provide additional evidence.

1.2 General considerations on estimated toxicity parameters

Three toxicity parameters were used to describe the effect of the compounds on *D. suzukii*.

The dose lethal for 50% of the exposed individuals, usually called LD_{50}, was used to estimate the level of contact toxicity of test compounds within a certain time (Porteus 2008). LD_{50} values are usually given in milligrams of product per kilogram of animal body mass. For small animals like flies, LD_{50} values are sometimes given as micrograms of product per individual.

The lethal concentration (LC_{50}) is the concentration of a substance in air or water that is sufficient to kill 50% of a sample population within a certain time (Porteus 2008). This parameter was used to measure the fumigant toxicity.

The half-maximally effective concentration, also called EC_{50}, is the concentration at which 50% of the maximum effect is produced or the concentration of drug at which the drug is half-maximally effective (Lowe and Balis 2012). This parameter was used to measure contact and fumigant toxicities.

Whenever the magnitude of effects of natural compounds on *D. suzukii* had to be estimated from graphs published by other authors, the software tool WebPlotDigitizer version 4.1 was used.

2 Repellents

Potential repellents were tested using either T-maze assays, choice trap assays, impregnated cotton wicks or direct airborne repellent assays. The results of repellent tests are summarized by assay in the following paragraphs.

2.1 T-maze and choice trap assays

A T-maze assay is based on a T-shaped apparatus: a test odorant is positioned into one arm of the T-maze and a control odorant into the opposite arm. Flies are released into the T-maze apparatus and after a predetermined experimentation time, the position of flies is recorded and a preference index is calculated (Eq. 1) (Krause Pham and Ray 2015).

$$\text{Preference index} = \frac{\text{number of flies in test arm} - \text{number of flies in control arm}}{\text{number of flies in test arm} + \text{number of flies in control arm}} \tag{1}$$

A trap assay is set up in a closed arena; for a no-choice assay, only one trap is arranged (treatment and control studied separately) and for a choice assay, at least two traps are arranged (treatment and control). Generally, test compounds are applied to a filter paper. Traps can have several designs. To test the effect of pyridine and DEET substitutes, the treated filter paper was placed at the entry of the trap and flies had to crawl over it to reach the lure in the trap. After a predetermined experimentation time, the number of flies in each trap was counted and the preference index was calculated (Eq. 1) (Krause Pham and Ray 2015). To study the repellence of octenol, geosmin and benzaldehyde, the filter paper was arranged in the trap and after a predetermined time, the number of flies in each trap recorded (Renkema et al. 2016; Wallingford et al. 2016b).

Carbon dioxide and pyridine (an animal skin odorant) are known to repel other *Drosophila* species and therefore, their effect against *D. suzukii* was assessed in a T-maze assay (Krause Pham and Ray 2015). Carbon dioxide concentration (concentration tested = CT = 0; 0.34; 0.67 and 1.34% v/v) in the air had no repellent effect on *D. suzukii* with a similar preference index for all concentrations tested, whereas CO_2 was strongly avoided by *D. melanogaster*. Pyridine (CT = 1% v/v) slightly attracted the flies. A complementary experiment, a two-choice trap assay, was also conducted to study the longterm effect of pyridine; *D. suzukii* showed no significant avoidance for this product (Krause Pham and Ray 2015).

Most *Drosophila* species are repelled by DEET (*N*,*N*-diethyl-meta-toluamide), a commonly used synthetic insect repellent. The repellent activity of three natural substitutes to DEET (butyl anthranilate (BA), methyl *N*,*N*-dimethylanthranilate (MDA) and ethyl anthranilate (EA)) (CT = 1 and 10% v/v) was assessed in a two-choice trap assay and their preference index were estimated. At 1%, the most repellent product was DEET followed by BA, MDA and EA with preference index of − 0.8, − 0.6, − 0.3 and − 0.05, respectively. At a concentration of 10%, all the products showed a repellent activity with preference index of − 0.6 for DEET and EA, and − 0.4 for BA and MDA. Thus, at 1%, only BA had a repellent effect comparable to DEET, while at 10%, all the natural substitutes repelled *D. suzukii* as DEET (Krause Pham and Ray 2015).

Two-choice trap assays were conducted to ascertain whether octenol, geosmin and benzaldehyde (CT = 0.1; 1 and 10% in mineral oil v/v) could repel *D. suzukii* from crushed raspberries mixed with yeast. Octenol and geosmin significantly repelled flies at 1 and 10% but not at a lower concentration. Benzaldehyde did not repel *D. suzukii* (Wallingford et al. 2016b). Interestingly, octenol and geosmin are known to be produced by necrotrophic fungi, such as *Penicillium expansum* and *Botrytis cinerea* on infected grape berries (La Guerche et al. 2005). It may be speculated that flies are repelled by these substances to avoid oviposition into already decaying fruits that may not allow the full development of the larvae.

2.2 Impregnated cotton wicks

The repellent effect of the EO of *Pelargonium asperum*, *Mentha × piperita*, *Zingiber officinale*, *Eucalyptus radiata*, *Cymbopogon winterianus*, *Lavandula angustifolia*, *Rosmarinus officinalis*, *Thymus vulgaris*, *Thuja occidentalis*, *Abies balsamea*, *Picea glauca* and *Pinus strobus* was assessed against *D. suzukii* (Renkema et al. 2016). A cotton wick was soaked with the EO and transferred into a vial containing fresh raspberry juice. The flies could choose between an untreated cotton wick and the treated one, and their position was recorded after 1, 6 and 24 h. The EO of *P. asperum*, *Z. officinale*, *Mentha × piperita*, *C. winterianus*, *L. angustifolia* and *T. vulgaris* significantly repelled the flies for 24 h while the other tested EO showed a weaker repellent activity (Renkema et al. 2016). In a similar experiment, the repellent effect of the EO of *C. winterianus*, *E. radiata*, *P. asperum*, *Mentha × piperita* and *T. vulgaris*, their major compounds (at the rate in the EO) and a blend of the major compounds (at the rate in the EO) was assessed against *D. suzukii* (Renkema et al. 2017). The only difference compared with the previous experiment was the use of a blueberry juice as the lure instead of raspberry juice. The flies could choose between an untreated cotton wick and the treated one; their position was recorded after 2, 6 and 24 h. The most efficient EO were extracted from *C. winterianus*, *P. asperum* and *T. vulgaris*, which significantly repelled *D. suzukii* males and females for at least 24 h. Among the major compounds of the EO, only thymol (CT = 35% w/v) showed a significant repellent activity against both sexes until 24 h when tested individually. Other compounds such as geraniol (CT = 22%) and citronellol (CT = 34%) significantly repelled males for 24 h and females for 6 h. The blends made of the major compound of *P. asperum* and *T. vulgaris* significantly repelled the flies for 24 h. Following these results, three blends of compounds were prepared, one dominated by thymol, one dominated by citronellol and a four-compound blend (thymol, citronellol, menthol and geraniol). Cotton wicks were soaked with the blends and placed between two fresh raspberries. Choice and no-choice assays were conducted. In the choice assay, the thymol blend significantly repelled landing on raspberries for 6 and 24 h whereas the repellent effect of the citronellol blend was only significant at 24 h. The four-compound blend had no repellent activity. In the no-choice assay, the repellent activity of the thymol blend was the same; it significantly repelled flies from landing on raspberries after 6 and 24 h. The citronellol blend had no repellent activity whereas the four-compound blend had a significant repellent effect only at 24 h (Renkema et al. 2017).

2.3 Direct airborne repellent assay

The direct airborne repellent test is suitable for volatile compounds that could be confounded by responses from the taste system. In a 20-cm length tube, a filter paper is placed at each end, one is treated with the tested compound and the other one with the control. A brass screen prevents contact between flies and the filter paper. Flies are introduced into the tube and after a predetermined experimentation time, their position is recorded (5 cm near the treated or the untreated end) (Krause Pham and Ray 2015). Citronellal (CT = 0.1 and 1% v/v), a compound present in numerous EO, is a known repellent so it has been tested against *D. suzukii*. At the lower concentration, citronellal attracted *D. suzukii* and, at 1%, it slightly repelled the flies; thus, this product did not have a significant effect on the behaviour of *D. suzukii* (Krause Pham and Ray 2015).

2.4 Conclusion on repellents

The most promising repellents tested against *D. suzukii* so far were butyl anthranilate, octenol, geosmin, the EO of *P. asperum*, *C. winterianus* and *T. vulgaris* and the EO compound thymol.

3 Contact toxicants

Contact toxicity was assessed by different methods. The most frequently used method was direct application of the product to the flies with a syringe. This method will subsequently be referred to as topical application and was mainly employed for EO, their major compounds and fungal metabolites. For formulations based on bacteria or entomopathogenic fungi, products were transferred to absorbent materials such as cotton or felt and *D. suzukii* was exposed to them in a closed arena.

3.1 Topical application

The experimental protocol for topical application was described previously (Kim et al. 2016b). The flies were kept in the following environmental conditions to obtain the results summarized below 23–27 °C, 60–70% relative humidity and 16:8 L:D (16-h light, 8-h darkness).

Among the tested substances, the most effective were *Leptospermum ericoides* and *Leptospermum scoparium* EO, the polar fraction of those EO and *L. scoparium* EO triketone fraction with LD_{50} values between 0.13 and 0.71 μg/fly for males and 0.22 and 1.23 μg/fly for females (Fig. 2, Jang et al. 2017; Kim et al. 2016a, 2016b; Park et al. 2017, 2016). The contact toxicity of the non-polar fraction, made up of sesquiterpene hydrocarbons, was significantly lower than the toxicity of the polar fraction. The triketone fraction as part of the polar fraction was mainly composed of flavesone, isoleptospermone and leptospermone (Park et al. 2017). For *Leptospermum ericoides*, the polar fraction was 67-fold more effective than the non-polar fraction for males and 134-fold more effective for females. For *Leptospermum scoparium*, the factor between the efficiency of the two fractions was 19 for males and 39 for females.

Cypermethrin, a pyrethroid insecticide, was used as a positive control. The contact toxicity of this product was very high with LD_{50} values ranging from 0.05×10^{-3} to 0.13×10^{-3} μg/fly for *D. suzukii* males and from 0.06×10^{-3} to 0.44×10^{-3} μg/fly for females, indicating that this synthetic product has an insecticidal activity approximately 10^3-fold higher than the most efficient of the tested EO or their compounds (Jang et al. 2017; Kim et al. 2016b; Park et al. 2017, 2016).

Other EO had a significant contact toxicity compared to the control at the highest concentration tested but were not promising enough to estimate their LD_{50}, such as the EO of *Leptospermum citratum*, *Pimenta dioica*, *Syzygum aromaticum* (Park et al. 2017), *Hyssopus officinalis*, *Mentha piperita*, *Ocimum basilicum*, *Origanum majorana* (Park et al. 2016), *Eucalyptus polybractea*, *Melaleuca alternifolia*, *M. dissitiflora*, *M. ericifolia*, *M. viridiflora* (Jang et al. 2017), *Croton anisatum*, *Aniba roseodora*, *Jasminum sambac*, *Amyris balsamifera*, *Illicium verum* and *Styrax tonkiensis* (Kim et al. 2016b).

Finally, some EO tested showed no contact toxicity, such as the EO of *Lavandula angustifolia*, *Rosmarinus officinalis*, *Salvia sclarea*, *Vitex agnus castus* (Park et al. 2016), *Eucalyptus globulus*, *E. radiata*, *E. smithii*, *M. leucadendron*, *M. uncinata* (Jang et al. 2017), *Rhus taratana*, *Bursea delpechiana*, *Boswellia carterii*, *Chamaecyparia obtusa*, *Cryptomeria japonica*, *Cupressus sempervirens*, *Juniperis communis*, *Thujopsis dolabrata*, *Gaultheria fragrantissima*, *Cedrus atlantica*, *Pinus sylvestris* and *Citrus limonum* (Kim et al. 2016b).

Fungal metabolites (sparassol, methyl orsellinate and methyl 2,4-dimethoxy-6-methylbenzoate (DMB)) were applied

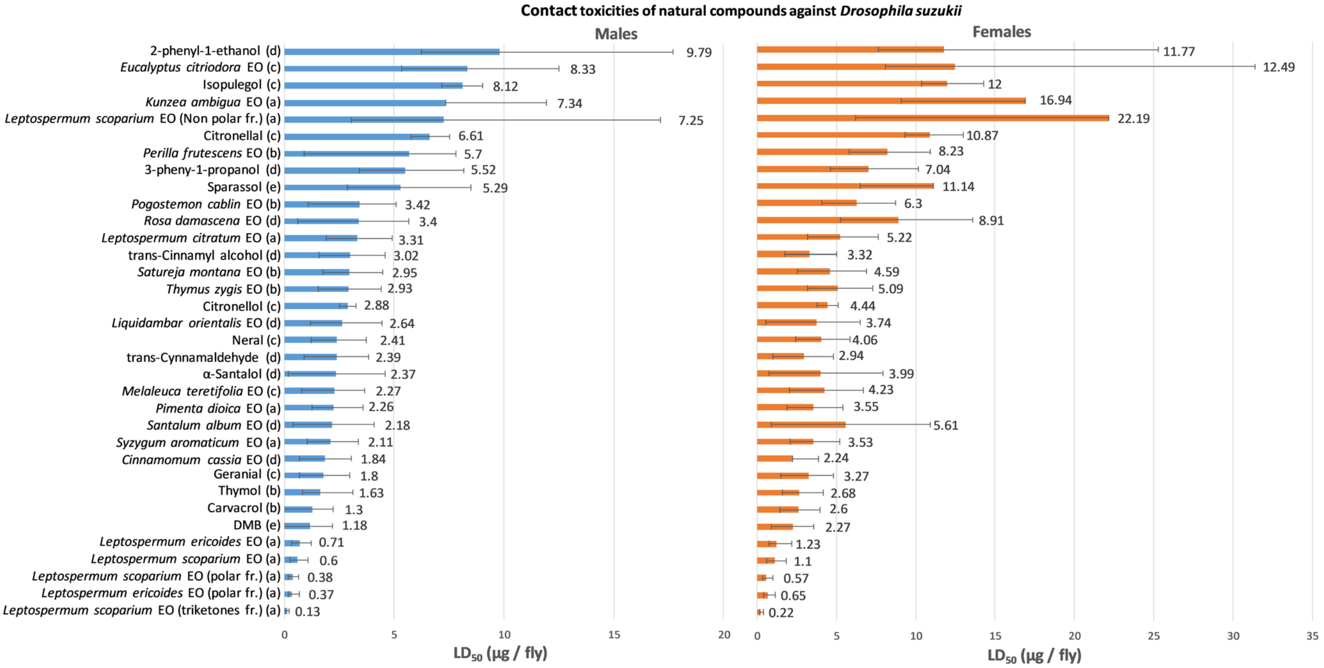

Fig. 2 Reported contact toxicities of natural compounds versus *Drosophila suzukii*. EO = essential oil; fr. = fraction. Error bars represent 95% confidence limits. Data were published by (a) Park et al. (2017); (b) Park et al. (2016); (c) Jang et al. (2017); (d) Kim et al. (2016b) and (e) Kim et al. (2016a)

topically to *D. suzukii*. Only DMB and sparassol showed an interesting contact toxicity with LD_{50} of 1.18 and 5.29 µg/fly for males, respectively, and 2.27 and 11.14 µg/fly for females, respectively (Fig. 2, Kim et al. 2016a).

Generally, LD_{50} values were higher for females than for males (Fig. 2, Jang et al. 2017; Kim et al. 2016a, b; Park et al. 2017, 2016). Females tend to be bigger than males (average body length when raised with cherry: females 2.5 mm; males 2.25 mm or with grapes: females 4.0 mm; males 3.0 mm (Walsh et al. 2011 adapted from Kanzawa)), but there seems to be no evidence supporting a role of body size for the differential sensitivity at present.

The EC_{50} was also used to compare the contact toxicity of some EO. All the EOs tested had a significant insecticidal activity, except that of *Aleurites moluccana*. *Persea americana* EO, 1,8-cineole and *L. latifolia* EO showed the highest insecticidal activity with EC_{50} values of 0.54, 0.67 and 0.69% of the product when 0.5 ml was applied per fly (Fig. 3, Erland et al. 2015). The EO of *Azadirachta indica*, *Macadamia integrifolia*, several cultivars of *Lavandula* and the compounds δ-carene and linalool showed a weaker contact toxicity (Fig. 3, Erland et al. 2015).

3.2 Use of impregnated matrices

In a series of studies, the contact toxicity of selected compounds was assessed with the test compounds being impregnated into a support matrix like a cotton wick or a piece of felt, and the percentage of dead flies counted after predetermined time intervals was used to compare the products.

The entomopathogenic fungus *Metarhizium brunneum* (strain EAMa 01/58-Su) was tested on a felt cone impregnated with conidia ($CT = 3 \times 10^{10}$ conidia). An artificial diet positioned at the bottom of the cone attracted the flies, such that the flies had to crawl over the inoculated felt when trying to reach the feed. After 5 days of exposure, this fungal strain had a significant contact toxicity compared to the control, inducing 62.2% and 57.7% of mortality with a black and a red felt, respectively. Treated adults had an average survival time (AST) of 3.6 days. The horizontal transmission of the entomopathogenic fungus was also studied. Flies (males and females separately) were transferred into the device described above for 24 h. Then, the following combinations were tested for 7 days: infected males with non-infected females, infected females with non-infected males, both infected or both non-infected. When males were infected, 72% of them died within 7 days and induced a mortality of 24% in untreated females with an AST of 6.3 days. When females were infected, 84% of them died and induced the mortality of 48% in untreated males with an AST of 5.6 days. When both were infected, mortality was 88% and 84% for males and females, respectively. When both were untreated, only 8% of males and 7% of females died during the experiment. The horizontal transmission of the entomopathogenic fungus induced significant mortality when only males, only females or both are infected compared to uninfected. In the same experiment, the sub-lethal effect of the entomopathogenic fungus was studied by counting the number of emerged pupae. When males were infected, the number of pupae was similar that of when males and females were healthy with a mean of 22 pupae. When either both sexes or only females were infected, the number of pupae was significantly lower with a mean of four pupae, corresponding to a reduction of 84.7% (Yousef et al. 2018).

D. suzukii was exposed to commercial formulations of *Bacillus thuringiensis* on cotton wicks. None of the tested products induced mortality in the tested populations suggesting their lack of insecticidal activity against *D. suzukii* (Biganski et al. 2018).

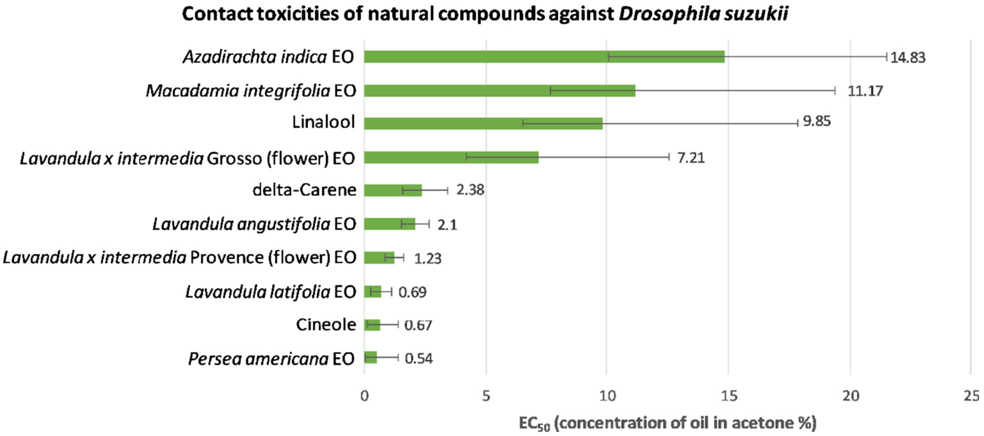

Fig. 3 Reported contact toxicities of natural compounds versus *Drosophila suzukii*. EO = essential oil. Error bars represent 95% confidence limits. Data were published by Erland et al. (2015)

3.3 Conclusion on contact toxicants

By topical application, the EO of *L. scoparium* and *L. ericoides* applied fully or partially (e.g. only the polar fraction) were the most promising. The entomopathogenic fungus *Metarhizium brunneum* had an interesting insecticidal effect with medium rates of horizontal transmission and sub-lethal effects.

4 Ingestion or contact toxicants

Some experimental set-ups do not allow a clear distinction between the effects of ingestion and contact. These cases will be discussed together in the following paragraphs.

4.1 Feeding and development on a supplemented medium

The insecticidal effect of a chitinase extracted from the latex of *Euphorbia characias* was tested against *D. suzukii* larvae. The chitinase was mixed with an artificial diet (CT = 0.005% and 0.025% w/v) in which larvae could feed and develop. At 0.005%, the chitinase caused 93% mortality among the larvae and only 2% developed into adults. At 0.025%, larvae neither survived nor pupated after 10 days of treatment. Both tested chitinase concentrations induced a significant mortality in the brood compared to the control. They were as efficient as the synthetic insecticide diflubenzuron (Dimilin®, CT = 2% v/v) which had a slower activity inducing 20% of larval mortality and 100% of pupal mortality (Martos et al. 2017).

The insecticidal activity of a crude extract of *Metarhizium brunneum* (EAMb 09/01-su), an entomopathogenic fungus, was assessed on *D. suzukii* adults. The crude extract was mixed with an artificial diet and had a significant contact/feeding toxicity with 88.8% of mortality after 48 h compared to 3.3% in the control. Exposure periods of between 6 and 9 h were needed to achieve 50% mortality. The crude extract was also tested in a lure-and-kill trap-device: in this case too, the crude extract showed a significant insecticidal activity with 61.6% of dead flies compared to 3.3% in the control (Yousef et al. 2018).

The toxicity of erythritol (Truvia®, CT = 0 to 2 M) to *D. suzukii* was assessed by allowing flies to feed on supplemented artificial media. Within a 4-day exposure period, the LC_{50} of erythritol was 1.15 M and the LC_{90} was 1.82 M. When larvae were feeding on the same treated artificial diet media, they died before pupation at an erythritol concentration in the media of 0.5 M (Sampson et al. 2017b). As erythritol may be cost-prohibitive, the efficiency of lower cost derivatives has been investigated against *D. suzukii* (Sampson et al. 2019). Flies were allowed to feed on a medium supplemented with pentaerythritol, dipentaerythritol, tripentaerythritol, erythritol (CT = 0.25, 0.5 or 1 M) or water as a negative control for 7 days. Then, the media were kept two more weeks for counting pupae and emerging adults. Only erythritol and pentaerythritol induced a significant adult mortality with respective rates of 90% and 100% at 1 M. Concerning adult emergence, erythritol had a significant effect with a reduction of 90% at a concentration of 0.25 M. At 1 M, pentaerythritol and dipentaerythritol induced a reduction of 60% and 80% of adult emergence, respectively. However, under laboratory conditions, only erythritol was able to prevent the increase of the population whereas pentaerythritol and dipentaerythritol only slowed it down (Sampson et al. 2019). The insecticidal activity of erythritol may be explained by a dual mode of action: (i) starvation when it is the sole food source and (ii) desiccation induced by cytolysis. Indeed, erythritol is not metabolized and diffuses through the midgut membrane to reach the hemolymph where it induces a quick increase of osmotic pressure in the fly's body, which can be lethal. The higher efficiency of erythritol and pentaerythritol compared to dipentaerythritol and tripentaerythritol was linked to their smaller molecule size and their reduced number of hydroxyl groups which induce a greater osmotic pressure (Sampson et al. 2019).

The insecticidal activity of *Bacillus thuringiensis*-commercialized formulations against *D. suzukii* larvae and pupae was studied. These products were mixed with an artificial medium on which larvae feed and develop. The percentage of mortality of larvae and pupae was very low and not significantly different from the control for all the products tested so far, suggesting no significant toxicity against *D. suzukii* larvae (Biganski et al. 2018).

4.2 Feeding on and contact with a soaked cotton wick

The ethanolic seed extracts (ESE) of the *Annona* species were offered to the flies on an impregnated cotton wick as sole food source for 24 h (CT = 2000 mg/l of water). Five days after the exposure period, the mortality of the flies was assessed. ESE of *A. muricata* did not induce a significant mortality rate compared to the control whereas the ESE of *A. sylvatica* and *A. mucosa* did, with 35% and 94% of fly mortality, respectively. The ESE of *A. mucosa* showed an insecticidal effect comparable to the synthetic insecticide spinetoram (Delegate 250WG™, CT = 300 mg/l). The ingestion toxicity of the ESE of *A. mucosa* was influenced by the exposure time: the LC_{50} was 1666.13 mg/l for an exposure of 12 h and decreased to 500.43 mg/l for 120 h (Bernardi et al. 2017).

The insecticidal activity of non-nutritive sugars against *D. suzukii* was assessed with impregnated cotton wick assays. The sugars tested were erythritol, erythrose, xylitol, mannitol, sorbitol and nutritive sugar sucrose (positive control) (CT = 0.05; 0.1; 0.5 and 1 M). Water was used as a negative control. Irrespective of the concentration, erythrose and erythritol resulted in the highest rates of mortality without survivors after 7 days of experiment. Among all tested non-nutritive sugars, only these two had a significant ingestion toxicity with results comparable to the negative control (Choi et al. 2017). The most promising non-nutritive sugar, erythritol, was tested mixed with sucrose to stimulate feeding and thus increase its ingestion and possibly its efficiency (Choi et al. 2017; Cowles et al. 2015). Two experimental set-ups were arranged: in the first one, erythritol (CT = 0.5; 1 and 2 M) and sucrose (CT = 0.5 and 1 M) were offered separately each in one tube in different combinations of concentration. Only one combination (0.5 M erythritol in one tube and water in the other) showed a significant mortality rate compared to the positive control (0.5 M sucrose and water) with no survival after 6 days. The other combinations showed almost no fly mortality. In the second set up, erythritol (CT = 0.5; 1 and 2 M) and sucrose (CT = 0.5 and 1 M) were mixed in the same tube. In this experiment, several combinations showed a significant ingestion toxicity compared to the control but the most promising was the combination 1 M sucrose/2 M erythritol, followed by 0.5 M sucrose/2 M erythritol and 1 M sucrose/1 M erythritol with no survival after 3, 4 and 5 days, respectively (Choi et al. 2017). A similar procedure was used in another study: all the combinations tested showed a significant insecticidal activity against *D. suzukii* with the most promising combinations 1 M sucrose/2 M erythritol and 0.5 M sucrose/2 M erythritol resulting in 100% of mortality after 3 and 4 days of feeding, respectively (Tang et al. 2017). To better reflect field conditions where alternative feed sources are often available, the insecticidal activities of erythritol and its combination with sucrose were studied in the presence of wounded blueberries (Choi et al. 2019). Ten flies were allowed to feed on a cotton wick soaked with 0.5 M erythritol or 0.5 M sucrose or 2 M erythritol combined with 0.5 M sucrose in the presence of 0, 20 or 60% of wounded blueberries after a starvation period of 24 h. The survival was checked daily for 7 days. Erythritol alone induced comparable mortality rates (around 60%) regardless of the presence of wounded berries while sucrose alone had no insecticidal activity. The combination of erythritol and sucrose was the most effective treatment with 100% of mortality for berries with intact cuticle, 85% of mortality when 20% of the berries were wounded and 87% of mortality when 60% of the berries were wounded (Choi et al. 2019). The insecticidal activity of the combination of erythritol and sucrose against *D. suzukii* had already been reported by Choi et al. (2017) and Tang et al. (2017); however, this experiment showed that it had a significant lethal effect also in the presence of naturally occurring sugars provided by wounded berries (Choi et al. 2019).

The contact or ingestion toxicity of the EO of *P. asperum*, *Mentha × piperita*, *Z. officinale*, *E. radiata*, *C. winterianus*, *L. angustifolia*, *R. officinalis*, *T. vulgaris*, *T. occidentalis*, *A. balsamea*, *P. glauca* and *P. strobus* was tested against *D. suzukii* flies. A choice bioassay was set up where flies could choose between a vial containing raspberry juice and a treated (CT = 15 g/l) or untreated cotton wick. None of the EO tested showed a significant insecticidal effect (Renkema et al. 2016).

The toxicity by contact or ingestion of blends made of EO compounds was assessed. One was mainly composed of thymol, one of citronellol and the last one was composed by thymol, citronellol, menthol and geraniol. These blends were applied to a cotton wick and arranged near a raspberry. The mortality of flies was assessed in choice tests (1 treatment vs control) or no-choice tests. In the first case, no difference was observed in mortality rates between all the treatments. In the no-choice assay, the thymol dominated blend showed a mortality significantly higher than the control, the citronellol and the four-compound blends (Renkema et al. 2017).

4.3 Feeding on or contact with treated fruits

Blueberries were rolled in powdered sulphur (Bago d'Ouro®, CT = 2.6 ± 0.3 mg/fruit) or sprayed with kaolin (Surround®, CT = 5% w/v). Blueberries were available to the flies for 48 h and direct mortality was assessed. Afterwards, blueberries were removed and residual mortality was recorded after seven additional days. Powdered sulphur induced a significant direct mortality with 23.1% of dead flies (5.3% for females and 40% for males). Seven days after exposure, the residual mortality rates were 11.1% for females and 73.4% for males. Hence, powdered sulphur had a significant insecticidal activity primarily on *D. suzukii* males. Kaolin expressed no toxicity with mortality rates comparable to the ones observed in the control (Pérez-Guerrero and Molina 2016).

Kaolin (Surround®, CT = 2% w/v), clinoptilolite (Klinospray®, CT = 2% w/v) alone or mixed with the adjuvant Heliosol (CT = 0.5% v/v), calcium carbonate (CT = 1.7 g/l), calcium hydroxide (Nekapur®, CT = 1.7 g/l) and diatomaceous earth (Pflanzen-Aktivator® P2032, CT = 0.34 g/l) were tested against *D. suzukii*. Blueberries were sprayed with the products using a spinning table spray booth. A white coating was observed on the fruit after spraying. None of the tested substances showed insecticidal activity against *D. suzukii* after an exposure period of 24 h (Strack et al. 2017). In the studies of Pérez-Guerrero and Molina (2016) and Strack et al. (2017), kaolin showed no insecticidal activity against *D. suzukii*.

To assess the insecticidal activity of methyl benzoate (CT = 0.1; 0.5; 1 and 5% v/v) on *D. suzukii*, blueberries were dipped in the solution. The toxicity of this product was concentration-dependant. After 48 h of exposure, a concentration of 0.1% of methyl benzoate had no significant effect. For the higher concentrations, methyl benzoate had a significant insecticidal effect with 50% fly mortality at 0.5% and almost no survival at concentrations of 1% and 5% (Feng and Zhang 2017).

Since erythritol mixed with sucrose showed an interesting insecticidal activity against *D. suzukii* when added to an artificial media, a complementary test was made in a greenhouse with treated fruits. In a tent, a blueberry bush and commercialized blueberries arranged in a hanging basket were sprayed with the solutions of erythritol mixed with sucrose (CT = 0.5 M sucrose/2 M erythritol or 1 M sucrose/2 M erythritol). All the combinations were significantly different from the controls with the quickest mortality observed for the combination 0.5 M sucrose/2 M erythritol followed by 0.5 M erythritol and 1 M sucrose/2 M erythritol (Tang et al. 2017).

In another experiment, blackberries were dipped in erythritol (Truvia®, CT = 2 M) alone or mixed with a synthetic growth regulator (erythritol CT = 1 M + lufenuron CT = 0.5 ppm) before being offered to *D. suzukii* for oviposition. Erythritol alone induced 93% of male mortality and 83% of female mortality, while mixed with lufenuron, its insecticidal activity decreased slightly with respective mortality rates of 82.2% and 78.3%. These mortality rates were not statistically different from those observed with the negative control which was only water (72.6% of male mortality and 69.2% of female mortality) (Sampson et al. 2017b). However, a positive control seemed to be missing in the latter study.

4.4 Conclusion on ingestion or contact toxicants

Added to an artificial medium, the entomopathogenic fungus *M. brunneum* and the chitinase extracted from *E. characias* showed high toxicity against adults and larvae of *D. suzukii*, respectively. Erythritol mixed with sucrose had a high insecticidal activity as food source on a cotton wick or as fruit treatment. Powdered sulphur and methyl benzoate showed an interesting toxicity when used as a fruit treatment.

5 Fumigants

Fumigants are volatile poisonous chemicals released into the air or injected into the soil to kill pests. Fumigant toxicity has often been evaluated using impregnated paper allowing the release of the product into the air of a closed experimental chamber (Erland et al. 2015; Kim et al. 2016b). The experimental set-up protected the flies from coming into contact with the impregnated paper thanks to a sieve or a mesh. The products tested were mainly EO, some of their major compounds and fungal metabolites.

Against *D. suzukii* males, perilla aldehyde, geranial and neral had the highest insecticidal activity with LC_{50} values of 0.99, 1.36 and 1.52 mg/l air, respectively (Fig. 4). Against the females, the most efficient products were perilla aldehyde, geranial and menthol with LC_{50} values of 1.15, 1.88 and 1.94 mg/l air, respectively (Fig. 4). These compounds are the major components of the EO of *Perilla frutescens*, *Melaleuca teretifolia* and *Mentha* × *piperita* (Jang et al. 2017; Kim et al. 2016b; Park et al. 2017, 2016)

Dichlorvos, an organophosphorus insecticide, was used as a positive control. The fumigant toxicity of this product was very high with LC_{50} values ranging from 0.24×10^{-3} to 0.86×10^{-3} mg/l air for *D. suzukii* males and from 0.36×10^{-3} to 1.08×10^{-3} mg/l air for females. The insecticidal activity of this synthetic product is approximately 10^4 times higher than that of the EOs or their compounds (Jang et al. 2017; Kim et al. 2016b; Park et al. 2017, 2016).

Other EOs had a significant fumigant toxicity compared to the control at the highest concentration tested but were not promising enough to estimate their LD_{50} such as the EO *H. officinalis*, *L. angustifolia*, *O. basilicum*, *O. majorana*, *S. sclarea*, *S. montana*, *T. zygis* (Park et al. 2016), *M. alternifolia*, *M. dissitiflora*, *M. ericifolia* (Jang et al. 2017), *T. dolabrata*, *A. roseodora* and *J. sambac* (Kim et al. 2016b).

Some EO tested showed no fumigant toxicity such as the EO of *L. ericoides*, *L. scoparium*, *K. ambigua*, *P. dioica*, *S. aromaticum* (Park et al. 2017), *P. cablin*, *R. officinalis*, *V. agnus castus* (Park et al. 2016), *E. globulus*, *E. polybractea*, *E. radiata*, *E. smithii*, *M. leucadendron*, *M. uncinata*, *M. viridiflora* (Jang et al. 2017), *L. occidentalis*, *R. taratana*, *B. carterii*, *C. obtusa*, *C. japonica*, *C. sempervirens*, *J. communis*, *C. atlantica*, *P. sylvestris*, *R. damascena*, *A. balsamifera*, *C. limonum*, *S. album* and *S. tonkiensis* (Kim et al. 2016b).

As observed for contact toxicants with LD_{50}, females had higher LC_{50} values than males (Fig. 4, Jang et al. 2017; Kim et al. 2016b; Park et al. 2017, 2016).

Product efficiencies were also compared based on EC_{50} values for the EO of *P. americana*, *A. moluccana*, *M. integrifolia*, *A. indica*, several cultivars of *Lavandula* and the compounds 1,8-cineole, δ-carene and linalool. Among all these products, only the EO of *Lavandula* cultivars and the isolated compounds has a significant fumigant toxicity. Linalool, *L. latifolia* EO and leaf *L. intermedia* (cultivar: Provence) EO were the most effective products against *D. suzukii* with EC_{50} values of 1.85, 3.79 and 5.68 μl oil/l air, respectively (Fig. 5, Erland et al. 2015).

The fumigant toxicity of the fungal metabolites (sparassol, methyl orsellinate and DMB) was very low with mortality rates below 4% (Kim et al. 2016a).

6 Fumigants and contact toxicants

Several EO and their major compounds expressed both contact and fumigant toxicities. For the EO of *M. teretifolia*, *L. citratum*, *P. frutescens* and *E. citriodora* as well as their major compounds geranial, neral, citronellal and isopulegol, average LD_{50} values for contact toxicity and average LC_{50} values for fumigant toxicity were related (Fig. 6) with females being slightly less sensitive than males, particularly when the contact toxicity of citronellal, isopulegol and EO of *Eucalyptus citriodora* was concerned (Fig. 6). Approximately 2.1 μg and 2.5 μg of natural product per male and female were needed in contact toxicity assays to obtain the

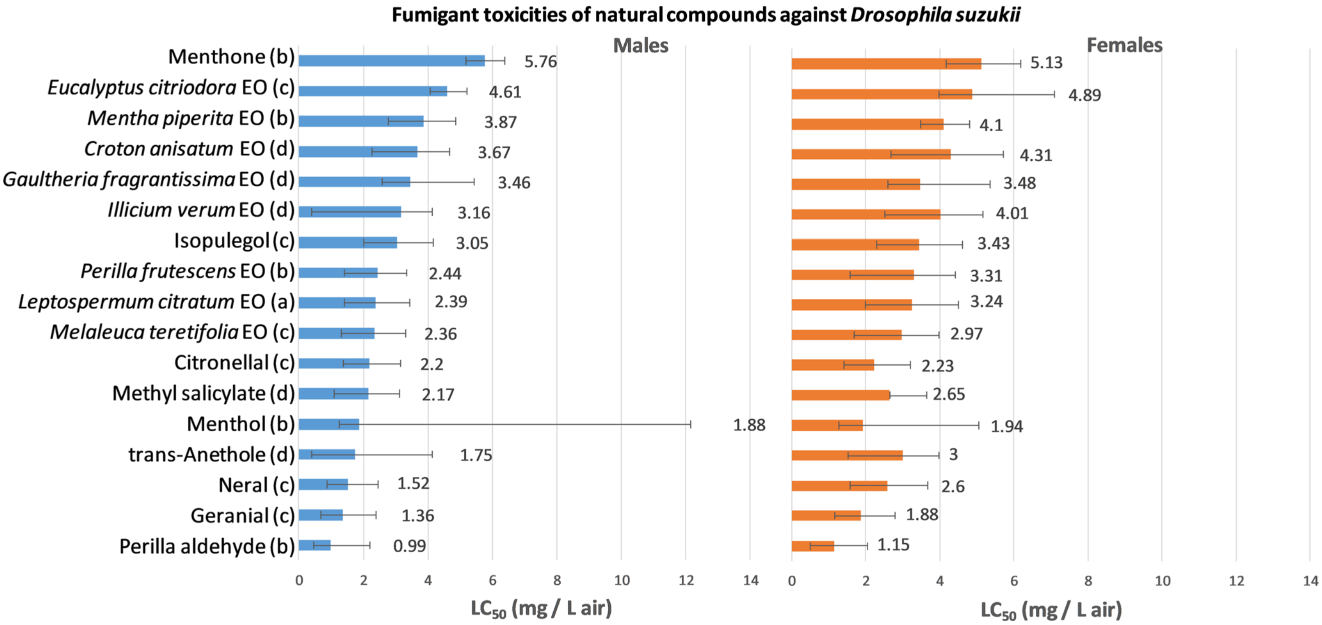

Fig. 4 Reported fumigant toxicities of natural compounds versus *Drosophila suzukii*. EO = essential oil. Error bars represent 95% confidence limits. Data were published by (a) Park et al. (2017); (b) Park et al. (2016); (c) Jang et al. (2017) and (d) Kim et al. (2016b)

effect of 1 mg natural product per litre of air in fumigant toxicity assays, respectively (Fig. 6, Jang et al. 2017; Kim et al. 2016b; Park et al. 2017, 2016). For the EO of *L. latifolia*, *L. angustifolia* and flowers of *Lavandula* × *intermedia* Provence and Grosso and the compounds linalool, delta-carene and 1,8-cineole (Erland et al. 2015), there was no correlation between contact and fumigant toxicities (data not shown).

7 Oviposition repellents and ovicides

Effects of tested compounds on oviposition were quantified by counting (i) the number of eggs deposited in fruit or (ii) the number of larvae or pupae that hatched or the number of adults that emerged from fruit. Numerous products such as EO, powders or bacterial formulations were tested. The most frequently used method was to treat fruits (such as raspberries, strawberries, blackberries or blueberries) directly. Other methods are usually based on the arrangement of the products close to the fruits to test potential repellent effects on the flies.

As fruits are not equally attractive for oviposition (Bellamy et al. 2013), the efficiency of the products will be described depending on the fruit that was used in the studies published so far.

7.1 Raspberries

The effect on the oviposition of EO blends was tested. One blend was mainly composed of thymol, another one of citronellol and the last one composed of thymol, citronellol, menthol

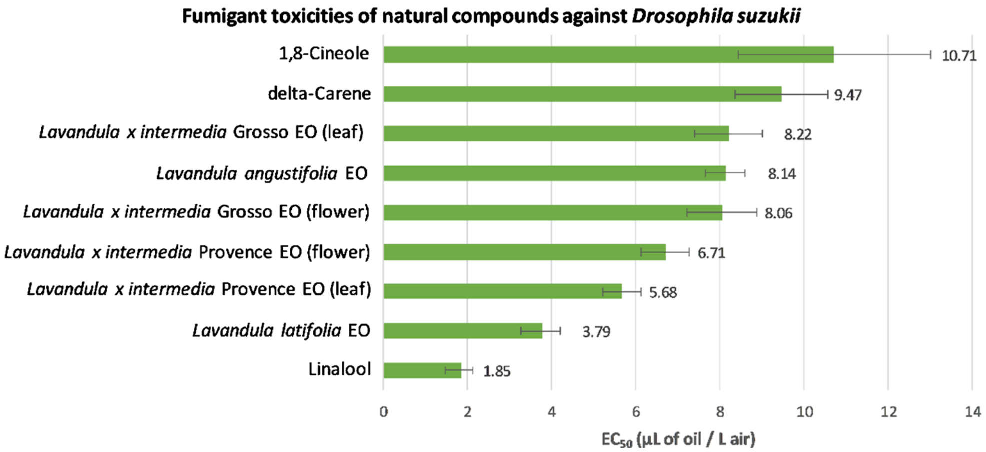

Fig. 5 Reported fumigant toxicities of natural compounds versus *Drosophila suzukii*. EO = essential oil. Error bars represent 95% confidence limits. Data were published by Erland et al. (2015)

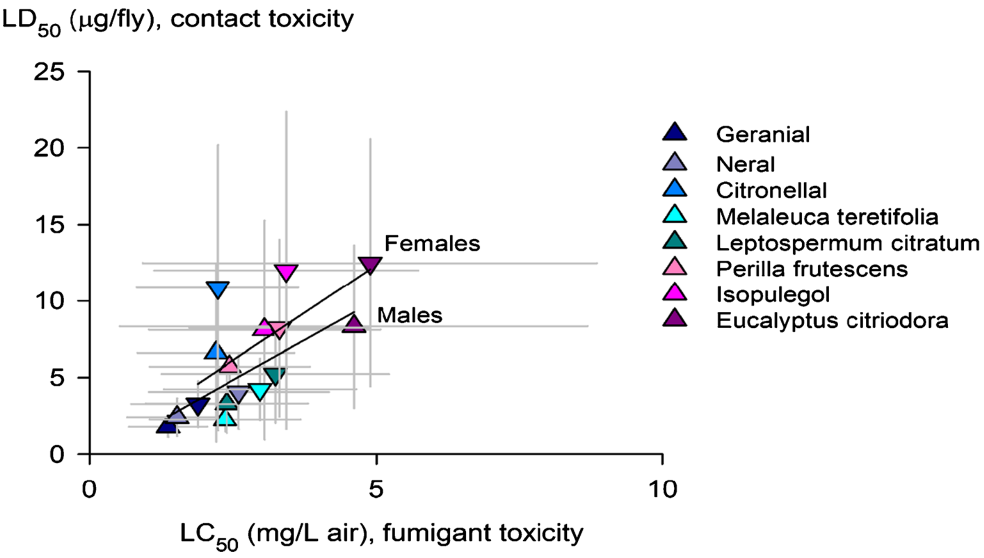

Fig. 6 Comparison of contact and fumigant toxicities of geranial, neral, citronellal, *Melaleuca teretifolia* EO, *Leptospermum citratum* EO, *Perilla frutescens* EO, isopulegol and *Eucalyptus citriodora* EO in *D. suzukii* males and females. Males are represented by up triangles and females by down triangles. Data were published by Jang et al. (2016), Kim et al. (2016b) and Park et al. (2016, 2017). Error bars represent the 95% confidence limits. Correlations were significant at $P = 0.0211$ for males and non-significant for females at $P = 0.1191$

and geraniol. Two raspberries were placed on either side of a treated cotton wick in no-choice and choice tests. In the no-choice experiment, the thymol blend was the only one with a significant effect on the larval infestation. In choice assays, all the blends induced a significant reduction (68–76%) of the number of larvae per berry compared to the fruits with an untreated wick. In the repellent part, all the blends showed a variable repellent effect on flies' landings on raspberries. It is possible that the reduction in larvae observed and subsequently of eggs laid is due to the reduction in landings (Renkema et al. 2017).

The effect of edible coatings (carnauba-based protective coating (PrimaFresh® 45), carnauba wax organically modified with kaolin clay (Raynox® Apple Sunburn Protectant) and calcium carbonate shade product (REFLECTIONS™)) on oviposition and brood survival has been studied in raspberries. Fruit were coated (CT = 1:40 to 1:1 product:water ratio) and offered for oviposition for 4 h in a cage. At the end of the oviposition time, eggs were counted and fruit were kept 21 additional days for monitoring adult emergence. Only Raynox® and PrimaFresh® significantly reduced the number of eggs laid in raspberries with a reduction of 62.3% and 65% respectively at 1:10 and almost 70% at 1:2. These products also significantly reduced the number of eggs reaching the pupal stage with no pupae from concentrations of 1:5 for Raynox and of 1:2 for PrimaFresh® (Swoboda-Bhattarai and Burrack 2014).

The effect of octenol and geosmin on *D. suzukii* oviposition was studied on several occasions. In a laboratory choice test, octenol and geosmin (CT = 1 and 10% in water v/v) were applied to cotton wicks and placed close to raspberries. Eggs laid in the berries were recorded. A significant avoidance for oviposition in fruits placed near a treated cotton wick was observed with reductions of 35% for octenol at 1%, 56% for octenol at 10% and 52% for geosmin irrespective of concentration (Wallingford et al. 2017). A similar experiment was conducted in a greenhouse. In a sleeve cage, raspberries were arranged around a cotton wick treated with octenol (CT = 1, 10 and 50% in mineral oil v/v). Octenol at 50% resulted in a significant reduction (49.8%) of the number of eggs laid in berries compared to the control (Wallingford et al. 2016a). In the field, octenol and geosmin were tested in various set-ups. Octenol (CT = 50% in mineral oil v/v), geosmin (CT = 50% in distilled water v/v) and a mix of both compounds was arranged in odour dispensers near ripening fruit clusters in an insecticide-free planting of raspberry. The number of eggs laid in fruits was counted and raspberries were kept until adult emergence for identification. Octenol and its combination with geosmin resulted in significantly fewer eggs compared with the control with reductions of 40% and 43%, respectively, while geosmin alone did not protect the fruit (Wallingford et al. 2017). In a comparable experiment (Wallingford et al. 2016b), octenol (CT = 50% in mineral oil v/v) led to a significant reduction (41.5%) of the eggs laid in the berries near an octenol odour dispenser compared to fruits near a control dispenser. Octenol also induced a significant reduction (47.6%) of adult emergence. In another experiment, octenol (CT = 20% v/v) was added to a specific pheromone and lure application technology (SPLAT) from ISCA technologies (Wallingford et al. 2016a). The system was mounted into the canopy at fruit height in a raspberry orchard. Ripe fruit were harvested and transferred to rearing containers until adult emergence for species identification and counting. Four days after establishing the system in the orchard, the treated plots showed significantly fewer offspring/g of fruit with reductions ranging from 28.8 to 49.5% compared to the control plots. However, 7 days after the deployment of the system in the planting, no differences in infestation levels were observed between treated and untreated plots any more (Wallingford et al. 2016a), suggesting a short-term efficacy of the latter method. Octenol was studied in the comparison of "push", "pull" and "push-pull" strategies. These strategies aimed to modify the geographical localization of the pest thanks to an aversive stimuli to "push" it or an attractive lure to "pull" it away from the crop (Wallingford et al. 2018). In the laboratory, experiments were carried out in a cage where octenol (CT = 25% in mineral oil v/v) was used as a repellent in the "push" and "push-pull" strategies and was applied to a cotton wick arranged near the raspberries. An attractive trap was used in the "pull" and "push-pull" strategies. Compared to the control, all the strategies show a significant reduction in the number of eggs per fruit. The "push" and the "pull" strategies had similar results with respective reductions of 66.2% and 69.6% whereas the "push-pull" strategy was the most effective with 87.6% fewer eggs per fruit. In the field, octenol (CT = 50% in mineral oil v/v) was arranged in an odour dispenser. The "push" and "push-pull" strategies showed a significant reduction in the number of eggs laid in fruits, 56.7% and 57.4% respectively. On the contrary, the "pull" system had an increase of 44.1% of infestation compared to the control. However, the latter result may be due to the use of a sticky card in the trap instead of a drowning solution, which may have diminished the efficacy of the "pull" system (Wallingford et al. 2018). Octenol had a repellent effect against *D. suzukii*.

7.2 Strawberries

The effect of ESE from *Annona* species on oviposition was also assessed. In a no-choice experiment, ripe strawberries were dipped in a solution of ESE (CT = 2000 mg of ESE/l) and deposited eggs were counted after 24 h. All the ESE tested showed a significant reduction in the number of eggs laid compared to untreated fruits (45% for *A. mucosa*, < 35% for *A. sylvatica* and *A. muricata*) and a higher oviposition repellence than spinetoram (Delegate 250WG™, CT = 300 mg/l), which induced a reduction of 26% (Bernardi et al. 2017).

The effect of three edible coatings on *D. suzukii* infestation was studied in a strawberry field. PrimaFresh® 45, Raynox® and REFLECTIONS™ (CT = 1:10 product:water ratio) were sprayed and 7 days later, ripe strawberries were harvested and monitored for 21 days for adult emergence and identification. None of these products reduced the number of adults that emerged from strawberries compared to untreated fruits (Swoboda-Bhattarai and Burrack 2014).

7.3 Blackberries

Blackberries were dipped in erythritol (Truvia®, CT = 2 M) alone or mixed with a synthetic growth regulator (erythritol CT = 1 M/lufenuron CT = 0.5 ppm) before being offered to *D. suzukii* for oviposition. These formulations showed a number of eggs laid that was comparable to the control but induced a significant reduction in the progeny survival. Erythritol alone led to an 88.9% reduction in survival and mixed with lufenuron, 99% mortality was observed. Eggs failed to hatch or larvae died shortly after hatching (Sampson et al. 2017b). In a field trial, erythritol (Truvia Baking Blend®, CT = 0.5 M), lufenuron (CT = 10 ppm) and the combination of both were applied on blackberry plants once a week for 3 weeks before fruit harvest. None of the treatments had a discernible effect on the number of eggs laid but they reduced larval infestation by 71 to 79% (Sampson et al. 2017a).

7.4 Blueberries

Blueberries were used in many studies even though according to Bellamy et al. (2013), they are not among the most attractive fruit for *D. suzukii*.

For products with a powder formulation, such as powdered sulphur (Bago d'Ouro®), blueberries were rolled in the powder. In a no-choice and a choice assay (CT = 2.6 ± 0.3 mg/fruit), powdered sulphur significantly reduced the number of eggs laid in blueberries by 76% and 97%, respectively (Pérez-Guerrero and Molina 2016).

Kaolin (Surround®, CT = 5% w/v) was sprayed on blueberries. This product had no effect on oviposition in no-choice and choice assays with a number of eggs laid in treated fruit similar to the control (Pérez-Guerrero and Molina 2016). In another study (Strack et al. 2017), kaolin (Surround®, CT = 2% w/v) sprayed on blueberries showed a significant reduction in the number of eggs deposited (86.4%) which was comparable to the effect of spinosad (Audienz®, CT = 0.025% v/v), a synthetic insecticide that quickly killed the flies inducing a reduction in the number of eggs laid by 95.2%. These studies showed contrasting effects of kaolin on oviposition that may be explained by the difference in the experimentation (variety and number of blueberries, number of flies, time of exposure, and method of spraying). Further studies are needed to clarify the effect of kaolin on *D. suzukii* oviposition.

Strack et al. (2017) also tested other powdered coatings, such as calcium carbonate (CT = 1.7 g/l), clinoptilolite (Klinospray®, CT = 2% w/v) alone or mixed with the adjuvant Heliosol (CT = 0.5% v/v), calcium hydroxide (also called lime, Nekapur®, CT = 1.7 g/l) and diatomaceous earth (Pflanzen-Aktivator® P2032, CT = 0.34 g/l). Calcium carbonate and the two formulations of clinoptilolite significantly reduced the number of eggs deposited, respectively by 80.5%, 74.2%, 75.6%. Only calcium hydroxide and diatomaceous earth had a non-significant effect on oviposition (Strack et al. 2017).

An experiment under semi field conditions with blueberry plants in pots under a mesh cage indicated that lime (Nekapur 2®, CT = 1.8 g/l) reduced the number of eggs laid in fruit. The product was sprayed once a week for 4 weeks. Each week, the treated plants showed a lower infestation than control plants but only the fourth week of treatment showed a significant difference with a reduction of 98.5% in the number of eggs laid (Dorsaz et al. 2017b). This study showed different results from the ones described by Strack et al. (2017) this may be due to the difference in the experimental conditions (blueberries variety, fly, time of exposure, treatment) or this can be linked to the way of working of lime with a slow effect not measurable in the study of Strack et al. (2017).

The effect of edible coatings (PrimaFresh® 45, Raynox® and REFLECTIONS™) on oviposition and brood survival has been studied in blueberries. Fruit were coated (CT = 1:40 to 1:1 product:water ratio) and offered for oviposition for 4 h in a cage. At the end of the oviposition time, eggs were counted and fruit were kept 21 additional days for monitoring adult emergence. Only Raynox® and REFLECTIONS™ significantly reduced the number of eggs laid in blueberries with reductions of 65.5% and 73% respectively at a 1:2 product:water ratio. However, these products had no effect on the number of eggs reaching the pupal stage and the number of pupae that emerged as adults inducing that they should be used before the presence of *D. suzukii* in the crop (Swoboda-Bhattarai and Burrack 2014).

Erythritol, a non-nutritive sugar, was assessed for its oviposition deterrence. Flies were allowed to lay eggs in untreated blueberries for 7 days while feeding on a cotton stud soaked with various erythritol solutions. Erythritol solutions alone (CT = 0.5 to 2.0 M) or mixed with sucrose solutions (CT = 0.5 or 1 M) led to a significant decrease in the number of eggs compared to the control (0.5 M sucrose). The most efficient formulations for avoiding oviposition were 0.5 M sucrose/2 M erythritol and 1 M sucrose/1 M erythritol with less than two eggs counted per blueberry. The result suggested that erythritol reduced female fecundity (Tang et al. 2017). In a similar experiment, flies were allowed to lay eggs in untreated blueberries for 48 h while feeding on a cotton stud soaked with erythritol (CT = 0.5 M), sucrose (CT = 0.5 M) or their combination (2 M erythritol + 0.5 M sucrose). Erythritol alone or mixed with sucrose induced a reduction of 43% of the number of eggs laid compared to sucrose (Choi et al. 2019) supporting previous results by Tang et al. (2017). To better understand the reason of the reduced fecundity, female flies were dissected to count the number of ovarian eggs. When studying the combination of eggs laid and ovarian eggs, females fed with erythritol alone had 12.4 eggs, on erythritol and sucrose 16.5 eggs and on sucrose alone 19.3 eggs. It was speculated that this reduction was caused by a deteriorated nutritional status of the flies since erythritol is not metabolized. Females fed with the combination of erythritol and sucrose laid fewer eggs but had a higher number ovarian eggs compared to sucrose fed flies showing a reduction of the oviposition activity (Choi et al. 2019). In a field trial, erythritol (Truvia Baking Blend®, CT = 0.5 M), lufenuron (CT = 10 ppm) and the combination of both compounds was applied on blueberry bushes once a week for 3 weeks before fruit harvest (Sampson et al. 2017a). None of the treatments had a discernible effect on the number of eggs deposited but they reduced larval infestation. Indeed, erythritol induced 100% of mortality for the first instar of larvae and 43% for the second instar. In untreated blueberries, for each larvae that survived, 8 eggs had to be laid. When blueberries were treated with erythritol, 54 eggs were necessary and with the combination of erythritol and lufenuron, 59 eggs were needed to obtain one surviving larva. None of the treatments prevented oviposition and crop damage completely but they induced an average reduction of 75% of larval infestation and thus the population decreases (Sampson et al. 2017a). The lower cost derivative of erythritol, pentaerythritol, showed an interesting efficiency against *D. suzukii* in laboratory trials and was therefore selected for testing in a blueberry field (Sampson et al. 2019). Weekly treatments were applied using a backpack sprayer (untreated control or 0.5 M of erythritol in water + soap or 0.5 M of pentaerythritol in water + soap or 0.25 M of erythritol +0.25 M of pentaerythritol in water + soap) for the last 3 weeks prior to harvest. A similar effect of erythritol and pentaerythritol (both of them tested at 0.5 M) was observed with a significant reduction of the number of eggs laid (64%) as well as the number of hatching larvae (94%). The combination of erythritol and pentaerythritol induced a higher reduction in the number of eggs deposited (82% of reduction) and a similar control of larvae (94% of reduction) (Sampson et al. 2019).

To learn if butyl anthranilate (BA) (CT = 1; 2.5; 5 and 10% v/v), a DEET substitute, has an effect on oviposition, blueberries were painted with the product or its solvent and offered to the flies for 1 week. Then, the number of eggs, larvae and pupae was counted. A dose-dependent effect was found with a reduction in the offspring emergence ranging from 12% at 1% of BA; 47% at a concentration of 2.5%; 77% with a 5% concentration and 97% at 10% (Krause Pham and Ray 2015).

The effect on oviposition of the EO of *P. americana*, *A. moluccana*, *L. angustifolia*, *L. latifolia*, *Lavandula* × *intermedia* (cultivars: Grosso and Provence) (leaf or flower), *M. integrifolia* and *A. indica* and their major compound cineole, δ-carene and linalool (CT = 1; 5; 10 and 20% v/v) was assessed by dipping blueberries and counting the number of oviposition marks after a 48-h period of oviposition. None of these EO had a significant effect on oviposition (Erland et al. 2015).

The effect on oviposition of *Bacillus thuringiensis* formulations was tested by dipping blueberries in the solutions in a choice experiment. The mean number of larvae per fruit was not significantly different between treated and untreated fruits, suggesting that these products had no effect on oviposition at the concentrations and conditions used so far (Biganski et al. 2018).

To assess the ovicidal effect of a product, blueberries were offered for oviposition until eggs were laid. Subsequently, half of the fruit was dipped in a solution of the test product. The number of offspring was compared between treated and untreated blueberries. This method was used to assess the ovicidal effect of methyl benzoate (CT = 1% v/v) (Feng and Zhang 2017) and lime (Nekapur 2®, CT = 1.8 g/l) (Dorsaz et al. 2017a). Methyl benzoate showed a significant toxicity against *D. suzukii* offspring as no larvae or pupae developed in treated blueberries (Feng and Zhang 2017). Lime also induced a significant reduction in adult emergence: 24% of eggs developed further to adults in treated fruit compared with 57% in untreated fruits (Dorsaz et al. 2017a).

7.5 Conclusion concerning the effect on oviposition

Since just a few larvae can render the crop useless, the efficacy of treatments against *D. suzukii* oviposition needs to be high. Treatments that resulted in more than 90% of efficiency were powdered sulphur (Bago d'Ouro®, CT = 2.6 mg/fruit) applied directly on fruit, erythritol (CT = 1 M) + sucrose (CT = 1 M), erythritol (CT = 2 M) + sucrose (CT = 0.5 M) and erythritol (CT = 0.5 M) in the feed. These products were primarily applied to blueberries. More testing is needed because the efficiency of the products varies depending on the fruit and because the vast majority of experiments were no-choice tests that do not reflect field conditions. Even though *D. suzukii* can inflict heavy damage on red vine cultivars, studies on the prevention of oviposition in this economically important crop are scarce.

8 Limitations of using natural compounds for controlling *D. suzukii*

This review shows that several structurally diverse natural compounds had promising repellent or insecticidal effects on *D. suzukii*. However, some points currently limiting a widespread use were also noted.

8.1 High concentrations needed for efficacy

To obtain a similar level of protection as provided by synthetic insecticides, most of the natural compounds tested need to be approximately 1000 times more concentrated. For example, the most effective contact toxicant showed that the triketone fraction of the EO of *Lesptospermum scoparium* had LD_{50} of 0.13 μg/fly for males and 0.22 μg/fly for females whereas the LD_{50} of the synthetic insecticide cypermethrin is below 0.06×10^{-3} μg/fly irrespective of the sex (Park et al. 2017). These high concentrations imply financial and technical challenges. The rather high requirement of natural compounds can easily render their use non-profitable as discussed by Sampson et al. (2017a, b) for erythritol. Since the production of the plants or fungi that contain the interesting natural compounds is also associated with (ecological) costs, life cycle analyses are needed to understand whether producing the most effective natural compounds on a large scale in plants or fungi is ecologically and economically sustainable. The risk of phytotoxicity and thus crop damage usually increases with concentration, a point that has rarely been addressed and tested in the studies published so far, but that may easily render effective compounds useless for crop protection.

8.2 Transfer to and deposition of natural compounds on crops

More efficient methods for transferring and depositing natural compounds onto the crops than those used in the papers summarized here need to be established and optimized without efficacy losses during the process. For example, for spray applications, natural compounds need to be diluted with a non-toxic, cheap and generally available carrier liquid (usually water). However, lipophilic compounds such as oils are not mixable with water. Appropriate formulations must be developed; or, carrier liquids other than water are required. Technologies are needed for depositing powders or waxy compounds in a homogenous manner on fruit surfaces. Concerning ingestion toxicants, erythritol and sucrose combinations are very sticky, limiting uptake by the flies (Tang et al. 2017). The physicochemical properties of the compounds need to be adapted for instance by developing formulations for widespread use with commercially available equipment.

8.3 Competition for use

Many of the tested compounds are "generally considered as safe" (GRAS) and are already used in food, pharmaceuticals or cosmetics, like EO (flavour and fragrance in food and beverages, perfumes, personal care products) and erythritol (calorie-reduced food, candies, toothpaste). Competition for the resource is likely, and again, life cycle analyses that consider this aspect are needed to better understand the contribution that the natural compounds can make when taking economic boundary conditions into consideration.

8.4 Occasional lack of specificity

Some of the tested products have multiple activities beyond the insecticidal one against *D. suzukii*. For example, the triketones fraction of the *Leptospermum* EO had an insecticidal contact activity against *D. suzukii* but triketones and more particularly leptospermone has an herbicidal activity and its synthetic derivatives belong to the ß-triketone class of herbicides. The mode of action of these herbicides is the inhibition of the enzyme p-Hydroxyphenylpyruvate dioxygenase (Dayan et al. 2007). Flavesone, another triketone, is the active component of Flavocide™, an insecticide used against various pests (Miller and Peters 2017). Erythritol inhibits tomato and corn seed germination and decreases tomato growth at insecticidal doses showing a potential herbicidal effect (Scanga et al. 2018). A lack of specificity with regard to biological activity implies a huge group of non-target organisms that are likely to be exposed to additional risks. This aspect needs to be investigated thoroughly before widespread use, particularly of those natural compounds that have a rather broad spectrum of biological activity.

8.5 Lack of knowledge of the (molecular) modes of action

The mode of action of the products and their target site(s) have rarely been investigated and hardly ever determined. The inhibitory activity of EO and their major compounds on acetylcholinesterase (AChE) and/or glutathione-S-transferase (GST) has been assessed (Jang et al. 2017; Kim et al. 2016b; Park et al. 2016). Only a few compounds show a potent inhibition activity against AChE, such as perilla aldehyde, thymol, carvacrol and trans-cinnamaldehyde whereas neral and geranial inhibit GST. However, these inhibitory activities do not unambiguously indicate that these enzymes are the factual and only target site of the tested products. More generally, the exact mode of action of EO is unknown but a likely target site is the octopaminergic system (Enan 2001). The mode of action of the coatings discussed in the present paper is also largely unknown. They may modify the fruit surface characteristics such as the pH or the colour and render it unsuitable for oviposition (Swoboda-Bhattarai and Burrack 2014), but evidence supporting these assumptions is scarce, so far.

The efficacy of many products summarized in the present paper has not been confirmed under field conditions, so far. Repellent products not applied directly to the fruits but to a cotton wick or in a dispenser may act differently in the field (dilution in the air or by rain, decomposition by heat) reducing their efficiency. Contact toxicants may be sprayed but the probability that they directly reach a fly in the field is low. Ingestion products may express a very variable performance because of the competition with natural non-toxic food sources. Fumigants are most effective in closed compartment, not under open field conditions. Organic compounds may be quickly colonized and metabolized by microorganisms. More information on the effects of environmental and biotic factors on the performance of the natural compounds is needed.

8.6 Waiting time until effects unfold

The period between the application of the treatment and its effects can be critical. Actually, because *D. suzukii* females lay between 7 and 48 eggs per day from the second day of their adult life, and have a short generation time (Cini et al. 2012), it is necessary to kill or repel them before oviposition or to kill the eggs once they have been laid and before they develop to larvae. For example, following the exposure to the entomopathogenic fungus *Metarhizium brunneum*, *D. suzukii* adults had an average survival time of 3.6 days (Yousef et al. 2018), which is enough for the infestation of several fruits and may allow the survival or even increase of the population.

As *D. suzukii* finds a shelter in wild hosts near crops, it is necessary that the products keep an insecticidal effect to avoid a quick re-infestation of the crop and to increase the interval between the treatments.

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Compliance with ethical standards

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

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